The life histories of platynothrus peltifer (Koch 1839) and damaeus clavipes (Hermann 1804)(Acarina:cryptostigmata) in soils of Pennine moorland

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THE LIFE HISTORIES OF *PLATYNOTHRUS PELTIFER* (KOCH 1839) AND *DAMAEUS CLAVIPES* (HERMANN 1804) (ACARINA : CRYPTOSTIGMATA) IN SOILS OF PENNINE MOORLAND

BY

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INTRODUCTION.

Since the pioneer studies of MICHAEL (1883-87) on the life histories of Oribatei, many laboratory culture studies have made by JACOT (1936), GRANDJEAN (1950), RIHA (1951), SENGBUSCH (1954, 1958), PAULY (1956) and WOODRING and COOK (1962). The attention of workers later turned to the study of life cycles of mites in the field, and HAARLØV (1960) worked out the life cycles of soil-inhabiting species from data collected by regular sampling. More recently, HARTENSTEIN (1962, 1962 a-c) has given life history data for several species of Cryptostigmata.

The present studies were undertaken to obtain information on the biology and life histories of oribatid mites in the soils of the Moor House National Nature Reserve in Westmorland, England (National Grid Reference : 35/758329). The area is typical Pennine moorland over 1,800 ft. O. D. (: 549 m.), covered by blanket bog and experiencing a sub-arctic climate (MANLEY, 1952). General descriptions of the Nature Reserve are given by CONWAY (1955), NICHOLSON (1957) and CRAGG (1961).

METHODS OF STUDY.

The material for life history studies was obtained by monthly sampling in 1961 of two sites at Moor House : for *Platynothrus peltifer* from an area of *Festuca-Agrostis* grassland, and for *Damaeus clavipes* from the litter of *Juncus effusus* L. The Acarina were extracted from cores of soil and litter in a high-gradient extractor

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MACFADYEN, 1961). As the methods for identification of the immature stages were different in the two species studied, these are described separately.

Platynothrus peltifer (Koch 1839).

This species occurs in soils throughout the Palaearctic region (KARPPINEN, 1958 ; DALENIUS, 1960 ; and HAARLØV, 1960) and in Greenland (HAMMER, 1946). The life cycle of *P. peltifer* has been previously studied by Grandjean (1960), HAARLØV (1960) and HARTENSTEIN (1962 c).

The adult of *P. peltifer* was first described and figured by SELLNICK (1928), and as *Hermannia bistriata* (MICHAEL, 1887). The adult mite deposits eggs singly or in batches of three or four (GRANDJEAN, 1950), and feeds on decaying leaf or wood tissues and fungi (HARTENSTEIN, 1962 c).

The juvenile forms of *P. peltifer* collected at Moor House were identified with the help of descriptions and figures by GRANDJEAN (1950), TÜXEN (1962) and HARTENSTEIN (1962 c). The four immature stage were separated, initially, by biometric measurements using arithmetic probability paper (HARDING, 1949). Table 1 shows the mean length of the first leg obtained for each stage by this method. The separation into instars was consistent with differences in the genital discs, and the setation of the anal and genital plates.

TABLE 1.

Mean length of the first leg (from distal part of the coxa to the end of the tarsus) of instars of *P. peltifer* obtained by probability analysis. The mean measurements are given in millimetres with the standard deviation, and the geometric increase for each moult is shown.

Instar	Mean length of first leg (mm.)	Geometric increase
Larva	0.131 ± 0.007	
		1.37
Protonympha	0.180 ± 0.018	
		1.31
Deutonympha	0.236 ± 0.024	
		1.28
Tritonympha	0.303 ± 0.023	
		1.25
Adult	0.380 ± 0.017	

Analysis of twelve monthly samples gave information on the life cycle of this mite under moorland conditions, and this is shown in Fig. 1. The histograms indicate the percentage of each instar in the total number of all stages on each monthly sampling date. Larvae were found in the period January-April, and in August, September and December, 1961. The species overwintered mainly as eggs, larvae, protonymphae and adults at Moor House. This does not confirm

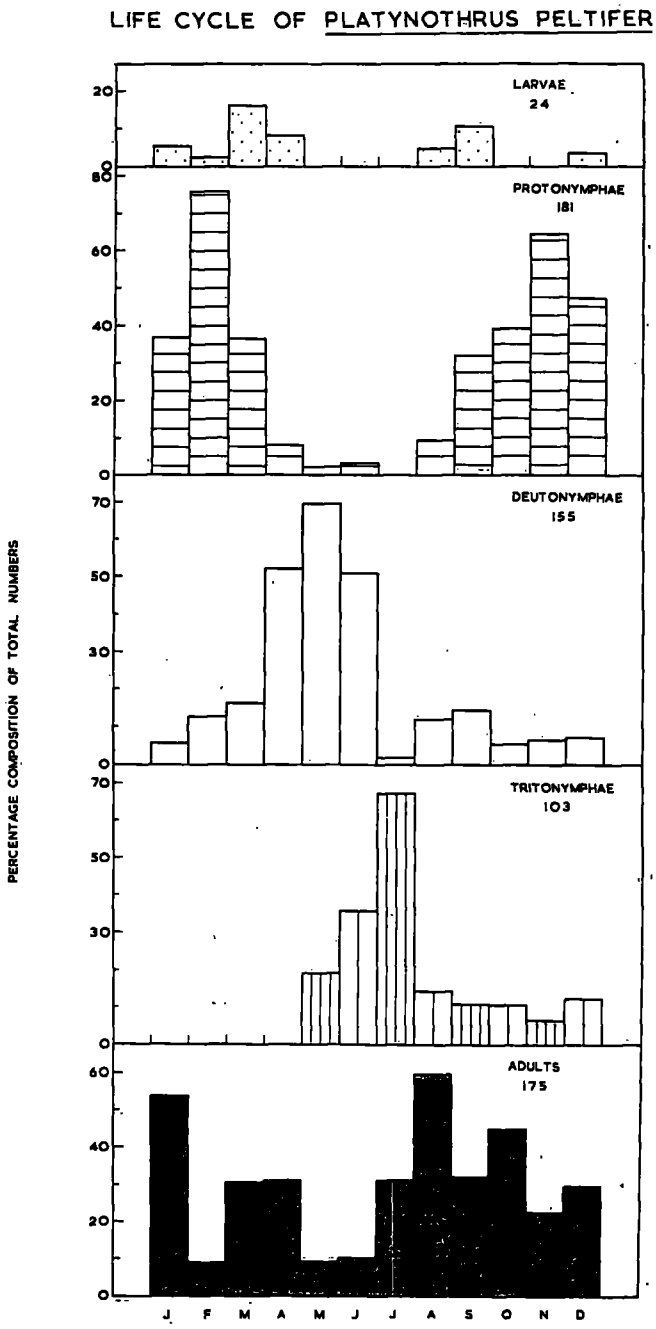

FIG. 1. — Life cycle of *Platynothrus peltifer* at Moor House in 1961. The material was collected from *Festuca-Agrostis* grassland. The histograms indicate the percentage of each instar, in the total number of all stages, on each monthly sampling date.

the results of NOORDAM and VAN DER VAART-DE VLIEGER (1943) in the Netherlands, who recorded that *P. peltifer* overwintered only in the adult stage and that nymphs occurred from February to June. Peaks of relative abundance of protonymphae occurred in February and November, and of deutonymphae in May, and of tritonymphae in July at Moor House. A relative increase in adult density was recorded for *P. peltifer* in August and January.

It can be seen from Fig. 1. that *P. peltifer* has a single generation per year in moorland soils, the eggs hatching in autumn and the rest of the life cycle being completed in the following 11-12 months. HAARLØV (1960) also concluded that *P. peltifer* had a single generation each year in hawthorn litter in the Jaegersborg Park, Denmark. Similar results were reported by HARTENSTEIN (1962 c) for this species in leaf litter of the Tully Forest, New York.

Damaeus clavipes (Hermann 1804).

The adult of this species has been described as *Belba clavipes* by MICHAEL (1883-87), and by KULCZYNSKI (1902). PAULY (1956) studied the biology of *D. clavipes* in culture, but no data are available on the life cycle in the field.

The immature material of *D. clavipes* collected at Moor House during 1961 was separated into instars by the number of genital discs, and the setation of the anal and genital plates. To confirm the separation of the stages measurements were made on each instar of *D. clavipes* and these are given in Table 2.

The geometric increase has been calculated for each moult, and it is interesting to note that the greatest growth increase was recorded between the proto- and deuto-nymphal stages for all the characters measured, with the exception of the length of the first tarsus. The protonymphal stage is also estimated to be the longest in duration from the field data shown in Fig. 2. The adult female is signicantly larger than the male, which was observed by JACOT (1934).

The life cycle of *D. clavipes* at Moor House is shown in Fig. 2. The percentage composition of each stage of the total number of specimens collected on each sampling date is shown, and the data are grouped on a bimonthly basis. Larvae were present from July to October, 1961, indicating that in this species egg laying is confined to the summer months under subarctic conditions. Protonymphae were present from September to February. Deutonymphae were absent from the samples in July and August, but this stage had a spring and autumn peak of relative abundance. Tritonymphae were present throughout the year, but were a high percentage of the total numbers of this species in November, December, May and June.

Adults were recorded from all the monthly samples, and had maximum density in July and August caused by the maturation of tritonymphae. *D. clavipes* overwintered in all stages except the larva and commonly in the tritonymphal stage, and had a single generation per year at Moor House.

Adult females of *D. clavipes* were most numerous in the May and June samples. Eggs were observed in adult females of *D. clavipes* using normal clearing methods, and the data are given in Table 3. It can be seen that the percentage of females recorded carrying newly fully developed eggs was highest in the period September to December, but most of the egg laying took place in May and June. The mean number of eggs recorded per female was eight. PAULY (1956) calculated that a single female of this species in culture laid 70 eggs in her lifetime.

TABLE 2.

Mean measurements with standard deviations (in millimetres) of all stages of *Damaeus clavipes*. The geometric increase for each moult is shown.

Instar	Larva	Protonympha	Deutonympha	Tritonympha	Adult	
					Female	Male
Number of specimens measured	5	11	22	21	24	21
Width of propodosoma	0.115 ±0.019	0.149 ±0.004	0.195 ±0.016	0.250 ±0.024	0.285 ±0.027	0.268 ±0.023
Geometric increase		1.29	1.31	1.28	1.10	
Length of body	0.360 ±0.057	0.465 ±0.031	0.676 ±0.039	0.839 ±0.092	1.067 ±0.033	0.958 ±0.044
Geometric increase		1.29	1.45	1.24	1.20	
Length of first tarsus	0.163 ±0.031	0.240 ±0.017	0.271 ±0.029	0.323 ±0.040	0.345 ±0.028	0.330 ±0.009
Geometric increase		1.47	1.13	1.19	1.04	
Length of anal plate	0.064 ±0.006	0.081 ±0.009	0.125 ±0.008	0.161 ±0.013	0.185 ±0.011	0.166 ±0.018
Geometric increase		1.27	1.55	1.28	1.09	
Length of genital plate	Genital plate absent	0.058 ±0.004	0.087 ±0.007	0.117 ±0.010	0.193 ±0.011	0.165 ±0.011
Geometric increase		—	1.51	1.34	1.53	

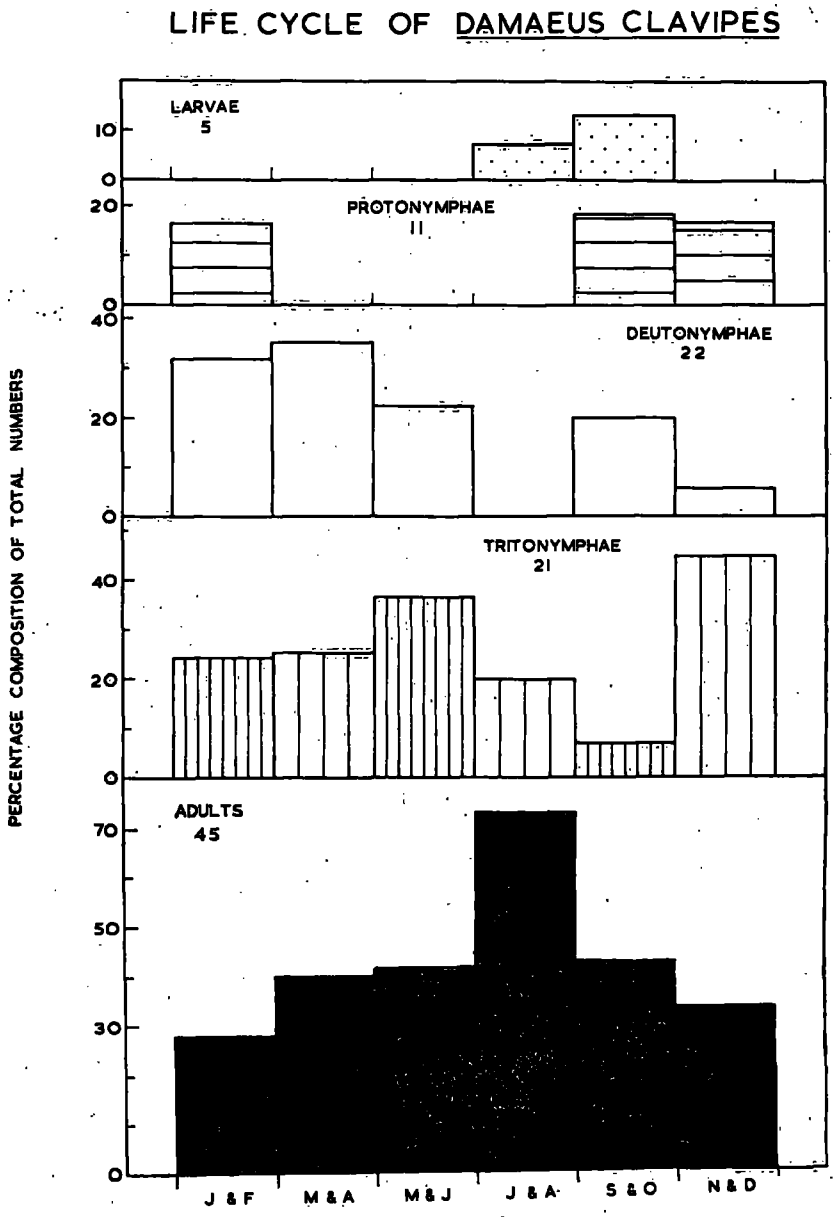

FIG. 2. — Life cycle of *Damaeus clavipes* at Moor House in 1961. The material was collected from litter of the rush, *Juncus effusus*. The histograms indicate the percentage of each instar, in the total number of all stages, on each sampling date. The data are presented in bimonthly groups.

TABLE 3.

Percentage of adult females of *D. clavipes* with eggs during 1961. The data are grouped on a bimonthly basis, and the number of eggs per female is also given.

Date	Number of adult females recorded	Percentage of females with eggs	Mean number of eggs per female
16. 1.61 13. 2.61	4	50	4
13. 3.61 26. 4.61	6	67	7
29. 5.61 5. 6.61	7	71	9
18. 7.61 28. 8.61	5	60	9
25. 9.61 23.10.61	4	100	8
24.11.61 11.12.61	4	100	9

DISCUSSION.

The postembryonic development of both *P. peltifer* and *D. clavipes* was 11-12 months at Moor House where the average daily temperature is 5.0° C. (: 40.9° F.). PAULY (1956) has recorded that this period is 75 days for *D. clavipes* in culture at 25° C and 95 per cent relative humidity. Several workers have observed that lowering of the temperature extends the postembryonic development period. SENGBUSCH (1958) found this in *Galumna nervosus* (Nicolet) (a drop of 1° C. lengthened development by four days), and it was recorded in *Ceratozetes cisalpinus* Berlese (a drop of 1° C. lengthened development by two days) by WOODRING and COOK (1962).

The estimated duration of the instars from Fig. 1 and 2 for the two species studied is one month for the larva, 4-5 months for the protonympha, 2 months for the deutonympha and 1-2 months for the tritonympha at Moor House. The postembryonic development for both species is 11-12 months under these subarctic conditions. The protonymphal stage has the greatest duration, the moult from proto- to deuto-nympha stage shows the largest geometric increase for the characters measured (see Tables 1 and 2).

Since adults of nearly all species were found in every month of the year at Moor House, it seems likely that the duration of adult life must be about a year or more, rather than a few weeks. Records of the duration of adult life for species of oribatids are non-existent in the literature, except for that of 10-12 months for *Ceratozetes cisalpinus* by WOODRING and COOK (1962). It was not possible to determine for the two species studied at Moor House whether eggs were present in newly moulted females. However, WOODRING and COOK (1962) recorded that females of *Ceratozetes cisalpinus* laid mature eggs 15-20 days after emergence from the tritonymphae in culture, *Scheloribates laevigatus* Koch 20 days after emergence, and *Oppia neerlandica* Oudemans 7 days after maturing to the adult.

These life history studies show that the duration of postembryonic development of Acarina is much longer in species which are subject to a severe sub-arctic climate, than in species which experience a milder climate in lowland habitats and that uni-voltine species are common amongst the Cryptostigmata at Moor House.

ACKNOWLEDGEMENTS.

Thanks are due to Professor J. B. CRAGG for initiating this research, to Dr. J. C. COULSON for continued direction and encouragement, to Mr. D. MACFARLANE for taxonomic help, and also to Professor David BARKER who kindly made available the facilities of the Zoology Department of Durham University. The Nature Conservancy allowed access to the Moor House National Nature Reserve, and this is gratefully acknowledged. The study forms part of a thesis for the degree of Doctor of Philosophy of the University of Durham, and was carried out whilst the writer was in receipt of a grant from the East Suffolk County Education Committee.

SUMMARY.

Information is given of the biology and life histories of two species of oribatid mites in soils of Pennine moorland under a sub-arctic climate. By examination of the immature stages from monthly samples, it is shown that both species have a single annual generation. *Platynothrus peltifer* bred both in the spring and autumn, and *Damaeus clavipes* only in the autumn.

REFERENCES

CONWAY (V. M.), 1955. — The Moor House National Nature Reserve, Westmorland. *Handb. Soc. Prom. Nat. Res.*, III : 1-7.

CRAGG (J. B.), 1961. — Some aspects of the ecology of moorland animals. *J. Ecol.*, 49 : 477-506.

DALENIUS (P.), 1960. — Studies on the Oribatei (Acari) of the Torneträsk Territory in Swedish Lapland. I. A list of the habitats, and the composition of their oribatid fauna. *Oikos*, II (1) : 80-124.

GRANDJEAN (F.), 1950. — Observations éthologiques sur *Camisia segnis* (Herm.) et *Platynothrus peltifer* (Koch). *Bull. Mus. Hist. nat. Paris*, 2e sér. 22 (2) : 224-231.

HAARLØV (N.), 1960. — Micro-arthropods from Danish soils. Ecology, Phenology. *Oikos*, supplementum 3 : 1-176.

HAMMER (M.), 1946. — Oribatids in : The zoology of east Greenland. *Medd. Grønland*, BD. 122, NR. 1 : 1-39.

HARDING (J. P.), 1949. — The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. Mar. biol. Ass.* U. K. 28 : 141-153.

HARTENSTEIN (R.), 1962. — Soil Oribatei. II. *Belba kingi*, (Acarina : Belbidae), and a study of its life history. *Ann. ent. Soc. Amer.*, 55 (4) : 357-361.

HARTENSTEIN (R.), 1962 *a*. — Soil Oribatei. III. Studies on the development, biology and ecology of *Metabelba montana* (Kulcz.) (Acarina : Belbidae) and *Eremobelba nervosa* n. sp. (Acarina : Eremaeidae). *Ann. ent. Soc. Amer.*, 55 (4) : 361-367.

HARTENSTEIN (R.), 1962 *b*. — Soil Oribatei. IV. Observations on *Ceratozetes gracilis* (Acarina : Ceratozetidae). *Ann. ent. Soc. Amer.*, 55 (5) : 583-586.

HARTENSTEIN (R.), 1962 *c*. — Soil Oribatei. V. Investigations on *Platynothrus peltifer* (Acarina : Camisiidae). *Ann. ent. Soc. Amer.*, 55 (6) : 709-713.

JACOT (A. P.), 1934. — Some Hawaiian Oribatoidea (Acarina). *Bull. Bishop Mus., Honolulu*, 121 : 1-99.

KARPPINEN (E.), 1958. — Über die Oribatiden (Acar.) der Finnischen waldboden. *Ann. Zool. Soc. 'Vanamo'*, 19 (1) : 1-43.

KULCZYNSKI (V.), 1902. — Species Oribatinarum (Oudms.) (Damaeinarum Michael) in Galicia collectae. *Bull. Acad. Sci. Cracovie, Classes Math. et Nat.* 2 : 89-96.

MACFADYEN (A.), 1961. — Improved funnel-type extractor for soil arthropods. *J. Anim. Ecol.*, 30 : 171-184.

MANLEY (G.), 1952. — Climate and the British scene. Collins, London.

MICHAEL (A. D.), 1883. — British Oribatidae, I. Ray Society, London.

MICHAEL (A. D.), 1887. — British Oribatidae, II. Ray Society, London.

NICHOLSON (E. M.), 1957. — Britain's Nature Reserves. H.M.S.O., London.

NOORDAM (D.) and VAN DER VAART-DE VLIEGER (S. H.), 1943. — Een onderzoek naar samenstelling en beteekenis van de fauna van eikenstooisel. *Ned. BoschbTijdschr.*, 16 : 470-492.

PAULY (F.), 1956. — Zur Biologie einiger Belbiden (Oribatei, Moosmilben) und zur Funktion ihrer Pseudostigmatischen Organe. *Zool. Jb. Abt. Syst.*, 84 : 275-328.

RIHA (G.), 1951. — Zur Ökologie der Oribatiden in Kalksteinböden. *Zool. Jb. Abt. Syst.*, 80 : 407-450.

SENGBUSCH (H. G.), 1954. — Studies on the life history of three oribatid mites with observations on other species. *Ann. ent. Soc. Amer.*, 47 : 646-667.

SENGBUSCH (H. G.), 1958. — The development of *Nanhermannia nana* (Nicolet) (Acarina, Oribatei) ; life history studies of Oribatei II. *Ant. Rec.*, 132 (3) : 504.

TUXEN (S. L.), 1952. — Die Jugenstadien der nordischen Camisiiden (Acar. Orib.) Und etwas über die Systematic der Erwaschsenen. I. Die Gattungen *Nothrus*, *Platynothrus* und *Heminothrus*. *Ent. Medd.*, 26 : 392-403.

WOODRING (J. P.) and COOK (E. F.), 1962. — The biology of *Ceratozetes cisalpinus* Berlese, *Scheloribates laevigatus* Koch, and *Oppia neerlandica* Oudemans (Oribatei), with a description of all stages. *Acarologia*, 4 (1) : 101-137.

Pedobiologia, Bd. 5, S. 244—251 (1965)

Department of Zoology, University of Durham[1])

Distribution of Soil Mites (Acarina) on the Moor House National Nature Reserve, Westmorland, with Notes on their Numerical Abundance

By William C. Block

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Contents

1. Introduction

The micro-arthropod fauna of British uplands has received scant attention from zoologists, and the records of soil mites (Acarina) from such areas are few: Hull (1916), Seyd (1958, 1962). This paper gives a preliminary list of soil mites recorded from the Moor House National Nature Reserve in Westmorland during 1960—63.

The greater part of the Reserve's 10,000 acres (4,000 hectares) is over 1,800 ft. (550 m.), and consists of fells covered with blanket bog which are typical of the northern Pennines. Mineral soils are confined to the fell tops, limestone outcrops and stream sides. The climate of the area has been described as sub-arctic (Manley, 1952), and general descriptions of the Reserve are given by Conway (1955), Nicholson (1957) and Cragg (1961).

2. Sample Sites and Methods

Four sample sites characteristic of distinctive vegetative and soil types were selected for study at Moor House. The limestone grassland site has a mineral soil of the brown earth type, and is a typical *Festuca-Agrostis* upland grassland (Pearsall, 1950). The mixed moor sample site is blanket peat overlying a gleyed mineral soil with *Calluna vulgaris* (L.) as the dominant plant species. The *Juncus squarrosus* moor sample site is on thin, poorly drained peat, with *Juncus squarrosus* L. and *Festuca ovina* L. being dominant. The *Nardus stricta* grassland sample site is an imperfectly drained peaty alluvium and *Nardus stricta* L. is the dominant plant whilst *Galium saxatile* L. occurs abundantly.

The Acarina were extracted from soil cores in a high gradient apparatus (Macfadyen, 1961). The sample size was 10 cm^2 in surface area and 3 cm in depth, and 15 sample units were collected at random on each sample site on each sampling occasion. A total of 24 monthly samples were collected from each of the limestone grassland and the mixed moor sites (1961—62). The *Juncus squarrosus* moor and *Nardus stricta* grassland sites were sampled four times each in one year (*J. squarrosus* moor in 1961 and *N. stricta* grassland in 1962).

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3. Faunal List

The faunal list of soil mites recorded from the four sample sites at Moor House is given in Table 1. The list is arranged following the order of TURK (1953). All the collected material has not been identified to the species, and some difficult groups have been determined only to the genus. The term species/genera therefore refers to the total number of species and genera so far identified for any particular sample site. From the list it can be seen that there are few differences in the species composition of the four areas sampled. The *Juncus squarrosus* moor had 39 species/genera recorded and was the poorest area in this respect. The peat soil of the mixed moor and the mineral soil of the limestone grassland supported similar numbers of species/genera of Acarina (65 and 66 respectively). This situation was reflected in the oribatid mites, but the Mesostigmata showed a marked preference for the limestone grassland habitat with a total of 30 species/genera recorded compared with 20 species/genera for mixed moor.

Table 1 Faunal list of Acarina for the four sample sites at Moor House. + indicates that species or genus recorded on that sample site.
LG: Limestone grassland sample site.
NG: *Nardus stricta* grassland sample site.
MM: Mixed moor sample site.
JS: *Juncus squarrosus* sample site.

Sample site	LG	NG	MM	JS
CRYPTOSTIGMATA				
1. *Nanhermannia nana* sensu WILLMANN, 1931	+	+	+	+
2. *Hypochthonius rufulus* C. L. KOCH, 1836	.	.	+	+
3. *Trimalaconothrus foveolatus* WILLMANN, 1931	+	+	.	+
4. *T. novus* SELLNICK, 1921	.	.	.	+
5. *Nothrus palustris* C. L. KOCH, 1836	+	+	+	.
6. *N. silvestris* NICOLET, 1855	.	+	+	+
7. *Camisia segnis* (HERMANN, 1804)	.	.	+	+
8. *C. spinifer* (C. L. KOCH, 1836)	+	.	+	+
9. *C. horrida* (HERMANN, 1804)	.	.	+	.
10. *Platynothrus peltifer* (C. L. KOCH, 1839)	+	+	+	+
11. *P. punctatus* (L. KOCH, 1879)	.	.	+	.
12. *Hermannia reticulata* THORELL, 1888	.	.	.	+
13. *Damaeus clavipes* (HERMANN, 1804)	.	+	.	.
14. *D. gracilipes* (KULCZYNSKI, 1902)	.	.	.	+
15. *Eremaeus oblongus* C. L. KOCH, 1836	.	.	+	.
16. *Suctobelba trigona* (MICHAEL, 1888)	+	.	.	.
17. *S. subtrigona* (OUDEMANS, 1900)	.	.	+	.
18. *Suctobelba* spec. PAOLI, 1908	+	.	+	.
19. *Oppia splendens* C. L. KOCH, 1841	+	+	+	.
20. *O. subpectinata* OUDEMANS, 1901	+	+	.	.
21. *O. obsoleta* (PAOLI) sensu WILLMANN, 1931	.	.	+	.
22. *O. ornata* (OUDEMANS, 1900)	+	.	+	.
23. *O. quadricarinata* (MICHAEL, 1885)	.	.	.	+
24. *O. neerlandica* OUDEMANS, 1900	+	+	+	.
25. *Oppia* spec. KOCH, 1836	+	+	.	.
26. *Hydrozetes lacustris* (MICHAEL, 1882) [Tritonymph only]	.	.	+	.
27. *Thyrisoma lanceolata* (MICHAEL, 1888)	+	+	+	.
28. *Pantelozetes paolii* (OUDEMANS, 1917)	.	.	+	.
29. *Ceratoppia bipilis* (HERMANN, 1804)	+	+	+	+
30. *Tectocepheus velatus* (MICHAEL, 1880)	+	+	+	+
31. *Cepheus dentatus* (MICHAEL, 1888)	.	+	+	.
32. *C. latus* KOCH, 1836	.	+	.	.
33. *Carabodes marginatus* (MICHAEL, 1884)	+	.	+	+
34. *C. minusculus* BERLESE, 1923	+	+	+	+
35. *Adoristes ovatus* (C. L. KOCH, 1840)	.	+	.	.

Table 1 (Continued)

Sample site	LG	NG	MM	JS
36. *Oribatula tibialis* (NICOLET, 1855)	+	+	+	.
37. *Zygoribatula exilis* (NICOLET, 1855)	.	+	.	.
38. *Liebstadia similis* (MICHAEL, 1888)	+	+	+	+
39. *Minunthozetes semirufus* (C. L. KOCH, 1840)	+	.	.	.
40. *Melanozetes mollicomus* (C. L. KOCH, 1840)	+	.	+	.
41. *Edwardzetes edwardsii* (NICOLET, 1855)	+	.	+	+
42. *Chamobates incisus* VAN DER HAMMEN, 1952	+	.	.	.
43. *C. schützi* (OUDEMANS, 1902)	+	+	+	+
44. *Ceratozetes gracilis* (MICHAEL, 1884)	+	+	+	+
45. *Limnozetes sphagni* (MICHAEL, 1884)	.	.	+	+
46. *Pelops planicornis* (SCHRANK, 1803)	+	+	+	+
47. *P. plicatus* (C. L. KOCH, 1836)	+	.	+	+
48. *Peloptulus phaenotus* (C. L. KOCH, 1844)	+	+	.	.
49. *Achipteria coleoptrata* (LINNAEUS, 1758)	+	.	+	.
50. *Notaspis punctatus* NICOLET, 1855	+	.	+	.
51. *Galumna* spec. VON HEYDEN, 1826	+	+	+	.
52. *Phthiracarus piger* (SCOPOLI, 1763)	+	.	+	.
53. *P. ligneus* WILLMANN, 1931	+	.	+	+
54. *Rhysotritia duplicata* (GRANDJEAN, 1934)	.	.	+	.
55. *Pseudotritia minima* (BERLESE, 1904)	.	.	+	.
Total of species/genera of Cryptostigmata recorded per sample site:	33	25	40	23
MESOSTIGMATA				
1. *Zercon zelawaiensis* SELLNICK, 1944	+	.	.	.
2. *Z. colligans* BERLESE, 1920	+	+	+	+
3. *Zercon* spec. C. L. KOCH, 1836	+	+	+	+
4. *Prozercon kochi* SELLNICK, 1943	+	+	.	.
5. *Parazercon sarekensis* WILLMANN, 1939	+	+	.	.
6. *Veigaia nemorensis* (C. L. KOCH, 1839)	.	.	+	.
7. *V. cervus* (KRAMER, 1876)	.	.	+	+
8. *V. transisalae* (OUDEMANS, 1902)	+	.	+	+
9. *V. kochi* (TRÄGÅRDH, 1901)	.	.	.	+
10. *Euryparasitus emarginatus* (C. L. KOCH, 1839)	+	.	.	.
11. *Gamasodes spiniger* OUDEMANS, 1936	.	+	.	
12. *Parasitus* spec. LATREILLE, 1795	+	+	+	.
13. *Eugamasus cornutus* (G. et R. CANESTRINI, 1882)	+	.	+	.
14. *Eugamasus* spec. BERLESE, 1892	.	+	.	.
15. *Amblygamasus septentrionalis* (OUDEMANS, 1902)	+	.	.	.
16. *Holoparasitus* spec. OUDEMANS, 1936	+	.	.	.
17. *Pergamasus* (*Pergamasus*) *crassipes* (L.) BERLESE, 1906	+	.	+	.
18. *P.* (*Pergamasus*) *longicornis* BERLESE, 1906	+	+	.	.
19. *P.* (*Paragamasus*) *robustus* (OUDEMANS, 1902)	.	+	.	.
20. *P.* (*Paragamasus*) *decipens* (BERLESE, 1904)	+	.	.	.
21. *Digamasellus* spec. BERLESE, 1905	+	+	+	.
22. *Hypoaspis* spec. G. CANESTRINI, 1885	.	.	+	.
23. *Ololaelaps placentula* (BERLESE, 1887)	.	+	.	
24. *Proctolaelaps levis* (OUDEMANS et VOIGHTS, 1913)	.	.	+	.
25. *Lasioseius* spec. BERLESE, 1916	.	+	.	.
26. *Platyseius* spec. BERLESE, 1916	+	.	.	.
27. *Sejus serratus* (HALBERT, 1915)	.	.	.	+
28. *S. necorniger* (OUDEMANS, 1903)	+	.	.	+
29. *S. laelaptoides* (BERLESE, 1887)	.	.	+	.
30. *Plesiosejus italicus* (BERLESE, 1905)	.	.	+	.
31. *Eviphis ostrinus* (C. L. KOCH, 1836)	+	.	+	.
32. *Pachylaelaps longisetis* HALBERT, 1915	+	.	.	.
33. *Pachylaelaps* spec. BERLESE, 1888	+	.	.	+
34. *Sphaerolaelaps* (?) *holothyroides* (LEONARDI, 1897)	.	+	.	.

Table 1 (Continued)

Sample site	LG	NG	MM	JS
35. *Macrocheles submotus* FALCONER, 1923	+	+	+	+
36. *M. glaber* (MÜLLER, 1860)	+	+	.	.
37. *Geholaspis longispinosus* (KRAMER, 1878)	.	.	+	.
38. *Rhodacarus roseus* OUDEMANS, 1902	+	+	.	.
39. *Trachytes pyriformis* (KRAMER, 1876)	+	+	+	+
40. *T. minima* TRÄGÅRDH, 1910	+	.	+	+
41. *Dinychus perforatus* KRAMER, 1882	+	.	.	.
42. *Dinychus* spec. KRAMER, 1882	.	.	+	.
43. *Polyaspinus cylindricus* BERLESE, 1916	+	.	.	.
44. *Phaulocylliba* spec. BERLESE, 1904	+	.	.	+
45. *Cilliba cassidea* (HERMANN, 1804)	+	.	.	.
46. *Olodiscus minima* (KRAMER, 1882)	+	+	+	+
Total of species/genera of Mesostigmata recorded per sample site:	30	18	20	13
PROSTIGMATA				
1. *Pachygnathus villosus* DUGÈS, 1834	+	.	+	+
2. *Ledermuelleria* spec. OUDEMANS 1923	.	.	+	.
3. *Soldanellonyx chappuisi* WALTER, 1917	.	.	+	.
4. *Platytrombidium* spec. THOR, 1936	.	.	+	+
Total of species/genera of Prostigmata recorded per sample site:	1	0	4	2
ASTIGMATA				
1. *Rhizoglyphus echinopus* FUMOUZE et ROBIN, 1868)	+	.	+	+
2. Anoetidae OUDEMANS 1906 — hypopi	+	+	.	.
Total of species/genera of Astigmata recorded per sample site:	2	1	1	1
Total of species/genera of Acarina recorded per sample site:	66	44	65	39

A total of 13 species/genera were restricted to the limestone grassland (3 being Oribatei, the remainder being Mesostigmata), and 18 species/genera were recorded only from mixed moor (9 Oribatei, 7 Mesostigmata and 2 Prostigmata). Thus the sites generally had a similar species spectrum for Acarina, as BANAGE (1962) has observed for the Nematoda at Moor House; but unlike that of the Tipulidae (Diptera) (COULSON, 1959) and the Collembola (HALE, pers. comm.) on the same area.

According to VAN DER HAMMEN (1952), *Nothrus silvestris* has been recorded mostly from forest soils, but SEYD (1962) also collected this species from moss and heather litter on Kinder Scout, Derbyshire. Trees are absent from both areas at the present time. The normal distribution of *Platynothrus punctatus* has been described as arctic and sub-arctic. SEYD (1958) first recorded this species in Britain in Derbyshire, and considers that BAGNALL (reported by HULL, 1916) unknowingly collected *P. punctatus* from Cheviot Hill in southern Scotland and that it was incorrectly described as a new species, *Heminothrus valentianus* HULL, 1916. Thus there are three records of *P. punctatus* from high ground in Britain.

Limnozetes sphagni was recorded only from wet clumps of *Sphagnum* moss at Moor House. A notable absence from the Oribatei recorded from the Reserve is *Calyptozetes sarekensis* (TRÄGÅRDH, 1910), which has been found on Kinder Scout in Derbyshire. It has further been postulated by SEYD (1962) that the discontinuous distribution of species

of oribatid mites (e. g. *Platynothrus punctatus* and *Calyptozetes sarekensis*) may be due to their being part of a relict fauna of the Ice Age. Species which today may be described as arctic and sub-arctic, would have been widely distributed in Europe during the Upper Pleistocene glaciation. With the return of warmer post-glacial conditions, the only habitats suitable for the survival of such forms would be the upland areas and mountains. The collection of *Platynothrus punctatus* at Moor House above 1,800 ft. (ca. 550 m.) supports this theory.

4. Quantitative Results

The abundance of the common species or groups collected from the four study sites at Moor House is considered here. The mean annual density of each of the four groups of Acarina, and the proportion of each of these groups in the total mite fauna are given in Table 2. These data show that the *Nardus stricta* grassland site had the highest mean density of Acarina (77.82 ± 4.24 thousands per m^2), and that the limestone grassland in 1961 had the lowest mean density of Acarina (28.74 ± 1.09 thousands per m^2).

Table 2 Mean annual density and percentage composition of the major groups of Acarina on four sample sites at Moor House. The figures are the mean density per 10 cm^2 with the standard error, and the percentage composition.

Group Site and year	Total Acarina	Crypto-stigmata	Meso-stigmata	Pro-stigmata	Astigmata
Limestone Grassland, 1961	28.74 ± 1.09	17.91 ± 0.79 62%	9.88 ± 0.43 34%	0.94 ± 0.14 3%	0.61 ± 0.03 2%
Limestone Grassland, 1962	45.29 ± 1.41	28.24 ± 1.29 62%	9.41 ± 0.38 20%	6.87 ± 0.49 15%	2.41 ± 0.21 4%
Mixed *Calluna* moor, 1961	41.86 ± 2.16	38.78 ± 2.12 93%	2.85 ± 0.16 7%	0.22 ± 0.08 0.5%	0.14 ± 0.03 0.3%
Mixed *Calluna* moor, 1962	65.79 ± 3.19	62.01 ± 3.50 94%	2.86 ± 0.18 4%	0.87 ± 0.12 1%	0.28 ± 0.07 0.4%
Juncus squarrosus moor, 1961	43.01 ± 3.09	40.34 ± 3.04 93%	2.55 ± 0.30 5%	0.10 ± 0.04 0.2%	0.50 ± 0.10 1.2%
Nardus stricta grassland, 1962	77.83 ± 4.24	65.96 ± 3.82 85%	9.91 ± 0.69 13%	1.46 ± 0.16 1%	0.51 ± 0.12 0.6%

Species or families which had mean annual densities in excess of 1,000 individuals per m^2 are shown in Table 3. In the routine analysis of the extracted fauna, the Mesostigmata specimens were identified only to the family, and data are given for the density of individual species only for the Cryptostigmata. From Table 3 the following conclusions can be drawn from the density distribution of the common species of Acarina on the sample sites at Moor House. There were six species and one family which had their highest mean densities on limestone grassland; namely: *Pelops planicornis*, *Pelops plicatus*, *Liebstadia similis* and *Thyrisoma lanceolata* of the Oribatei; and the Mesostigmata were *Olodiscus minima*, *Trachytes pyriformis* and the Parasitidae. *Platynothrus peltifer*, the Oppia-Suctobelba groups and the Zerconidae dominated the fauna of the *Nardus stricta* grassland. *Nanhermannia nana* occurred in its highest recorded mean density of 7.64 ± 1.76 thousands per m^2 on the *Juncus squarrosus* moor site. The highest mean densities of *Chamobates schützi*, *Carabodes minusculus*, *C. marginatus* and *Tectocepheus velatus* were recorded from the peat soil of mixed moor. In general, it can be concluded that there was no tendency for the density of individual species to vary in a constant proportion in the main environments of the habitats studied at Moor House.

Table 3 Mean annual densities of Acarina per 10 cm². on four sample sites at Moor House. The standard error of the mean density is given. Note: + indicates that species present; but less than 1,000 individuals per metre².

Species or Group	Limestone grassland 1961	Limestone grassland 1962	Mixed *Calluna* moor 1961	Mixed *Calluna* moor 1962	*Juncus squarrosus* moor 1961	*Nardus stricta* grassland 1962
Platynothrus peltifer	1.14 ± 0.11	1.64 ± 0.18	1.41 ± 0.13	0.54 ± 0.08	2.18 ± 0.31	8.37 ± 1.87
Pelops planicornis	1.04 ± 0.13	1.06 ± 0.17	0.44 ± 0.05	0.24 ± 0.04	+	+
Pelops plicatus	1.16 ± 0.12	1.57 ± 0.24	0.30 ± 0.06	0.12 ± 0.07	+	absent
Chamobates schützi	0.15 ± 0.09	0.01 ± 0.001	6.80 ± 0.55	3.09 ± 0.26	+	+
Nanhermannia nana	0.43 ± 0.07	1.20 ± 0.17	2.36 ± 0.23	2.24 ± 0.21	7.64 ± 1.76	6.08 ± 1.74
Carabodes minusculus	0.67 ± 0.08	0.63 ± 0.08	8.66 ± 1.35	11.79 ± 1.88	+	+
Carabodes marginatus	0.62 ± 0.01	2.26 ± 0.03	1.75 ± 0.14	2.20 ± 0.45	+	absent
Liebstadia similis	7.72 ± 0.09	9.57 ± 0.12	0.05 ± 0.01	0.16 ± 0.03	+	2.94 ± 0.33
Thyrisoma lanceolata	5.51 ± 0.68	6.09 ± 0.69	0.41 ± 0.07	0.61 ± 0.05	absent	+
Oppia — Suctobelba	1.49 ± 0.14	1.62 ± 0.16	2.00 ± 0.14	1.66 ± 0.21	+	2.77 ± 0.64
Melanozetes mollicomus	0.07 ± 0.02	1.94 ± 0.13	0.75 ± 0.12	1.03 ± 0.15	absent	absent
Tectocepheus velatus	1.18 ± 0.13	1.37 ± 0.14	5.46 ± 0.40	5.80 ± 0.40	2.97 ± 0.25	+
Cryptostigmata juveniles	9.88 ± 0.53	14.71 ± 0.91	15.15 ± 0.85	33.15 ± 1.81	26.93 ± 2.44	42.18 ± 2.70
Olodiscus minima	2.55 ± 0.18	1.62 ± 0.14	0.19 ± 0.03	0.22 ± 0.03	0.16 ± 0.04	2.20 ± 0.26
Trachytes pyriformis	2.16 ± 0.17	1.63 ± 0.14	0.11 ± 0.03	0.14 ± 0.04	0.05 ± 0.01	0.65 ± 0.09
Parasitidae	3.25 ± 0.18	3.26 ± 0.19	1.28 ± 0.08	1.77 ± 0.13	2.50 ± 0.24	3.07 ± 0.28
Zerconidae	0.72 ± 0.10	1.92 ± 0.15	0.13 ± 0.02	0.19 ± 0.05	0.05 ± 0.01	2.90 ± 0.26

5. Comparison of Moor House Fauna with other Areas

The closest similarity of the Oribatei species from Moor House and other British studies exists with the faunal list of MACFADYEN (1952) for a *Molinia* fen in Berkshire, and with the species recorded by SEYD (1962) from Kinder Scout, Derbyshire. From the former study there are 16 oribatid species (30 per cent of the Moor House fauna) in common with the present study; and in the list of SEYD (1962) there are 20 species out of a total of 23 recorded in common with Moor House fauna (i. e. 36 per cent of the Moor House fauna). It is to be expected that a similarity exists in the composition of the oribatid fauna of two areas of high Pennine moorland, and the results given here confirm this. The similarity of the Pennine mite fauna with that of the lowland *Molinia* fen (MACFADYEN, 1952) is probably due to the predominant peat soils of both areas.

A comparison of the Moor House oribatid fauna with continental studies reveals that 50 per cent (27 species) of the moorland fauna were also recorded by KARPPINEN (1962) in north Finland; and 45 per cent (25 species) of the Moor House fauna are in common with the Iceland records of TUXEN (1943). Similarities also exist with the mite fauna of Swedish Lapland (DALENIUS, 1963) and east Greenland (HAMMER, 1944).

6. Acknowledgements

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7. Summary

Records are given of soil mites collected from the Moor House National Nature Reserve, Westmorland, England during a survey in 1960—63. A total of at least 107 species is recorded belonging to the following groups:

Cryptostigmata (55), Mesostigmata (46), Prostigmata (4) and Astigmata (2). Data are given also of the abundance of the common species on the four sample sites studied. The Moor House fauna is compared with other areas in Britain and Europe.

7. Zusammenfassung

Verteilung der Bodenmilben (Acarinen) in dem Moor-House-National-Naturschutzgebiet Westmorland, mit Angaben über ihre zahlenmäßige Abundanz

von WILLIAM C. BLOCK

Es wird über Bodenmilben berichtet, die während einer Bestandsaufnahme in den Jahren 1960—63 in Moor-House-National-Naturschutzgebiet, Westmorland in England, gesammelt wurden. Eine Gesamtzahl von mindestens 107 Arten, die zu folgenden Gruppen gehören, wurde festgestellt: Cryptostigmata (55), Mesostigmata (46), Prostigmata (4) und Astigmata (2).

Auch über die Abundanz der gemeinen Arten an vier untersuchten Probenentnahmestellen wurden Angaben gemacht. Die Moor-House-Fauna wird mit der anderer Gebiete in Britannien und Europa verglichen.

8. Literature

BANAGE, W. B., 1962. Some nematodes from the Moor House National Nature Reserve, Westmorland. Nematologica, **7**, 32—36.

CONWAY, V. M., 1955. The Moor House National Nature Reserve, Westmorland. Handb. Soc. Prom. Nat. Res., III, 1—7.

COULSON, J. C., 1959. Observations on the Tipulidae (Diptera) of the Moor House Nature Reserve, Westmorland. Trans. R. ent. Soc. Lond., **3**, 157—174.

CRAGG, J. B., 1961. Some aspects of the ecology of moorland animals. J. Ecol., **49**, 477—506.

DALENIUS, P., 1963. Studies on the Oribatei (Acari) of the Torneträsk territory in Swedish Lapland. IV. Aspects of the distribution of the moss-mites and the seasonal fluctuations of their populations. K. Fysiogr. Sällsk. Lund. Förh., **32** (10), 105—129.

HAMMEN, L. VAN DER, 1952. The Oribatei (Acari) of the Netherlands. Zool. Verh. Leiden, **17**, 1—139.
HAMMER, M., 1944. Studies on the Oribatids and Collemboles of Greenland. Medd. Grønland BD. **141**, Nr. 3, 1—210.
HULL, J. E., 1916. Terrestrial Acari of the Tyne province. Trans. nat. Hist. Soc. Northumb., **4**, 381—409.
KARPPINEN, E., 1962. Zur Kenntnis der Oribatidenfauna Nordfinnlands. Arch. Soc. 'Vanamo', **16** (1), 36—48.
MACFADYEN, A., 1952. The small arthropods of a *Molinia* fen at Cothill. J. Anim. Ecol., **21**, 87—117.
MACFADYEN, A., 1961. Improved funnel-type extractor for soil arthropods. J. Anim. Ecol., **30**, 171—184.
MANLEY, G., 1952. Climate and the British scene. Collins, London.
NICHOLSON, E. M., 1957. Britain's Nature Reserves. H. M. S. O. London.
PEARSALL, W. H., 1950. Mountains and Moorlands. Collins, London.
SEYD, E. L., 1958. An Oribatid mite new to the British fauna. Naturalist, Lond., 3—4.
SEYD, E. L., 1962. The moss mites of Kinder Scout, Derbyshire (Acari: Oribatei). J. Linn Soc. (Zool.), **44** (300), 585—591.
TURK, F. A., 1953. A synonymic catalogue of British Acari. Ann. Mag. nat. Hist., **61**, 1—26.
TUXEN, S. L., 1943. Die Zeitliche und räumliche Verteilung der Oribatiden-Fauna (Acar.) bei Maelifell, Nord-Island. Ent. Medd., 23, 321—336.

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Studies on the Distribution of some Phthiracarid Mites (Acari: *Oribatidae*) in a Coniferous Forest Soil

By A. J. HAYES

With one figure in the text

(Received March 26th, 1965)

Contents

1. Introduction

The Phthiracaridae are a small family of Oribatid mites (Acari: Cryptostigmata), of which six genera and a dozen species have so far been recorded in Britain (TURK, 1953a, b) and all occur in soil or decaying organic material. Many workers have suggested that as the Phthiracaridae feed mainly on litter and decaying wood and have biting mouthparts, the members of this family play an important part in the decomposition of organic debris (JACOT, 1936, 1939; FORSSLUND, 1938; RIHA, 1951; SPENCER, 1951; SCHUSTER, 1955, 1956; WALLWORK, 1958; and DUNGER, 1958). Even though the members of this family occur commonly, particularly in coniferous forest soils, there have been no detailed investigations of their distribution in different habitats in Great Britain, although EVANS (1951) investigated the distribution of mites in a Sitka Spruce [*Picea sitchensis* (BONGARD) CARRIÈRE] plantation.

It was therefore decided to investigate the distribution of Phthiracarid mites in the soil of Coed Marian y Winllan, a small plantation of mixed coniferous species near Bangor (HAYES, 1962). This wood formerly comprised about 30 acres of old mixed hardwood approximately 100 to 150 years old, consisting mainly of *Quercus petraea* (MATTUSCHKA) LIEBL, *Fagus sylvatica* LINNÉ, and *Castanea sativa* MILL., with occasional trees of *Acer pseudoplatanus* LINNÉ, and *Betula verrucosa* EHRH. About thirty to thirty-five years ago, part of this wood was felled and replanted with conifers; *Abies grandis* LINDLEY,

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The Distribution of Soil Acarina on Eroding Blanket Bog

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With 2 figures in the text

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Contents

1. Introduction

The micro-arthropod fauna of British uplands has received little attention from zoologists, and this paper contributes towards filling this gap in our knowledge by providing information on the distribution of Acarina in the peat soil of eroding blanket bog. The study was made in 1961 on Moss Flats, a part of the Moor House National Nature Reserve, Westmorland, England. A preliminary check list of the soil mites of the Reserve has been made (Block, 1965).

Blanket peat, reaching a thickness of 2 m or more and supporting a mixed moor vegetation (Pearsall, 1950), covers much of the upland region of the British Isles. The peat layer is often eroded and dissected by channels or haggs, which cut down to the bedrock, and because of these erosion processes the water content of the surface layers of peat, and thus the plant cover, change markedly over short horizontal distances. This paper presents a picture of the distribution of the main species of soil mites associated with the stages of erosion of the moor, and attempts to explain the differences.

An account of the zoology of the Reserve has been given by Cragg (1961), and a study of the Collembola of eroding blanket bog is reported by Hale (1963). The botanical nomenclature in this paper follows Clapham, Tutin and Warburg (1952) for higher plants, Watson (1953) for lichens, and Watson (1955) for mosses.

2. Sample sites

The following areas were selected for study:

I. The uneroded moor supporting a mixed moor vegetation.
II. The top of a residual peat hummock remaining after the surrounding moor has been eroded away.
III. The lip or overhanging edge of a hagg.
IV. An area of tussocks of *Eriophorum vaginatum* L. growing on bare peat.
V. An area of *Eriophorum angustifolium* Honck. growing on bare peat.

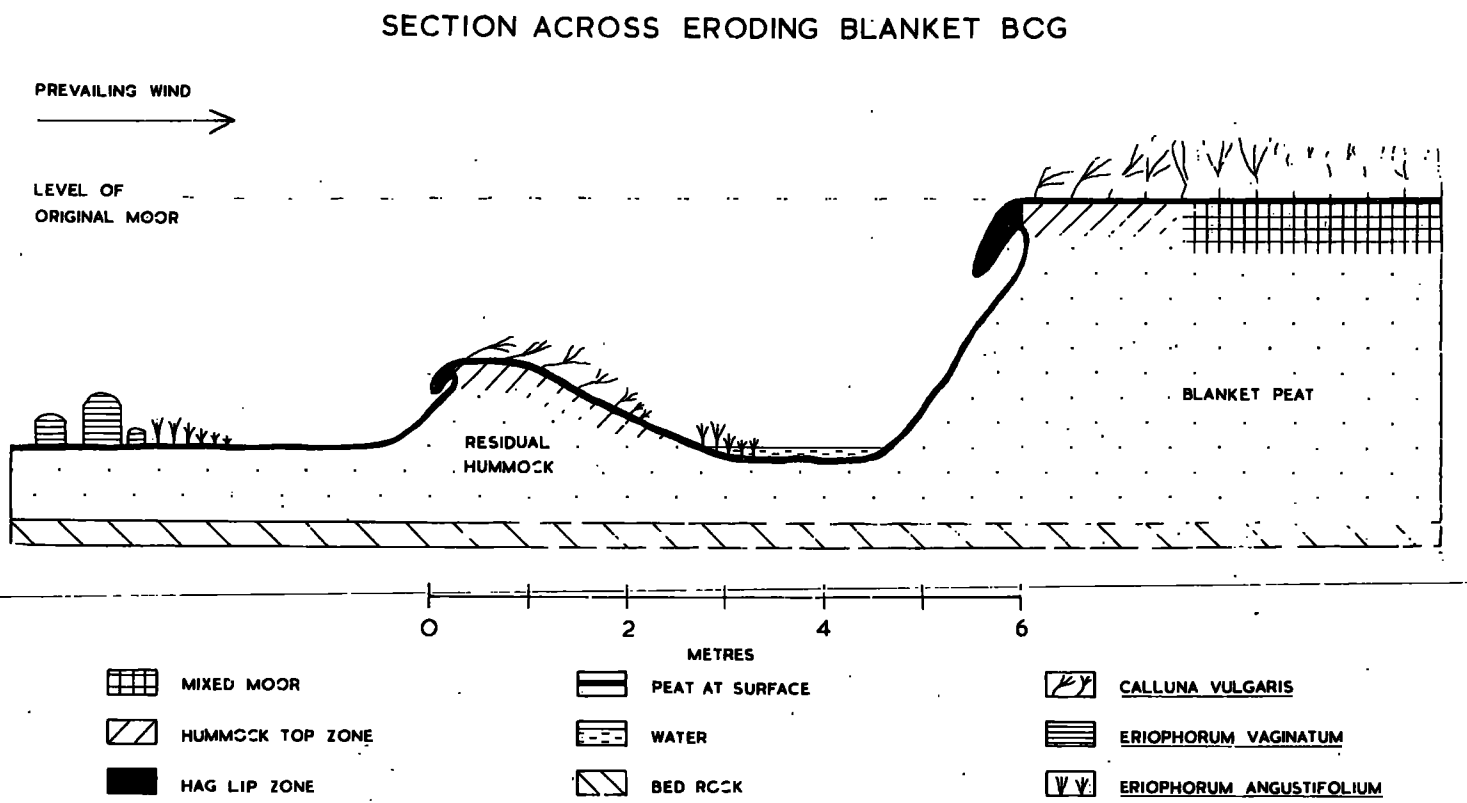

Figure 1. Diagrammatic section across eroding blanket bog showing the sample sites at Moor House.
Une coupe verticale diagrammatique de la tourbière ombrogienne erodée et il montre les situations des échantillons à Moor House.
Schematischer Schnitt durch das erodierende Hochmoor zur Kennzeichnung der Probenentnahmestellen bei Moor House.

Calluna vulgaris (L.) is the dominant plant of the mixed moor sample site with *Eriophorum vaginatum*, *E. angustifolium*, *Empetrum nigrum* L. *Vaccinium myrtilus* L. and *Rubus chamaemorus* L. occurring abundantly. *Sphagnum rubellum* WILS. is the dominant moss, and the following lichens also occur: *Cladonia sylvatica* (L.), *C. uncialis* (L.), *C. impexa* (L.) and *Hypogymnia physodes* L. The peat has a pH of 4.4—5.0 and overlies a gleyed mineral soil (JOHNSON and DUNHAM, 1963).

A hagg is formed by the progressive erosion of an area of blanket bog. At first a drainage channel is cut through the peat, and loose peat from its banks falls into it and is washed away; the vegetation binds the surface uneroded peat and a lip or overhang is formed at the edge of the hagg. The hagg lip is devoid of *Calluna* and mosses being mainly covered by the lichen *Cladonia coccifera* (L.); the peat here is no longer waterlogged and large populations of Collembola are found in this habitat (HALE, 1963). In some areas of Moss Flats, the peat erosion is so extensive that only a few *Calluna* covered hummocks remain on a shallow, bare peat surface, upon the top of which *Empetrum nigrum* becomes more common. Similar erosion on British and Irish bogs has been described by OSWALD (1949).

The erosion channels have cut down to the sandstone bedrock in places at Moor House, and elsewhere the bare redistributed peat forms a plane below the original moor level. In some areas stabilisation of this loose peat has occurred by the development of tussocks of *Eriophorum vaginatum*, and by the invasion of *Eriophorum angustifolium* into the wetter, bare peat areas.

It is suggested that sites I, II, IV and V represent the successive stages which occur in the erosion and primary recolonisation of the blanket bog studied. Site III (the hagg lip) is a special habitat as it is an area of much modified mixed moor, and it is not regarded as a true stage in the cycle of erosion. Figure 1 shows a transect across the eroding blanket bog with the sample sites indicated.

3. Sampling

In order to compare the Acarina of the erosion area with those of the mixed moor, regular samples were taken over one year (1961). The sites were sampled on the following dates during 1961: 27 February, 29 May, 5 September and 4 December. Fifteen sample units each 3 cm in depth and 11.35 cm^2 in surface area were taken with a soil auger from the dry hummock top, the hagg lip, the mixed moor and an area of *Eriophorum angustifolium*. Eight sample units each 6 cm in depth and 11.35 cm^2 in surface area were collected at the same time from *Eriophorum vaginatum* tussocks, as only in this habitat did preliminary studies show that mites occurred below 3 cm in depth. The Acarina were extracted from the soil samples in a high gradient extraction apparatus (MACFADYEN, 1961).

To compare differences between vegetation types, and species differences of Acarina, the data for the year are grouped. This reduces variations caused by the annual cycle of the mites, and differences arising from separate sampling dates. This gave data of 60 sample units from each site (hummock top, the hagg lip, mixed moor and *Eriophorum angustifolium*); except site IV (*Eriophorum vaginatum*) where 32 sample units were taken.

4. Soil Water Content

The soil samples were weighed in bulk before extraction; after extraction they were air dried at a temperature of 105 °C to constant weight. In Table 1 the soil water content is expressed as the ratio of the weight of water to the dry weight, and the figures are the means for all the sample units collected on the dates indicated. The high values for mixed moor are due to the water retaining properties of live *Sphagnum* mosses.

5. Distribution of Mites

Table 2 shows the mean density and the percentage composition of the groups of Acarina on the five sample sites of the erosion area compared with that on mixed moor.

Table 1 Soil water contents of samples from the erosion area of Moss Flats compared with the mixed moor.

Sampling date	Mixed moor	Hummock top	*Eriophorum vaginatum*	Bare peat	*Eriophorum angustifolium*	(Hagg lip)
27. 2. 1961	9.2	3.6	4.0	4.7	4.4	(2.5)
29. 5. 1961	7.7	1.0	3.4	3.2	3.6	(1.1)
5. 9. 1961	9.4	3.3	3.6	5.0	4.3	(1.8)
4. 12. 1961	8.9	3.4	7.3	5.0	5.7	(3.0)
Mean	8.8	2.8	4.6	4.5	4.5	(2.1)

The figures are the ratio of weight of water to dry weight and are the means of 15 sample units from all sites except the *Eriophorum vaginatum* site which are the means of 8 sample units.

Table 2 Mean density and percentage composition of the major groups of Acarina on the five sites of the erosion area compared with the mixed moor.

Group Site	Total Acarina	Crypto-stigmata	Meso-stigmata	Pro-stigmata	Astigmata	Collembola
Mixed moor	48.7 ± 4.2	45.3 ± 4.2 93.0 %	3.2 ± 0.2 6.6 %	0.2 ± 0.1 0.4 %	0.0	31
Hummock top	97.5 ± 7.2	92.8 ± 6.8 95.2 %	2.5 ± 0.2 2.6 %	1.4 ± 0.5 1.5 %	0.8 ± 0.3 0.7 %	39
Eriophorum vaginatum	34.0 ± 3.7	26.8 ± 3.5 78.8 %	4.1 ± 0.6 12.1 %	3.1 ± 1.1 9.0 %	0.0	24
Bare peat	0.0	0.0	0.0	0.0	0.0	0.0
Eriophorum angustifolium	26.0 ± 3.1	25.3 ± 3.1 97.4 %	0.6 ± 0.2 2.3 %	0.1 ± 0.03 0.4 %	0.0	5
Hagg lip	21.2 ± 3.1	18.9 ± 2.8 89.0 %	1.6 ± 0.2 7.6 %	0.2 ± 0.1 0.9 %	0.5 ± 0.3 2.5 %	125

The figures are the mean density per 10 cm² and the standard error. The data for Collembola are after HALE (1963).

The highest density of mites was found on the hummock top, and was significantly greater than that of the mixed moor ($P < 0.001$). The mean density of mites on mixed moor was also significantly greater than on the area of *E. vaginatum* ($P < 0.05$). There was no correlation between the abundance of mites and collembola recorded on these areas.

The Cryptostigmata formed at least 90 % of the total mite fauna on all sites with the exception of *E. vaginatum*, where the group was 79 % of the total fauna. The Mesostigmata were 2—8 % of the total numbers on all sites except, again, the area of *E. vaginatum* where they were relatively more abundant, reaching 12 %. The Prostigmata constituted approximately 1 % of the total mites on all sites except the *E. vaginatum* where they reached 9 %. The Astigmata were recorded only from the hummock top and the hagg lip zone.

The mean densities of mites per 10 cm² of surface (30 cc) on the sample sites of the eroding blanket bog are compared with the mixed moor in Table 3. The common species on the mixed moor and hummock top were *Chamobates schützi*, *Carabodes minusculus* and *Tectocepheus velatus*. *T. velatus* and *C. minusculus* were in significantly greater numbers on the hummock top and mixed moor than on any other site ($P < 0.001$, and $P < 0.02$ respectively). *C. schützi* had significantly higher ($P < 0.02$) densities on mixed moor, hummock top and *E. vaginatum* tussocks than on any other area. *Oppia* spp. and *Suctobelba* spp. were distributed similarly to *C. schützi* but in lower densities. The species confined mainly to both the *Eriophorum* areas was *Platynothrus peltifer*, and the densities of this species on these sites were not significantly different. *Ceratoppia bipilis* reached its

Table 3 Mean densities of Acarina per 10 cm² (30 cc) on the sample sites of the erosion area of Moss Flats compared with the mixed moor. The standard error of the mean is given.

Species or Family	Mixed moor	Hummock top	*Eriophorum vaginatum*	Bare peat	*Eriophorum angustifolium*	Hagg lip
Chamobates schützi	9.78	8.45	6.11	0.0	0.36	0.91
(Oudemans, 1902)	± 1.28	± 0.76	± 1.86		± 0.09	± 0.20
Oppia-Suctobelba	1.85	2,60	0.13	0.0	0.0	0.34
spp.	± 0.19	± 0.49	± 0.09			± 0.10
Carabodes minusculus	8.91	15.96	0.27	0.0	0.05	2.70
(Berlese, 1923)	± 1.21	± 3.27	± 0.20		± 0.01	± 0.88
Tectocepheus velatus	4,80	16.38	0.27	0.0	0.0	7.03
(Michael, 1880)	± 0.25	± 3.59	± 0.17			± 2.09
Platynothrus peltifer	0.80	0.63	3.38	0.0	6.69	0.04
(C. L. Koch, 1839)	± 0.12	± 0.19	± 1.49		± 1.55	± 0.01
Pelops planicornis	0.23	0.63	1.65	0.0	0.0	0.44
(Schrank, 1803)	± 0.05	± 0.16	± 0.46			± 0.25
Liebstadia similis	0.03	1.64	0.0	0.0	0.0	0.03
(Michael, 1888)	± 0.01	± 0.38				± 0.01
Ceratoppia bipilis	0.27	0.81	3.36	0.0	0.03	0.0
(Hermann, 1804)	± 0.07	± 0.13	± 0.85		± 0.01	
Phthiracarus ligneus	0.76	0.31	0.0	0.0	0.0	0.04
Willmann, 1931	± 0.14	± 0.09				± 0.01
Parasitidae	1.12	1.07	1.23	0.0	0.04	0.74
	± 0.25	± 0.20	± 0.13		± 0.01	± 0.09
Olodiscus minima	0.25	0.10	1.54	0.0	0.0	0.0
(Kramer, 1882)	± 0.05	± 0.02	± 0.51			
Trachytes pyriformis	0.15	0.10	0.33	0.0	0.0	0.06
(Kramer, 1876)	± 0.05	± 0.03	± 0.10			± 0.02
Zerconidae	0.04	0.06	0.0	0.0	0.0	0.45
	± 0.02	± 0.01				± 0.12
Veigaiaidae	0.82	0.54	0.22	0.0	0.06	0.23
	± 0.12	± 0.07	± 0.08		± 0.01	± 0.09
Pachylaelaptidae	0.38	0.18	0.66	0.0	0.0	0.12
	± 0.07	± 0.05	± 0.16			± 0.05

highest density on the *E. vaginatum* area. The distribution of some of the common species of mites on Moss Flats is shown in a diagrammatic form in Figure 2. The sample sites are arranged in what is considered to be the succession of erosion or degradation of mixed moor through to bare peat, and its initial recolonisation by *E. angustifolium*.

The bare peat did not support a permanent population of Acarina, but occasionally individuals could be found which presumably had been carried there by the wind from surrounding areas. In some parts of Moss Flats an algal mat is formed on the bare redistributed peat in the spring. As conditions become drier in early summer, the peat cracks and the algal mat flakes away from the peat surface. Beneath these flakes high humidities were maintained and *P. peltifer* occurred here. A similar habitat to this was beneath flat pieces of sandstone rock exposed by erosion on the peat surface, and here *P. peltifer* outnumbered all other species. Haarløv (1942), Hammer (1946) and Weis-Fogh (1948) all recorded this species from moist habitats. *C. bipilis* was also recorded from both these temporary habitats on the bare peat. It is suggested, therefore that the bare peat areas of Moss Flats lacked a permanent mite population only because it did not afford sufficient protection from adverse climatic conditions.

6. Discussion

The erosion processes of blanket bog cause a general drying out of the soils as is shown in Table 1. The distribution of Collembola on the same area of blanket bog has been shown to be correlated with the soil water content of the habitats (Hale, 1963).

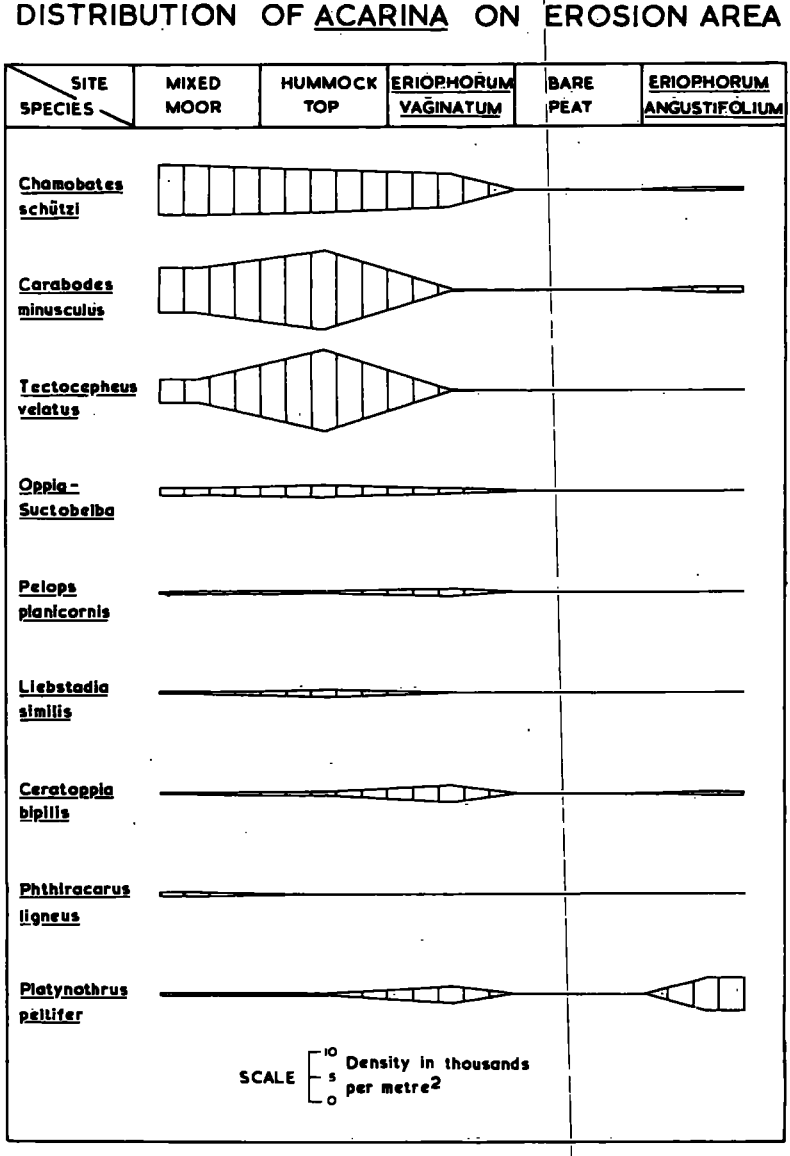

Figure 2. Diagram showing the distribution of the common species of soil mites (Acarina) on the eroding blanket bog at Moor House.
La diagramme montre la distribution des espèces ordinaires des acariens (Acarina) au sol de la tourbière ombrogienne erodée à Moor House.
Das Diagramm zeigt die Verteilung der gewöhnlichen Bodenmilben-Arten im erodierenden Hochmoor bei Moor House.

The density of Acarina and the species abundance were not determined solely by the soil water contents of the habitats sampled in the present study. The number of species present in each habitat were not related to the soil moisture. There were 15 species recorded from each of the mixed moor and hummock top; two habitats which had very differ-

ent soil water contents (see Table 1). Only six species were represented on *E. angustifolium* and twelve were present on the *E. vaginatum* area; two habitats with similar soil moisture contents.

In order to examine these faunal differences further, the samples from the special zone of the hagg lip were studied (Tables 2 and 3). The hagg lip was immediately adjacent to the mixed moor, which supported a population of 48.7 ± 4.2 Acarina per 10 cm². The hagg lip was the driest of the sample areas (a mean moisture content of 2.0 over the study year as compared with 8.8 of the mixed moor), and it supported less than half the mite population of the mixed moor, although 13 out of the 15 species found on mixed moor were also recorded from the hagg lip. The hagg lip zone had a similar soil water content to the top of the residual *Calluna* hummock, but supported less than a quarter of the hummock top mite population of 97.5 ± 7.2 per 10 cm². There was thus a paucity of mites on the hagg lip, which cannot be accounted for solely by the physical factors measured in this study. It is of interest to note that the highest density of Collembola (125.20 ± 8.8 per cm²) observed by HALE (1963) on Moss Flats was in the hagg lip zone.

It is suggested that biotic factors such as the changes in plant cover which take place as the moor is eroded, may determine the distribution of Acarina on the Moss Flats area at Moor House. Associated with changes in the vegetation are the changes in the microflora of the soil, and this may well be important to the mites as many species of the Oribatei are fungivorous. The difference between the hagg lip and the hummock top mite density could be caused by the different plant cover of the two areas. *C. minusculus* and *T. velatus* were the only mites able to resist desiccation and inhabit the micro-cavities of the lichens growing on the hagg lip.

Further evidence in support of this conclusion is given by the distribution on the study area of the three common species of Oribatei: *C. schützi*, *C. minusculus* and *T. velatus* shown in Figure 2. These species were all recorded with high densities in both wet and dry habitats; from the waterlogged mixed moor and the relatively dry hummock top. *T. velatus* has been found in high densities in a Swedish bog by TARRAS-WAHLBERG (1961), who placed it in the mesophilous hemiedaphon of the Gisin-Strenzke Lebensformen classification, showing that it requires a relative humidity of about 100 % for survival. KLIMA (1959), however, recorded this species from 'dry' habitats. Previously, STRENZKE (1952) termed *T. velatus* a 'plastic' species in relation to environmental factors such as water content, humus content, PH, litter cover and sodium chloride content of the soil. The distribution of *T. velatus* on the eroding blanket bog at Moor House suggests that this species can withstand great extremes of environmental conditions.

The erosion of the moorland with the concomitant changes of vegetation cover cause different densities and species of Acarina to occur. As the mixed moor is slowly degraded by the loss of its plant cover to a bare peat surface, the abundance of soil mites falls, both in respect of species and total numbers. The distribution of the characteristic species of Acarina with the stages of erosion and recolonisation of Pennine moorland may be summarised in the following manner:

Erosion			Recolonisation	
Mixed moor	→ Hummock top	→ *Eriophorum vaginatum*	→ Bare peat	→ *Eriophorum angustifolium*
Chamobates schützi		*C. schützi*	—	—
Carabodes minusculus		—	—	—
Tectocepheus velatus		—	—	—
—	—	*Ceratoppia bipilis*	—	—
—	—	*Platynothrus peltifer*	*Platynothrus peltifer* (rare)	*Platynothrus peltifer*

It should, however, be noted that the time scale of these changes is not known.

7. Acknowledgments

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8. Summary

Data are presented showing the distribution of the common species of soil mites (Acarina) associated with blanket bog in northern England. Changes in population density and species abundance were demonstrated during erosion and initial recolonisation of the blanket bog. It is suggested that these changes were directly related to biotic factors such as changes in plant cover or the microflora of the soil, and not to soil moisture.

8. Sommaire

Les données montrent la distribution des espèces ordinaires des acariens (Acarina) dans la tourbière ombrogienne d'Angleterre au nord. Les changements de la densité des populations et le nombre des espèces sont démontré pendant la érosion et la nouvelle colonisation de la tourbière ombrogienne. Il propose lesquels changements des populations des acariens et des espèces sont attaché à agents biologiques une telle la couverture des plantes ou la flore microscopique au sol, et ils ne sont pas attaché à la humidité au sol.

8. Zusammenfassung

Es werden Daten vorgelegt, aus denen die Verteilung von gewöhnlichen Bodenmilben-Arten in einem nordenglischen Hochmoor ersichtlich ist. Änderungen der Besatzdichte und des Vorkommens einzelner Arten während der Erosion und in den Anfangsstadien der Wiederbesiedlung des Hochmoores werden gezeigt. Es wird vermutet, daß diese Veränderungen direkt mit biotischen Faktoren — wie Veränderungen der Pflanzendecke oder mit der Mikroflora des Bodens — und nicht mit der Bodenfeuchtigkeit in Beziehung stehen.

9. Literature

BLOCK, W. C., 1965. Distribution of soil mites (Acarina) on the Moor House National Nature Reserve, Westmorland, with notes on their numerical abundance. Pedobiologia, **5**, 3/4, 252—261.

CLAPHAM, A. R., TUTIN, T. G., and WARBURG, E. F., 1952. Flora of the British Isles. Cambridge.

CRAGG, J. B., 1961. Some aspects of the ecology of moorland animals. J. Anim. Ecol., **30**, 205—234.

HAARLØV, N., 1942. A morphologic-systematic-ecological investigation of Acarina, and other microfauna around Mørkefjord, N. E. Greenland. Dansk N. E. Greenland Expedition 1938—39. Medd. Grønland, BD. **128**, NR. 1. Copenhagen.

HALE, W. G., 1963. The Collembola of eroding blanket bog. In Soil Organisms (ed. by DOEKSEN, J., and VAN DER DRIFT, J.): 406—413. North-Holland, Amsterdam.

HAMMER, M., 1946. Oribatids in: The zoology of east Greenland. Medd. Grønland, BD. **122**, NR. 1: 1—39.

JOHNSON, G. A. L., and DUNHAM, K. C., 1963. The geology of Moor House. Monograph of the Nature Conservancy, No. 2. H. M. S. O. London.

KLIMA, J., 1959. Die Zönosen in der Umgebung von Innsbruck. De Natura Tirolense, 197—208.

MACFADYEN, A., 1961. Improved funnel-type extractor for soil arthropods. J. Anim. Ecol., **30**, 171—184.

OSWALD, H., 1949. Notes on the vegetation of British and Irish mosses. Acta phytogeogr. suec., **26**, 1—62.

PEARSALL, W. H., 1950. Mountains and Moorlands. New Naturalist Monograph. Collins, London.

STRENZKE, K., 1952. Untersuchungen über die Tiergemeinschaften des Bodens: Die Oribatiden und ihre Synusien in den Böden Norddeutschlands. Zoologica, **104**, 1—172.

TARRAS-WAHLBERG, N., 1961. The Oribatei of a central Swedish bog and their environment. Oikos, Suppl. **4**, 1—56.

WATSON, E. V., 1955. British mosses and liverworts. Cambridge.

WATSON, W., 1953. Census catalogue of British lichens. Cambridge.

WEIS-FOGH, T., 1948. Ecological investigations on mites and collemboles in the soil. App.: Description of some new mites (Acari). Nat. Jutland. 1: 139—277.

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SEASONAL FLUCTUATIONS AND DISTRIBUTION OF MITE POPULATIONS IN MOORLAND SOILS, WITH A NOTE ON BIOMASS

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SEASONAL FLUCTUATIONS AND DISTRIBUTION OF MITE POPULATIONS IN MOORLAND SOILS, WITH A NOTE ON BIOMASS

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Department of Zoology, University of Durham

Free-living terrestrial mites occur in a great variety of habitats, and they are especially abundant in situations where organic detritus is present. Consequently an ecological study of mites in organic peat soils and in mineral soils was made in 1961 and 1962 on the Moor House National Nature Reserve, Westmorland, England, and the results of this are reported here. Apart from a few records (Hull 1914, 1916, 1918; Seyd 1962) little is known of the mite fauna of upland soils; and the present study forms part of a more comprehensive survey of the fauna of the Reserve initiated by Cragg (1961).

Block (1965a) gives a preliminary check list of the soil mites of Moor House, and Block (1965b, 1966a) reports life history studies and studies on the Acarina of eroding moor. Botanical nomenclature in this paper follows Watson (1953) for lichens, Watson (1955) for mosses, and Clapham, Tutin & Warburg (1952) for higher plants.

STUDY AREA

Most of the Moor House Reserve of 10 000 ac (4000 ha) is over 1800 ft ordnance datum (549 m), and it includes fells that are typical of the northern Pennines. The climate is characteristically cold and wet, and corresponds to that at sea level in southern Iceland (Manley 1952). The area has been further described by Conway (1955), Nicholson (1957) and Cragg (1961).

The bedrock underlying the Reserve consists of successive strata of sandstones, shales and limestones belonging to the Carboniferous Yoredale Series (Johnson & Dunham 1963). The area is mostly covered by blanket bog, mineral soils being confined to the fell tops, rock outcrops and stream sides. A description of the vegetation of these soil types is given below. Two sites, typical of the peat and mineral soil areas were selected for the main study, as it was considered that they would show the two extremes of the soil fauna.

Limestone grassland sample site

Situated close to the Moor House Field Station at 1850 ft (564 m), the site has a brown earth soil type. The soil rarely exceeds 50 cm in depth and has a high pH by moorland standards (5·0–5·8). The site is on a north-west-facing slope with good drainage, with a result that the soil is well aerated, some earthworms are found and arthropods may be present throughout the soil profile. The site is a typical *Festuca–Agrostis* upland grassland (Pearsall 1950), and is grazed heavily by sheep during the summer months. The vegetation and humus mat is approximately 3 cm thick, and was separated from the soil layer when sampling. The dominant plant species are *Festuca ovina* L. and *Agrostis tenuis* Sibth., with *A. canina* L., *Thymus drucei* Ronn., *Polytrichum commune* Hedw. and *Potentilla erecta* (L.) occurring abundantly (Eddy, personal communication, 1962).

During the 2-year study period there were greater fluctuations in the water content of the upper 3 cm layer of vegetation and humus than in the lower 4–6 cm soil layer. Indices of humidity ranged from 0·64 to 2·15 in the upper layer, and from 0·51 to 1·17

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in the lower layer. The driest soil samples were collected in June and the wettest in December and January in both study years.

Mixed moor sample site

This site, Dodgen Pot, is situated to the north-west of Great Dodgen Pot Sike, with an elevation of 1840 ft (561 m). The blanket peat which covers the site has a pH of 4·4–5·0 and it overlies a gleyed mineral soil. The site has typical blanket bog vegetation except that the *Sphagnum* cover is reduced due to the relatively low level of the water table on the sample site, compared with other areas nearby. The litter layer is approximately 2 cm thick, and consists of leaves and shoots of *Calluna*, lichens and mosses; and below this layer is undecayed humus which is usually waterlogged, but clumps of easily recognizable *Sphagnum* occur here. The driest soil samples were collected from this site in May and June of both years (indices of humidity ranged from 5·7 to 6·1), and the wettest samples in September 1961 (index of humidity of 9·4) and December 1962 (index of humidity of 11·8).

Calluna vulgaris (L.) is the dominant plant, with *Eriophorum vaginatum* L., *E. angustifolium* Honck., *Vaccinium myrtillus* L., *Empetrum nigrum* L. and *Rubus chamaemorus* L. occurring abundantly. The dominant moss is *Sphagnum rubellum* Wils., with the following lichens commonly present: *Cladonia sylvatica* (L.), *C. impexa* (L.) and *C. uncialis* (L.), (Eddy, personal communication, 1962).

Other sample sites

Two other sites were sampled for soil mites at Moor House, and are referred to in the section on biomass. An area of grassland at 1975 ft (602 m) on the west bank of Rough Sike, dominated by *Nardus stricta* L., with a 3 cm deep litter layer. The soil is an imperfectly drained peaty alluvium and the site is occasionally flooded by the nearby stream. Indices of humidity for soil samples from this site ranged from 1·3 to 4·0.

The *Juncus* moor sample site is situated to the north of the alluvial flats of Troutbeck at an elevation of 1840 ft (561 m), and has a south-facing sheltered aspect. *J. squarrosus* L. and *Festuca ovina* L. are the dominant plants. The underlying peat is thin and the site has poor drainage (indices of humidity recorded were from 5·5 to 7·5).

The chemical characteristics of these sites at Moor House are given in Cragg (1961).

METHODS

Monthly soil samples were taken on the two main study sites. Each sample consisted of fifteen randomly selected soil cores, each 11·35 cm^2 (1/881 m^2) in surface area and 6 cm deep. The cores were taken with a soil sampler similar to that decribed by Macfadyen (1961) and cut horizontally into halves which were extracted separately. The micro-arthropods were extracted from the soil cores in a high gradient apparatus (Macfadyen 1961), which extracted thirty cores at one time, the most suitable extraction period being 3 days. Block (1966b) gives some characteristics of this apparatus. The mites were counted and identified as soon as possible. A mean estimate of the populations of soil mites on the two sites was thus obtained each month during 1961 and 1962.

HORIZONTAL DISTRIBUTION OF SOIL MITES

Aggregation is a common feature of soil animals including mites (Macfadyen 1952; Hartenstein 1961; Nef 1962) and this is demonstrated also in the present study. Coefficients of dispersion (c.d.) or relative variances were calculated for total mites, juvenile Oribatei and six oribatid species for the twenty-four monthly samples from limestone

grassland and mixed moor. For total mites, the c.d. was significantly greater than unity for all samples, and for juvenile Oribatei and for the six species considered the c.d. were, in the main, significant, showing aggregation. Fig. 1 shows the relationship of mean population density to c.d. for total mites on the two sites. The c.d. increases slowly with the mean, up to a population density of 50–60 thousands/m^2, when it increases more steeply. The distinction, however, between a real increase in aggregation of the individuals of the populations, and the suggestion of an increase in aggregation produced by a

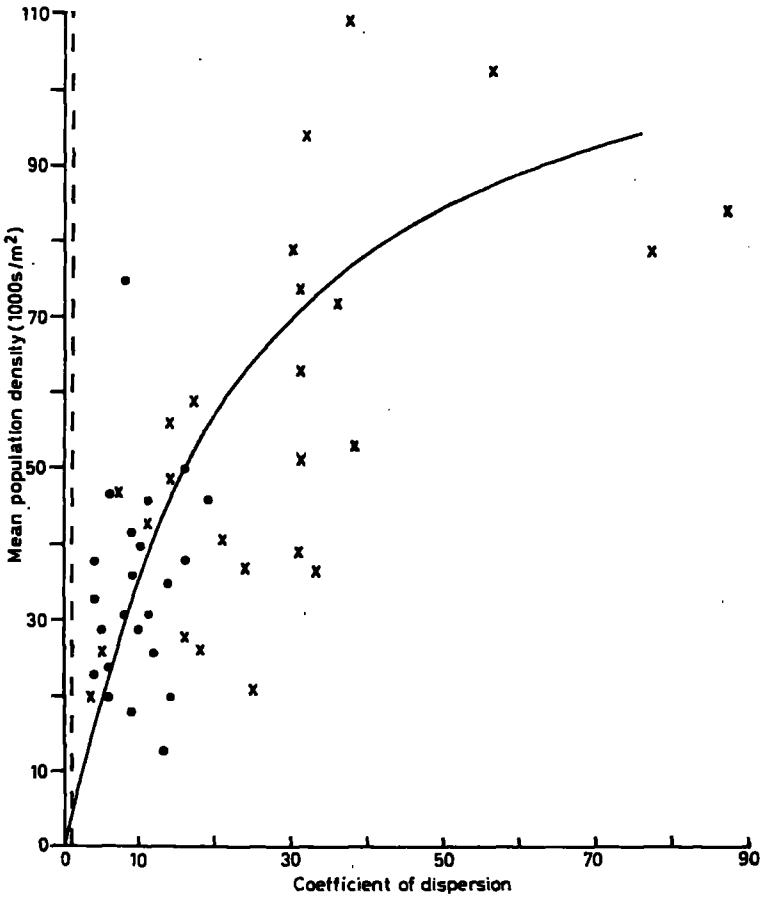

FIG. 1. Graph showing the relationship of the values of the coefficient of dispersion (c.d.) to the mean population density per sample for total Acarina. The samples were from the limestone grassland (●) and mixed moor (×) sites, collected in 1961 and 1962. The trend line has been drawn in by eye, and the Poisson line (variance equal to the mean) is indicated by a vertical broken line.

larger population, cannot be made using c.d. The coincidence of high values of c.d. with the presence of many juveniles in the populations suggests, however, that there are real increases in the degree of aggregation during the spring and autumn breeding periods.

In a comparison of the frequency distribution of the sample unit values for total Acarina with the normal distribution a non-normal distribution which was not Poisson was indicated. The comparison thus showed that there was a random distribution with a few discrete aggregations superimposed upon this basic pattern.

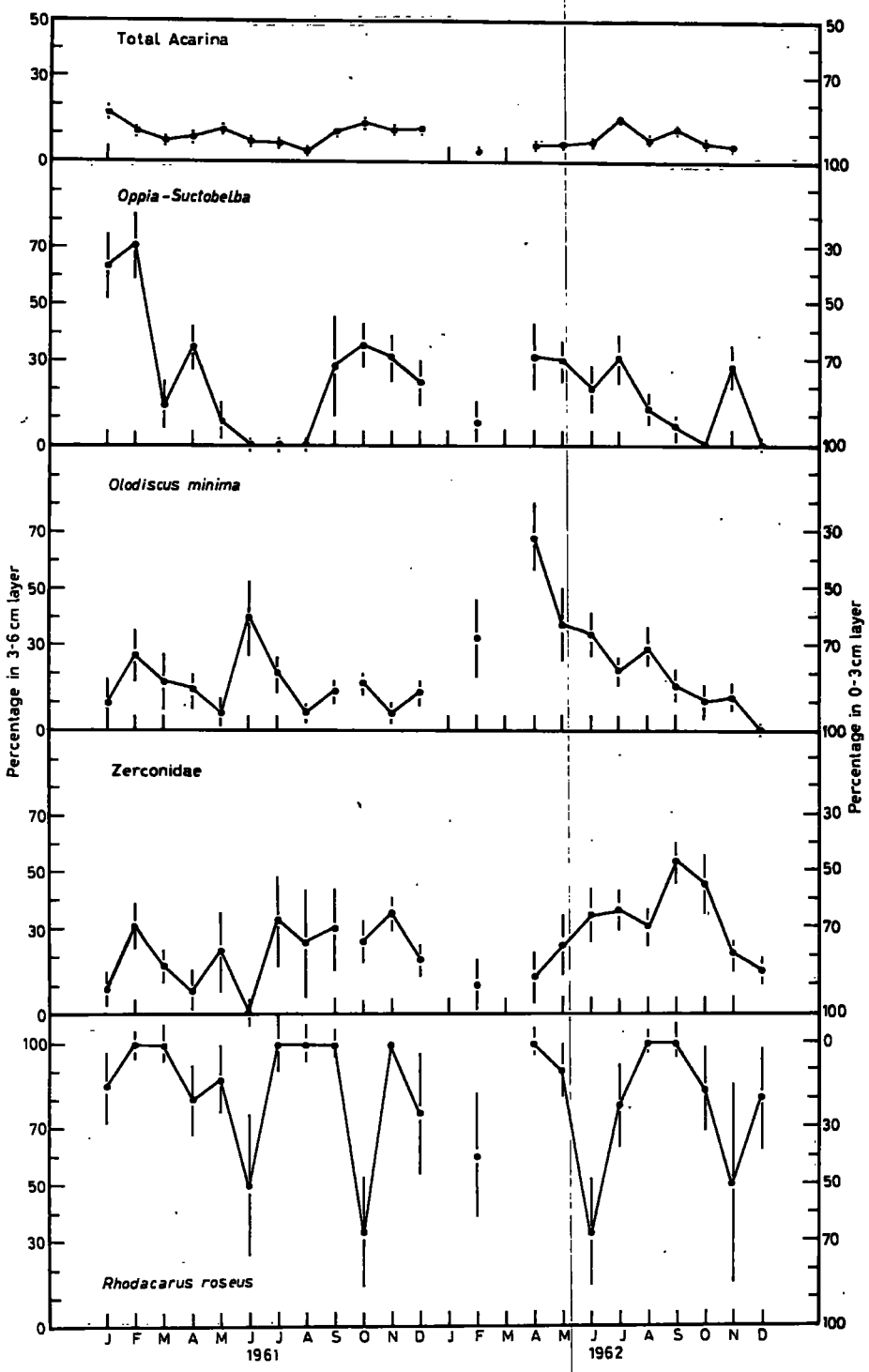
Total Acarina
Oppia-Suctobelba
Olodiscus minima
Zerconidae
Rhodacarus roseus
Percentage in 3-6 cm layer
Percentage in 0-3cm layer
J F M A M J J A S O N D J F M A M J J A S O N D
1961
1962

FIG. 2(a)

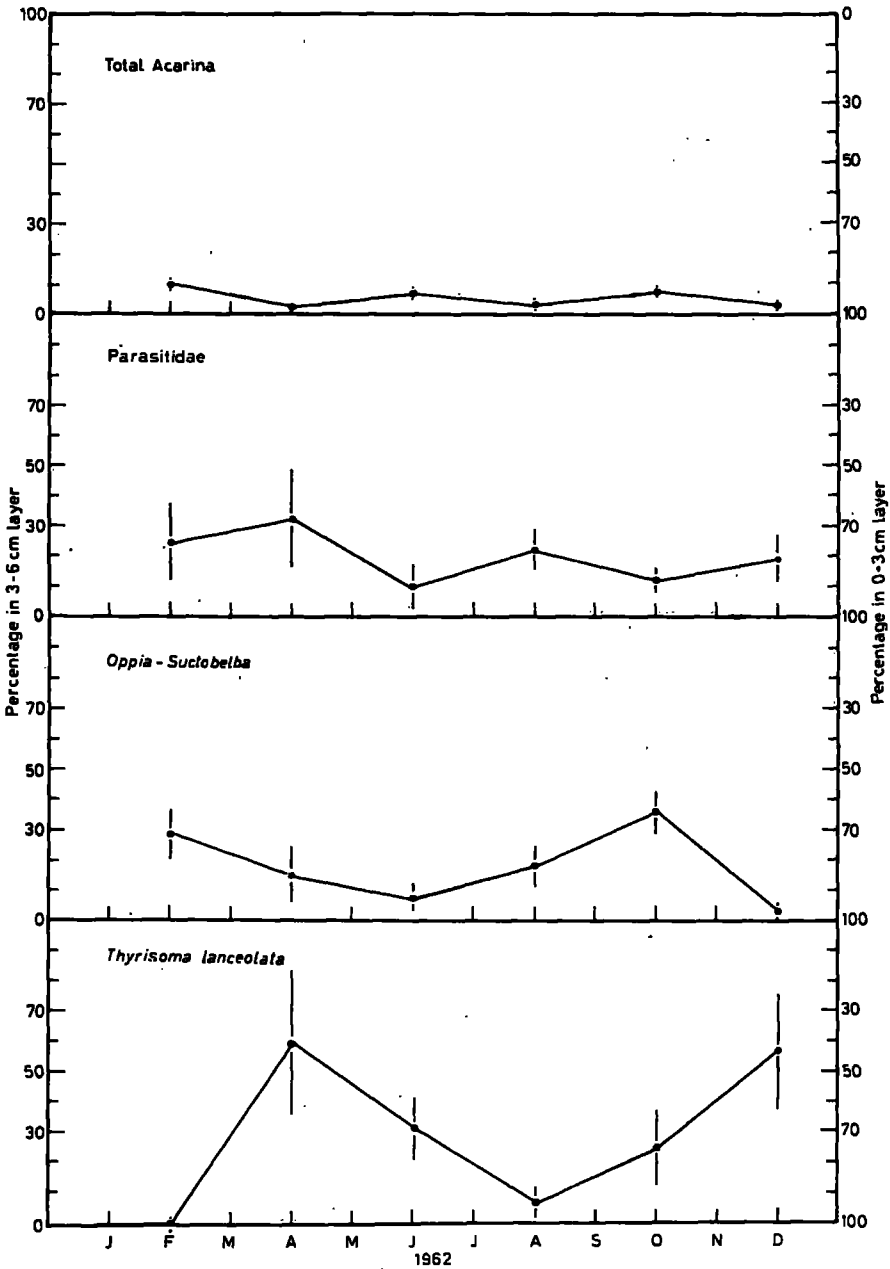

FIG. 2(b)

FIG. 2. Vertical distribution of Acarina in the mineral soil of limestone grassland during 1961 and 1962 (a) and in the peat soil of mixed moor during 1962 (b). The percentage of the total numbers of each species or group occurring in the two layers in each sample is shown. The 3–6 cm soil layer on limestone grassland was not sampled in January and March 1962 due to the soil being frozen. For mixed moor, the 3–6 cm soil layer was sampled bi-monthly, and the time scale is different from that of limestone grassland.

VERTICAL DISTRIBUTION OF SOIL MITES

Most groups of soil micro-arthropods are concentrated in the upper layers of the profile (van der Drift 1950; Macfadyen 1952), with some exceptions, e.g. Symphyla and Protura. Murphy (1953) and Dhillon & Gibson (1962) among others, have shown that there are more mites in the upper layers of the soil than the deeper layers.

In this study, soil samples were taken to a depth of 6 cm on limestone grassland in both years, but only in 1962 was the mixed moor sampled to this depth. The upper 3 cm layer consistently contained more mites than the lower layer (see Fig. 2). Only *Rhodacarus roseus* Oudemans 1902 was more abundant in the lower layer (3–6 cm depth) in limestone grassland. This correlates with Sheals (1957) who found that 49% of the Mesostigmata in upland grassland were Rhodacaridae, which were particularly abundant in the lower soil layers. In limestone grassland 24–32% of the Zerconidae were in the 3–6 cm layer. On mixed moor, during 1962, 27% of *Thyrisoma lanceolata* (Michael 1888) and 22% of *Oppia* and *Suctobelba* spp. were in the lower layer at maximum penetration. On either sample area, few juvenile Oribatei (2–7% of total) penetrated into the 3–6 cm layer.

There was little seasonal variation in the vertical distribution of mites on either site, although 70% of *Oppia* and *Suctobelba* spp. occurred in the lower layer of limestone grassland in February 1961, as compared with between 0 and 30% of its numbers throughout the remainder of the study period. *Rhodacarus roseus* was most abundant in the 3–6 cm zone of limestone grassland in February, March, July, August and September in 1961; and in April, August and September in 1962. This species was found only in the upper zone (0–3 cm) in June and October 1961, and June and November 1962, when about 50% of the population occurred there. This could be due to either a seasonal vertical migration or differential mortality, but it is not possible to differentiate between the two in the present study. In mixed moor soil, all the mites were confined to the upper layer except twice, in April and December 1962, when 50–60% of *Thyrisoma lanceolata* were found in the lower layer. Thus except for *Rhodacarus roseus*, there is no evidence of a seasonal vertical migration on either site.

SEASONAL FLUCTUATIONS IN ABUNDANCE OF SOIL MITES

Many previous workers (e.g. Thompson 1924; Ford 1935, 1937; Strenzke 1951; Evans 1951; Haarløv 1960) have shown that soil mites are usually most abundant in autumn and winter and least abundant in summer. Exceptions have been found in arctic soils (Hammer 1944) and alpine soils (Stockli 1957), where peak populations occurred in summer (July and August), probably due to the severe climate of such areas. However, since all population studies tend to be of limited duration, it is difficult to demonstrate a seasonal pattern for mites.

Figs. 3–7 show the population estimates, with standard errors, for the species or groups of mites with a mean annual population of more than 1000 individuals/m^2. There were eleven such species from limestone grassland and seven from mixed moor. Three-point running means have been plotted to show trends and seasonal changes.

In 1961, the population was greatest in May and December and smallest in August on both limestone grassland and mixed moor. In 1962, it was greatest in May and October on mixed moor, and in July and November on limestone grassland, where it was smallest in March and September. The later population peak on limestone grassland in 1962 may be due to the site being more exposed than mixed moor, and hence development of eggs, larvae and nymphae in spring may have been delayed. The Moor House

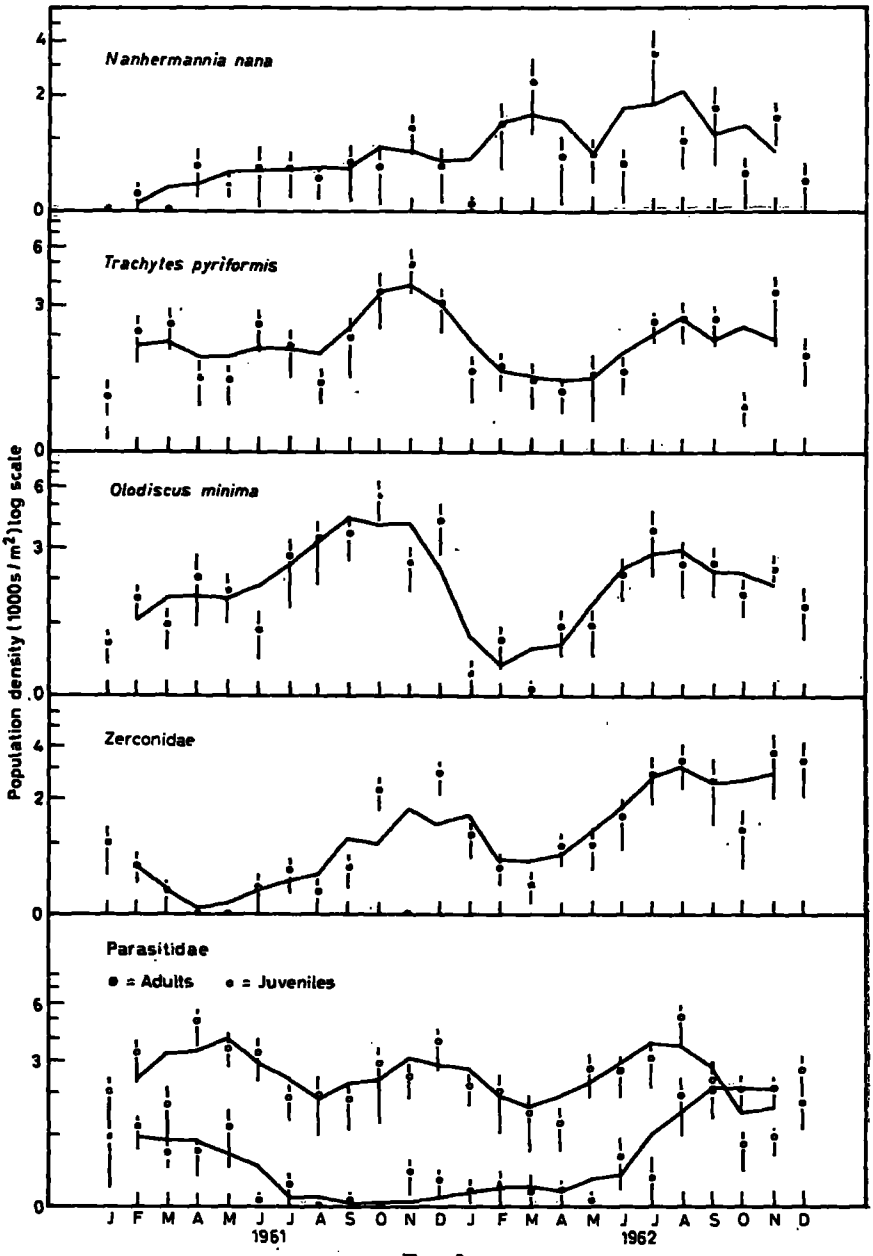

FIG. 3

FIGS. 3–7. Seasonal fluctuations in the abundance of soil Acarina, Figs. 3–5 in mineral soil of the limestone grassland site, Figs. 6 and 7 in peat of mixed moor. The data are of groups and species of soil mites which occur at Moor House. The horizontal axis shows the sampling months, and data for two complete years are given. The populations are plotted on a logarithmic scale on the vertical axis. The population scales are the same for all groups and species, but in some cases they do not begin at zero. The standard errors of the population means are shown also, and three-point running mean values are indicated by trend lines.

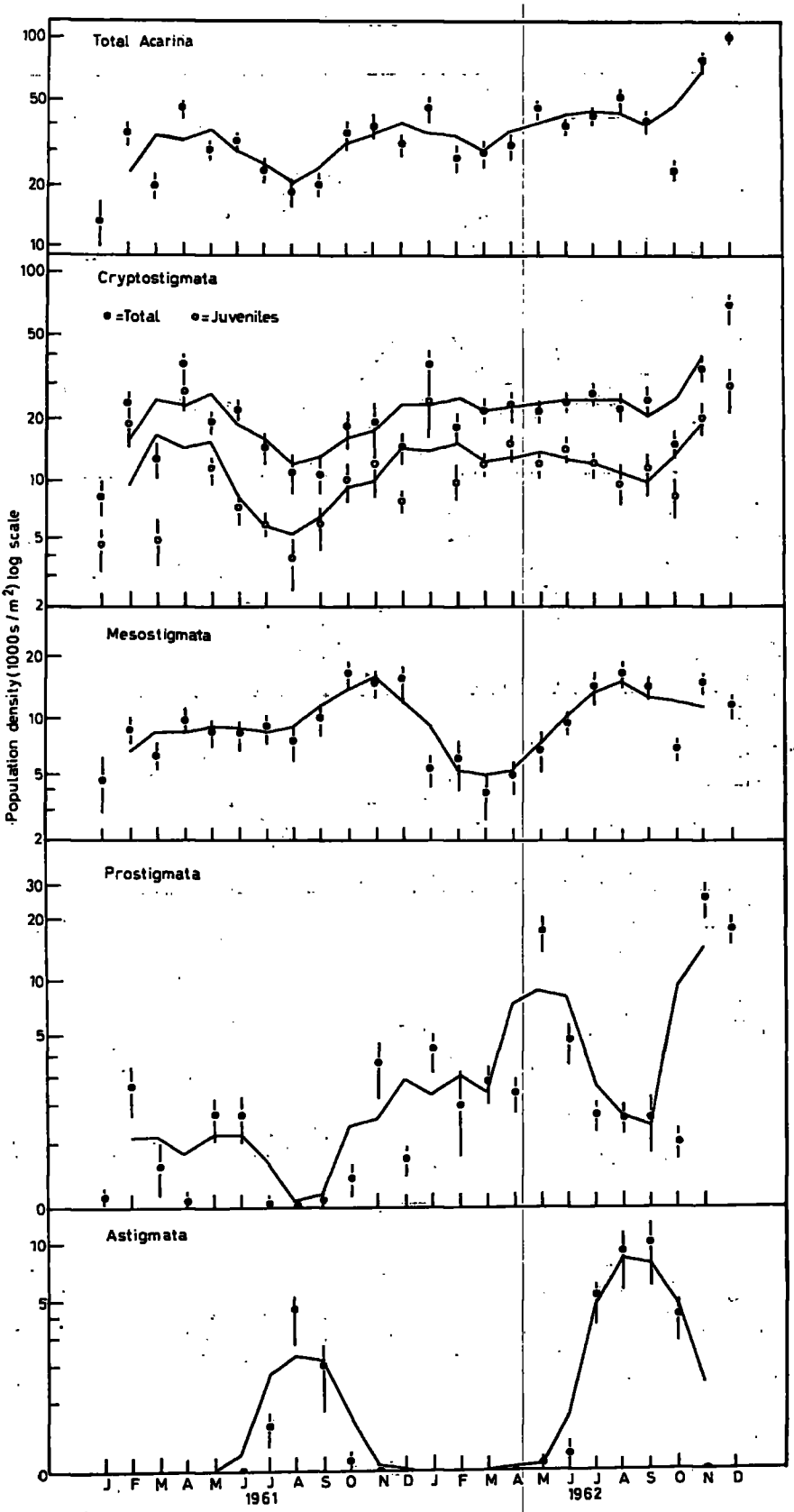

FIG. 4. (See legend beneath Fig. 3.)

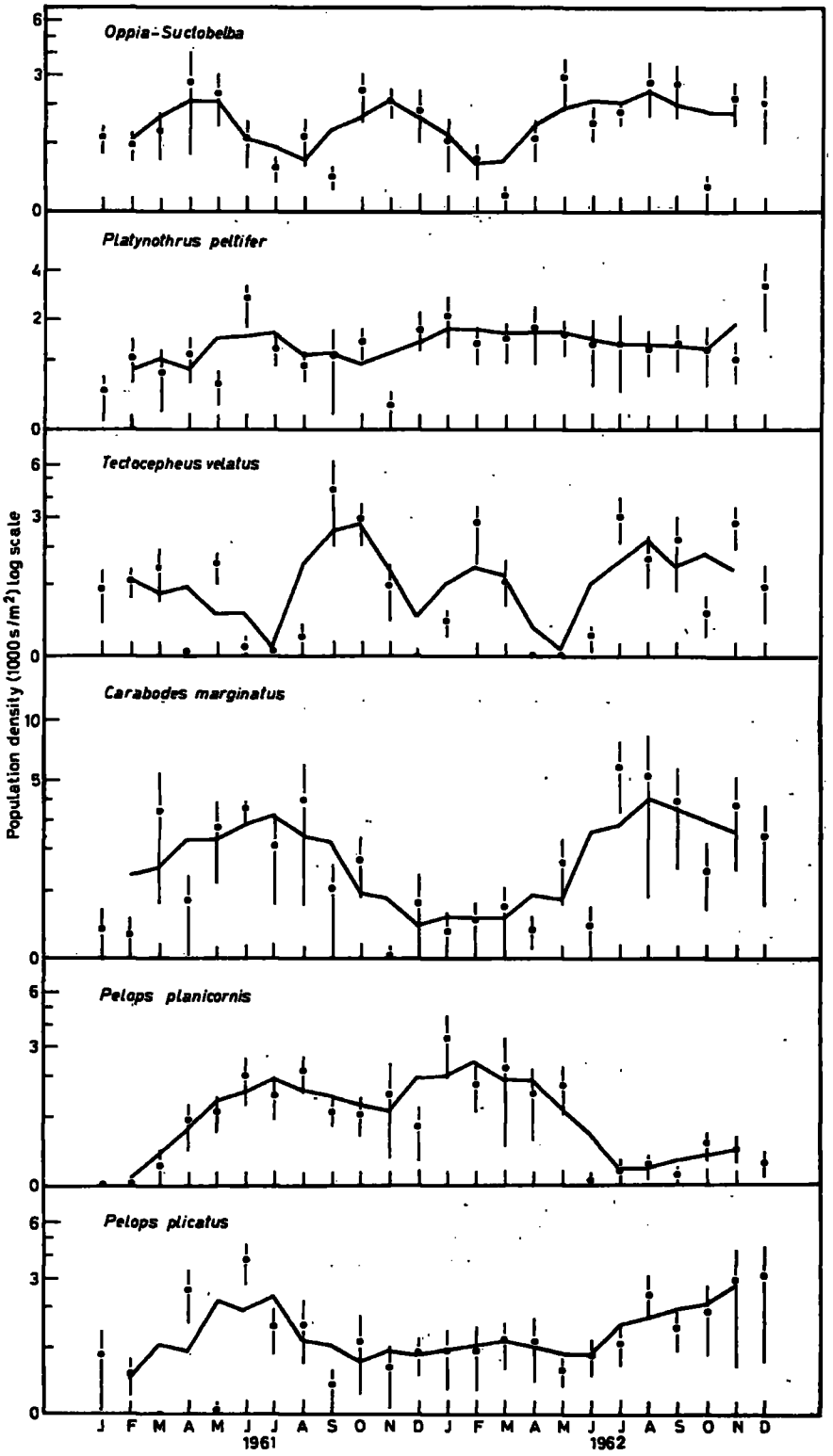

FIG. 5. (See legend beneath Fig. 3.)

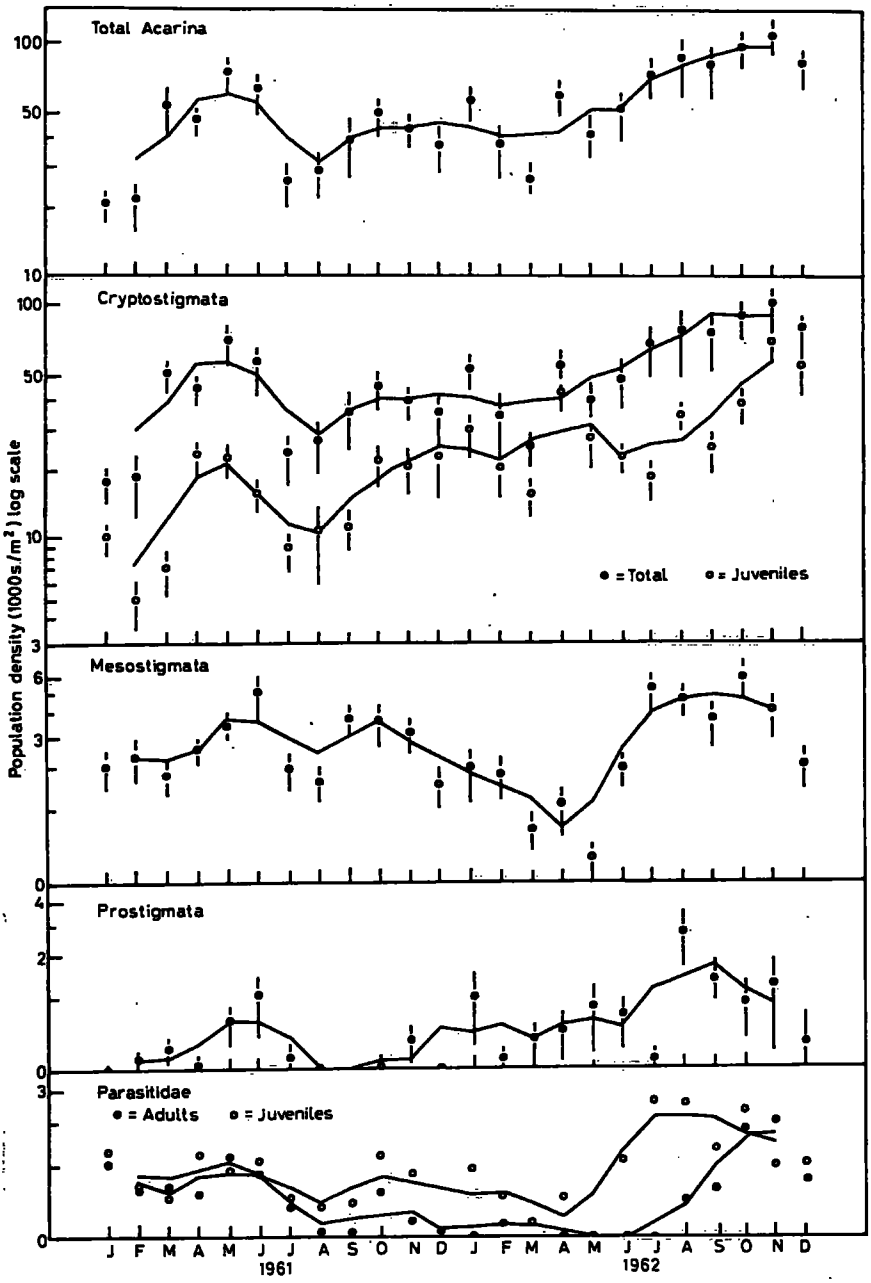

FIG. 6. (See legend beneath Fig. 3.)

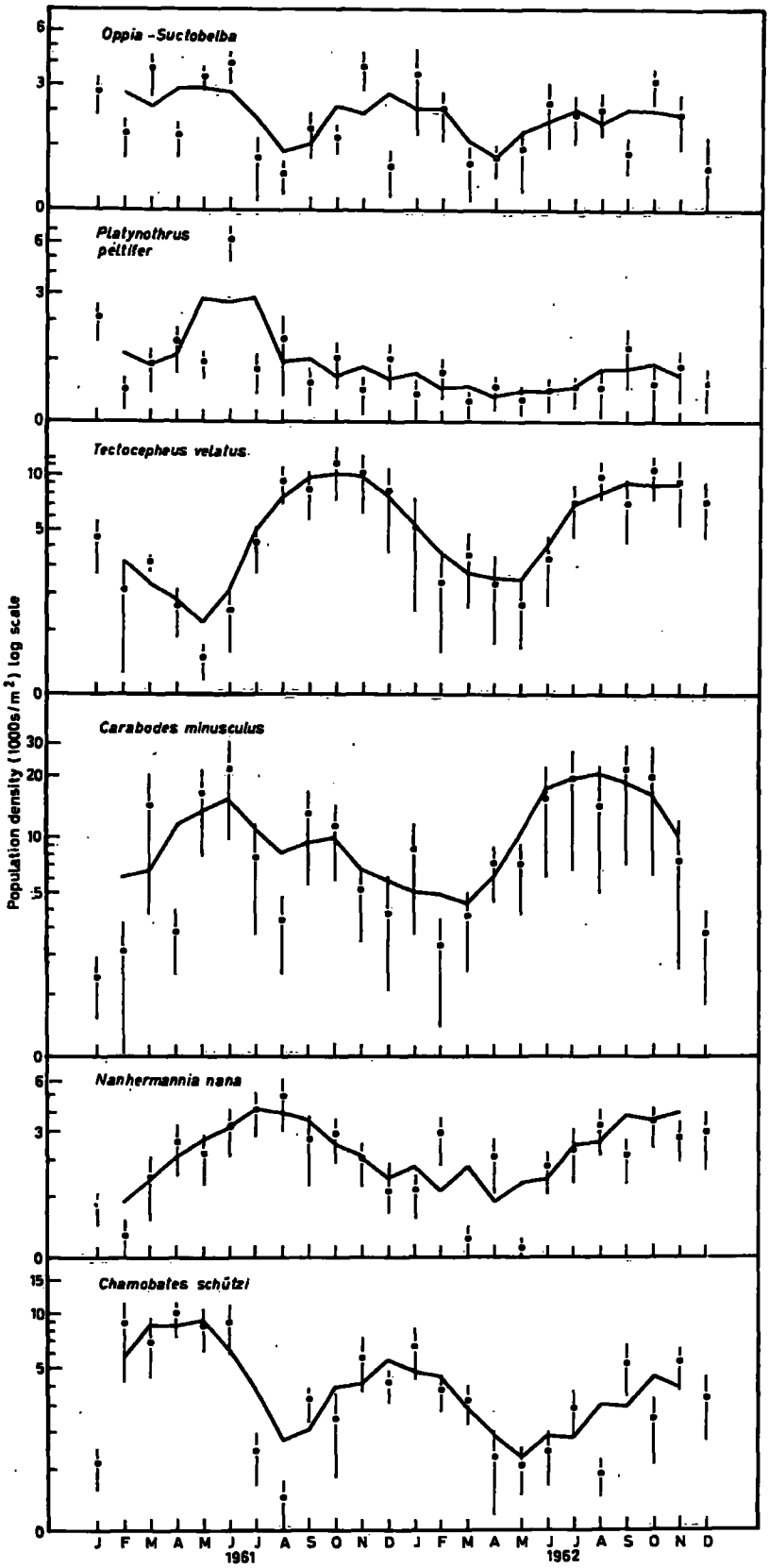

FIG. 7. (See legend beneath Fig. 3.)

results correspond with those for areas with a similar or more rigorous climate, e.g. Frenzel (1936) for mites in Silesia, Hammer (1944) for micro-arthropods of arctic soils, Riha (1951) for mites in Austria, Stockli (1957) for both mites and Collembola in the Alps, and Davis (1963) for mites in Northamptonshire. Spring comes earlier to the northern Pennines than in most of the other areas mentioned and this could account for the spring population peak being earlier at Moor House. The spring peak may have been due to a rapid hatch of eggs in April of both study years, for Figs. 4 and 6 show that immature mites were most abundant then. The air temperature rose rapidly at that time too. Possibly climatic factors affect the reproduction of the mites, so that eggs hatch at well-defined periods of the year, but this is discussed below.

Seasonal trends in the total mite populations follow closely those of the Cryptostigmata, which are the dominant group in the soils studied. Figs. 4 and 6 also show that there is a seasonal trend in the ratio of juvenile to adult Cryptostigmata on both sample sites. The highest ratios were in spring, autumn and early winter, when newly hatched juvenile forms were abundant. These high ratios could be the result of a decrease in the abundance of adults, but this is unlikely to be the sole factor. Sheals (1957) suggested that seasonal fluctuations in Oribatei populations of uncultivated grassland soil were caused partly by mites moving to other habitats for reproduction. Riha (1951), studying calcareous woodland soils near Vienna, showed that juvenile forms of several oribatid species lived in habitats other than soil, e.g. under the bark of trees and in leaf litter, but sticky traps and pitfull traps in the *Calluna* of mixed moor at Moor House gave no evidence of this. Juvenile Oribatei were present in large numbers in each monthly sample (Figs. 4 and 6). Although the total number of species on each site was the same for the 2-year study period (Block 1965a), there were considerable seasonal variations in the numbers of the common species (see Figs. 3–7), which correlates with the findings of Strenzke (1951) and Macfadyen (1952). As adult and juvenile Oribatei were found in all months, it suggests that a continuous recruitment takes place to the adult population from the juvenile forms. The peaks in abundance of juveniles could be caused by eggs hatching in response to climatic factors, such as temperature or rainfall.

Figs. 3, 5 and 7 show that, in 1961, the majority of the common species were most abundant in May and June and least so in August but, in 1962, they were most abundant in August and least abundant in March. There is a considerable seasonal variation in abundance of each species and there are differences between species; e.g. for *Pelops planicornis* (Schrank 1803) the trend line is almost the mirror image of those for *Carabodes marginatus* (Michael 1884), *Olodiscus minima* (Kramer 1882) and the Zerconidae. This may be related to food supply for these species, or some other environmental factor, but so little is known of the ecology and feeding habits of these mites that no explanation can be given at present. Two patterns, however, can be seen in these results; they are: (1) species that may have two generations per year at Moor House, e.g. *Carabodes minusculus* Berlese 1923, and *Oppia* and *Suctobelba* species; and (2) species that may have one generation per year at Moor House, e.g. *Platynothrus peltifer* (C. L. Koch 1839), *Tectocepheus velatus* (Michael 1880), *Carabodes marginatus*, *Nanhermannia nana* Willmann 1931, *Pelops plicatus* (C. L. Koch 1836), *P. planicornis*, *Chamobates schützi* (Oudemans 1902) and *Olodiscus minima*.

The three-point running means suggest that there is a seasonal pattern in the abundance of soil mites on the two areas studied which may be typical of moorlands. Meteorological data from the Annual Reports for the Reserve show that 1961 was a more typical year in respect of weather, whereas 1962 was exceptional. The late spring in 1962 probably

delayed the population peak in the soil mites until July, with the summer population minimum occurring in September on limestone grassland. On both sites, the autumn population peak was in October–November in 1962. Life history studies of *Platynothrus peltifer* and *Damaeus clavipes* (Hermann 1804) in Pennine moorland (Block 1965b) support the suggestion that the seasonal pattern of abundance is due mainly to breeding being limited to spring and autumn periods, usually with only a single generation each year.

BIOMASS OF SOIL MITES

An estimate of the biomass of mites in moorland soils was made by weighing representative samples of the common species and of all juveniles. The mean weights were then

Table 1. *Mean weights (± standard deviations) of adult specimens of Acarina (except where otherwise stated)*

Species or group	Mean weight (μg)		Percentage water content
	Live	Dry	
Nanhermannia nana Willmann 1931	17·2±1·4	7·4±0·5	57·0
Platynothrus peltifer (C. L. Koch 1839)	56·0±4·8	25·6±1·8	53·6
Oppia and *Suctobelba* spp.	2·0	1·0	50·0
Tectocepheus velatus (Michael 1880)	4·8	1·7	64·6
Phthiracarus ligneus Willmann 1931	76·5±4·6	22·5±1·8	70·6
Ceratoppia bipilis (Hermann 1804)	63·8±2·8	20·5±1·5	67·9
Chamobates schützi (Oudemans 1902)	8·3±0·4	2·5±0·6	69·9
Carabodes minusculus Berlese 1923	28·4	10·4	63·4
Immature Cryptostigmata	3·3±0·9	*	*
Olodiscus minima (Kramer 1882)	15·6	5·2	66·7
Parasitidae	258·4±39·9	103·2±25·7	60·0
Macrochelidae	408·4±96·6	150·9±45·5	63·1
Veigaiaidae	139·6±24·7	65·7±18·2	52·9

* Indicates no figure available.

Table 2. *Estimated average annual biomass of mites for the Moor House sample sites, compared with the mean annual population density (the weights are g/m², and the standard error of the mean population is given)*

Site and year	Live-weight biomass			Population density (×10³/m²)	Live-weight biomass of 1000 individuals (g)
	Crypto stigmata	Meso-stigmata	Total Acarina		
Limestone grassland (1961)	0·25	0·64	0·89	28·74±1·09	0·0307
Limestone grassland (1962)	0·36	0·72	1·08	45·29±1·41	0·0240
Mixed *Calluna* moor (1961)	0·69	0·42	1·11	41·86±2·16	0·0264
Mixed *Calluna* moor (1962)	0·72	0·40	1·12	65·79±3·19	0·0169
Juncus squarrosus moor (1961)	0·39	0·52	0·91	43·01±3·09	0·0210
Nardus stricta grassland (1962)	0·86	0·99	1·85	77·83±4·24	0·0237
EROSION AREA (1961)					
Hagg lip	0·17	0·15	0·31	21·22±3·11	0·0148
Hummock top	0·93	0·28	1·21	97·52±7·17	0·0125
Eriophorum angustifolium	0·44	0·10	0·54	26·01±3·14	0·0208
E. vaginatum	0·59	0·31	0·90	34·02±3·70	0·0265

multiplied by the mean number of each species for each sampling occasion, to give the biomass. Both live and dry weights were obtained and are given in Table 1. There is

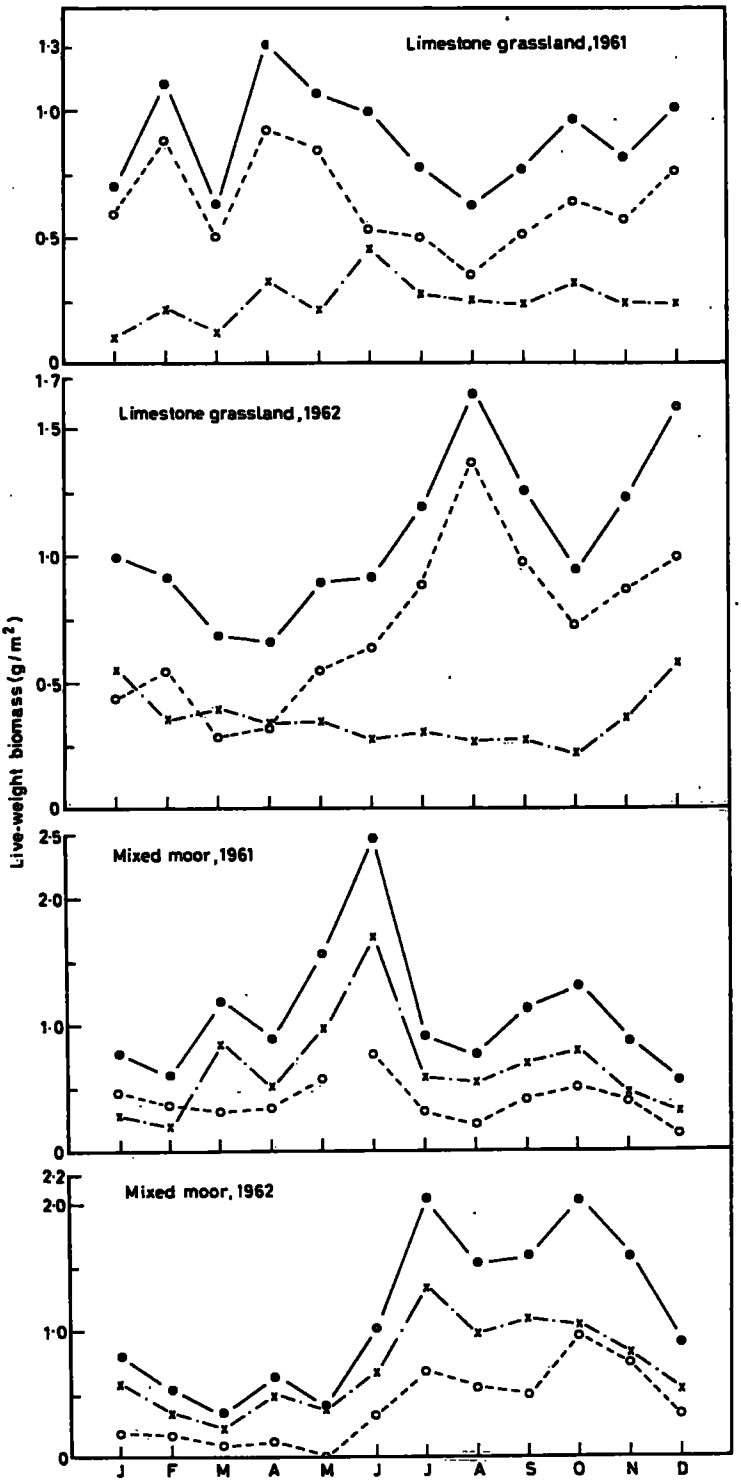

FIG. 8. Seasonal fluctuations in the estimated biomass of mites on limestone grassland and mixed moor areas at Moor House. The data are of two complete years, 1961 and 1962. ×, Cryptostigmata; ○, Mesostigmata; ●, total Acarina.

good agreement between the weights of Oribatei obtained in this study and those given by Berthet (1963). The biomass is expressed in g/m^2, and it is given in Table 2 for several sites at Moor House, ranging from mineral soil to peat moor.

In general, the biomass was greatest where mites were most numerous. It was greatest in *Nardus stricta* grassland (1·85 g/m^2), and least in the hagg lip zone of eroding blanket bog (0·31 g/m^2). The final column in Table 2 shows that, on average, the individual mites tend to be larger on limestone grassland. This is due to a higher proportion of large species rather than individuals of the same species differing in size. There was little change in total biomass between years on mixed moor (see Table 2), although the population increased; but there was an estimated increase of 0·29 g/m^2 in biomass on limestone grassland from 1961 to 1962. This increase in biomass can be attributed to the large population increase that was observed. Fig. 8 shows the seasonal variations in mite biomass for the two sites. In 1961, it was greatest in April on limestone grassland (1·3 g/m^2) and in June on mixed moor (2·5 g/m^2). In 1962, it was greatest in August on limestone grassland (1·6 g/m^2) and in July and October on mixed moor (2·0 g/m^2). These results reflect population changes and on both sites the biomass was greatest when young forms were maturing, and when Mesostigmata were abundant.

On limestone grassland Mesostigmata accounted for 69% of the biomass, and peaks in biomass were due mainly to increases in the numbers of Parasitidae (see Figs. 3 and 6). Cryptostigmata, whose biomass fluctuated little throughout the two years of study, accounted for 31% of the total biomass on limestone grassland. On mixed moor, however, Cryptostigmata accounted for 63% of the total biomass, and Mesostigmata for 37%, with the Oribatei causing the major seasonal fluctuations in biomass.

DISCUSSION

The estimates of biomass for the moorland sites in this work (0·3–1·8 g/m^2 for populations of 21–77 thousand mites/m^2) show great similarity with those for the Oribatei of a *Molinia* fen (Macfadyen 1952). These were of the order of 0·2–1·4 g/m^2 for similar populations. The maximum estimated biomass for mites at Moor House (1·8 g/m^2 on *Nardus stricta* grassland) compares well with 1·9 g/m^2 for mites of beech litter in the Netherlands (van der Drift 1950).

The importance of soil moisture for Acarina has been demonstrated by Ford (1938), and Weis-Fogh (1948). The fauna is said to owe its summer population minimum to drought and the winter population minimum, when it occurs, to low temperature and excessive moisture. The autumn or winter peaks of abundance are attributed to ideal moisture conditions. At Moor House, the population minimum for mites did not occur at the time of driest soil conditions in June, but in August and September, when the water content of soil samples was similar to those of the rest of the year. This supports the suggestion that soil moisture alone does not affect the abundance of mites on eroding moor (Block 1966a). Both Riha (1951) and Sheals (1957) have suggested that certain species of mites migrate from soil and litter onto herbage at certain times of the year giving an erroneous impression from soil samples that the population was at a minimum at this time, but evidence of this type of movement was not found at Moor House, although the vegetation was sampled on several occasions. Thus, the August–September population minima which occurred on mixed moor (with rank cover of *Calluna vulgaris*) and on limestone grassland (with closely cropped grass, which gave the mites little chance of vertical movement) were probably real.

It is likely that the seasonal abundance of mites is influenced by temperature restricting their breeding season. It limits the developmental period of eggs and therefore the recruitment to the populations studied. The hatching of eggs which have overwintered is an important factor in producing the population peak in May, and this is confirmed by the high ratio of juveniles : adults found in the Oribatei at this time. The second peak of hatching (and of overall abundance) in the autumn could be the result of mites which have matured in the spring laying eggs which hatch in the autumn. Thus there are two main periods of eggs hatching, in the late spring and autumn. There are, therefore, two types of life cycle in soil mites of moorlands, namely those which lay eggs in the autumn and which hatch in the spring, and those which lay eggs in the spring and which hatch in the autumn. These probably represent different species, although at lower altitudes, where more species may have two generations a year, they would represent a bivoltine annual cycle. From the life histories of the species studied (Block 1965b), this is an oversimplification, but it has been shown that *Platynothrus peltifer* contributes largely to a spring hatch while the eggs of *Damaeus clavipes* hatch mainly in the autumn.

Under more extreme climatic conditions than at Moor House, such as in the arctic, the season of activity for soil mites is so reduced that there is a single period of egg laying only. Under these conditions, hatching must occur in the summer and also this is the main, if not the only time of the year when recruitment can occur. Consequently, only a single peak of abundance can occur as has been demonstrated by Hammer (1944) for mites of Greenland, and by Stockli (1957) for alpine populations.

ACKNOWLEDGMENTS

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SUMMARY

Ecological studies on the Acarina of peat and mineral soils of the Moor House National Nature Reserve, Westmorland are reported. The mites were aggregated in all the twenty-four monthly samples. Most mites occurred in the top 3 cm layer of the soil cores compared with the 3–6 cm layer, except for *Rhodacarus roseus* in samples from limestone grassland. Mite populations ranged from 10 to 100 thousands/m^2 in both soils. Mites were most abundant in May and December and least abundant in August on both sites in 1961; but in 1962, peak and minimal populations occurred at different times and this is interpreted as the result of unusual weather. The peak populations are related to the breeding cycle of the mites which is limited by climate, and individual species may have one or two generations per year at Moor House. Estimates of the biomass of mites in moorland soils range from 0·31 to 1·85 g/m^2.

REFERENCES

Berthet P. (1963). Mesure de la consommation d'oxygène des Oribatides (Acariens) de la litière des forêts. *Soil Organisms* (Ed. by J. Doeksen and J. van der Drift), pp. 18–31. Amsterdam.

Block, W. (1965a). Distribution of soil mites (Acarina) on the Moor House National Nature Reserve, Westmorland, with notes on their numerical abundance. *Pedobiologia*, **5**, 244–51.

Block, W. (1965b). The life histories of *Platynothrus peltifer* (Koch 1839) and *Damaeus clavipes* (Hermann 1804) (Acarina: Cryptostigmata) in soils of Pennine moorland. *Acarologia*, **7**, 735–43.
Block, W. (1966a). The distribution of soil Acarina on eroding blanket bog. *Pedobiologia*, **6**, 27–34.
Block, W. (1966b). Some characteristics of the Macfadyen high gradient extractor for soil micro-arthropods. *Oikos*, **16** (In press).
Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1952). *Flora of the British Isles*. Cambridge.
Conway, V. M. (1955). The Moor House National Nature Reserve, Westmorland. *Handbk a. Rep. Soc. Promot. Nat. Reserves*, **111**, 1–7.
Cragg, J. B. (1961). Some aspects of the ecology of moorland animals. *J. Anim. Ecol.* **30**, 205–34.
Davis, B. N. K. (1963). A study of micro-arthropod communities in mineral soils near Corby, Northants. *J. Anim. Ecol.* **32**, 49–71.
Dhillon, B. S. & Gibson, N. H. E. (1962). A study of the Acarina and Collembola of agricultural soils. *Pedobiologia*, **1**, 189–209.
Drift, J. van der (1950). Analysis of the animal community in a beech forest floor. *Tijdschr. Ent.* **94**, 1–168.
Evans, G. O. (1951). *Investigations on the fauna of forest humus layers*. Forestry Commission Report on Forest Research for the year ending March, 1950, pp. 110–13. London.
Ford, J. (1935). The animal population of a meadow near Oxford. *J. Anim. Ecol.* **4**, 195–207.
Ford, J. (1937). Fluctuations in natural populations of Collembola and Acarina. I. *J. Anim. Ecol.* **6**, 98–111.
Ford, J. (1938). Fluctuations in natural populations of Collembola and Acarina. II. *J. Anim. Ecol.* **7**, 350–369.
Frenzel, G. (1936). Untersuchungen uber die Tierwelt des Wiesenbodens. Jena. (Original not consulted, reviewed by Ford, J. 1937, *loc. cit.*)
Haarløv, N. (1960). Micro-arthropods from Danish soils. Ecology, Phenology. *Oikos*, suppl. **3**, 1–176.
Hammer, M. (1944). Studies on the Oribatids and Collemboles of Greenland. *Meddr Grønland.* **141**, 1–210.
Hartenstein, R. (1961). On the distribution of forest soil micro-arthropods and their fit to 'Contagious' distribution functions. *Ecology*, **42**, 190–4.
Hull, J. E. (1914). Oribatidae (Beetle Mites) of the County of Durham, with special reference to the Derwent Valley. *Trans. Vale Derwent Nat. Fld Club*, **1**, 59–65.
Hull, J. E. (1916). Terrestrial Acari of the Tyne province. *Trans. nat. Hist. Soc. Northumb.* **4**, 381–409.
Hull, J. E. (1918). Terrestrial Acari of the Tyne province. *Trans. nat. Hist. Soc. Northumb.* **5**, 13–88.
Johnson, G. A. L. & Dunham, K. C. (1963). The geology of Moor House. *Monograph of the Nature Conservancy*, No. 2. London.
Macfadyen, A. (1952). The small arthropods of a *Molinia* fen at Cothill. *J. Anim. Ecol.* **21**, 87–117.
Macfadyen, A. (1961). Improved funnel-type extractors for soil arthropods. *J. Anim. Ecol.* **30**, 171–84.
Manley, G. (1952). *Climate and the British Scene*. London.
Murphy, P. W. (1953). The biology of forest soils with special reference to the mesofauna or meiofauna. *J. Soil Sci.* **4**, 155–93.
Nef, L. (1962). The distribution of Acarina in the soil. *Progress in Soil Zoology* (Ed. by P. W. Murphy), pp. 56–58. London.
Nicholson, E. M. (1957). *Britain's Nature Reserves*. London.
Pearsall, W. H. (1950). *Mountains and Moorlands*. London.
Riha, G. (1951). Zur Ökologie der Oribatiden in Kalksteinböden. *Zool. Jb.* (*Abt. Syst.*), **80**, 407–50.
Seyd, E. L. (1962). The moss mites of Kinder Scout, Derbyshire (Acari: Oribatei). *J. Linn. Soc.* (*Zool.*), **44**, 585–91.
Sheals, J. G. (1957). The Collembola and Acarina of uncultivated soil. *J. Anim. Ecol.* **26**, 125–34.
Stockli, A. (1957). Die Metazoenfauna von Wiesen- und Ackerboden aus der Umgebung von Zurich. *Landw. Jb. Schweiz*, **6**, 571–95.
Strenzke, K. (1951). Die Biozönotik der Oribatiden norddeutscher Böden. *Naturwissenschaften*, **38**, 284–5.
Thompson, M. (1924). The soil population. An investigation of the biology of soil in Aberystwyth. *Ann. appl. Biol.* **11**, 349–94.
Watson, E. V. (1955). *British Mosses and Liverworts*. Cambridge.
Watson, W. (1953). *Census Catalogue of British Lichens*. Cambridge.
Weis-Fogh, T. (1948). Ecological investigations on mites and collemboles in the soil. Appendix: Description of some new mites (Acari). *Natura jutl.* **1**, 139–277.

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RECOVERY OF MITES FROM PEAT AND MINERAL SOILS USING A NEW FLOTATION METHOD

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RECOVERY OF MITES FROM PEAT AND MINERAL SOILS USING A NEW FLOTATION METHOD

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Flotation methods have been described for extracting both micro-arthropods from mineral soils (Ladell 1936; Salt & Hollick 1944; Raw 1955), and Collembola from peat soils (Hale 1964). With peat, the plant material is made to sink in water by boiling under reduced pressure, and the arthropods are brought to the surface by stirring and aeration. In the present study, a test was made of the recovery of various arthropods in water in the Hale extraction apparatus, and then a comparison was made between the numbers of mites extracted by the Hale apparatus and those from a high gradient heat extractor (Macfadyen 1961) from samples of both peat and mineral soils.

Table 1. *Recovery of arthropods from water after pressure reduction and aeration for 5 h in the Hale flotation extractor*

Group	No. introduced	No. recovered	Percentage recovery
Cryptostigmata	100	98	98
Mesostigmata	36	32	89
Total Acarina	136	130	96
Collembola	60	49	82
Araneida	4	2	50
Pseudoscorpionida	5	4	80
Diptera—adults	3	2	67
Diptera—larvae	8	7	87
Coleoptera—adults	9	6	67
Coleoptera—larvae	21	15	71
Total Arthropoda	246	215	87

EXTRACTION TEST

The flotation extractor and procedure used in these experiments, which were exactly as described by Hale (1964), were tested initially by placing a known quantity of arthropods in water in one unit of the apparatus. The water was made to boil by pressure reduction, and the material was then aerated for 5 h, with additional water being added hourly to float the arthropods into a side arm where they were trapped in 360 meshes per inch phosphor–bronze gauze (aperture 0·042 mm). The results given in Table 1 show that the method gave a 96% recovery of Acarina compared with only 74% found by Hale (1964); Hale's result was probably affected by the operator's unfamiliarity with the group, and the relatively low recovery of Collembola in the present experiment (82%) can probably be attributed to the same cause.

COMPARISON OF HIGH GRADIENT AND FLOTATION EXTRACTORS

A comparison was made of the Hale flotation extractor and the high gradient heat extractor (Macfadyen 1961) for recovery of mites from both peat and mineral soils. The

comparison was made concurrently on a peat sample collected from an area of mixed moor and a sample of mineral soil from a *Festuca–Agrostis* upland grassland, both sites being on the Moor House National Nature Reserve, Westmorland. Fifteen sample units, each 11·35 cm^2 in surface area and 3 cm deep, were used for each extraction method from each site. The samples were collected on 12 November 1962, and both extraction processes began the following day. The mean numbers of Acarina delivered by the two methods for the two soils are shown in Table 2.

Table 2. *Mean and standard error of numbers of various Acarina delivered by high gradient and flotation extractors from fifteen sample units each of peat from mixed moor and of mineral soil from* Festuca–Agrostis *grassland, 12 November 1962 (each sample unit was 11·35 cm^2 in surface area and 3 cm deep)*

Group or species	Peat		Mineral soil	
	Macfadyen high gradient extractor	Hale flotation extractor	Macfadyen high gradient extractor	Hale flotation extractor
Total Acarina	106·60 ± 17·93	53·40 ± 11·00	72·13 ± 9·01	22·27 ± 4·63
Mesostigmata	4·07 ± 0·69	6·47 ± 1·96	14·46 ± 3·06	6·67 ± 1·14
Cryptostigmata	101·27 ± 32·45	46·93 ± 11·03	32·67 ± 5·27	11·13 ± 3·52
Prostigmata	1·27 ± 0·52	0·0	25·00 ± 7·25	4·47 ± 2·27
Carabodes marginatus (Michael)	3·67 ± 0·09	0·73 ± 0·28	0·53 ± 0·29	0·0
C. minusculus Berlese	7·33 ± 1·50	4·20 ± 0·97	0·0	0·0
Platynothrus peltifer (C. L. Koch)	0·80 ± 0·40	0·80 ± 0·47	1·07 ± 0·45	0·47 ± 0·35
Nanhermannia nana Willmann	2·67 ± 0·85	2·53 ± 0·90	1·47 ± 0·73	0·53 ± 0·29
Tectocepheus velatus (Michael)	9·20 ± 2·25	3·20 ± 1·29	2·80 ± 0·85	1·40 ± 0·62
Chamobates schützi (Oudemans)	5·33 ± 1·44	1·60 ± 0·65	0·0	0·0
Melanozetes mollicomus (C. L. Koch)	1·67 ± 0·75	0·0	0·0	0·0
Phthiracarus ligneus Willmann	0·67 ± 0·29	0·67 ± 0·60	0·0	0·0
Achipteria coleoptrata (Linnaeus)	0·0	0·0	1·47 ± 0·43	0·53 ± 0·21
Pelops plicatus (C. L. Koch)	0·0	0·0	2·93 ± 0·60	1·47 ± 0·57
Species of *Oppia* Koch and *Suctobelba* Paoli	1·80 ± 0·62	0·0	2·20 ± 0·52	1·13 ± 0·51
Juvenile Oribatei	68·13 ± 19·85	33·20 ± 11·67	20·20 ± 4·77	5·60 ± 2·70
Trachytes pyriformis (Kramer)	0·0	0·0	3·60 ± 1·81	2·00 ± 0·75
Olodiscus minima (Kramer)	0·0	0·0	2·40 ± 1·01	1·20 ± 0·54
Rhodacarus roseus Oudemans	0·0	0·0	1·60 ± 0·94	0·67 ± 0·30
Zerconidae	0·0	0·0	3·73 ± 1·54	0·0
Parasitidae	3·40 ± 0·69	4·80 ± 1·73	3·13 ± 1·35	2·80 ± 0·77

The high gradient apparatus extracted from samples of peat a mean number of mites twice as large as that delivered by the Hale flotation extractor. For mineral soil, approximately 3¼ times the mean number of mites were delivered by the heat extractor compared with the flotation method. More Mesostigmata were recovered from peat by the flotation extractor than by the heat extractor. Greater numbers of all the other sub-orders of mites were delivered by the high gradient apparatus than by the Hale method for both soils. For mite species, all were extracted in larger numbers from both soil types by Macfadyen's extractor than by Hale's flotation method, except for *Platynothrus peltifer* (C. L. Koch) and *Phthiracarus ligneus* Willman from samples of peat, which were extracted in the same numbers by both methods. Parasitid mites were recovered in greater numbers from peat by the flotation method.

In order to determine whether these differences were significant, the data of the fifteen replicates were pooled and subjected to an analysis of variance. First a square-root

transformation of the data was carried out; then the pooled data for mite sub-orders were analysed; and finally the pooled data for five species which were common to both soils were analysed. The results of these analyses are given in Table 3. For sub-orders of mites the extraction methods were just significantly different ($P<0{\cdot}10$), the total numbers of mites for each sub-order were significantly different ($P<0{\cdot}05$), and the soils had different

Table 3. *Results of analyses of variance of the transformed data of pooled counts of sub-orders of mites (A), and mite species common to both soils (B), which were delivered by Macfadyen high gradient and Hale flotation extractors from peat and mineral soils*

Source of variation	Degrees of freedom	Mean square	*F*	Significance
(A) Soil types	1	0·0028	<1	NS
Mite sub-orders	2	342·0010	40·85	*
Extraction methods	1	132·5664	15·83	+
Soil types × mite sub-orders	2	189·3658	22·62	*
Soil types × extraction methods	1	8·9484	1·07	NS
Mite sub-orders × extraction methods	2	23·4154	2·80	NS
Soil types × mite sub-orders × extraction methods	2	8·3722		
(B) Soil types	1	12·9563	8·93	*
Mite species	4	11·8112	8·14	*
Extraction methods	1	28·4149	19·58	*
Soil types × mite species	4	7·2000	4·96	+
Soil types × extraction methods	1	1·1095	<1	NS
Mite species × extraction methods	4	1·9911	1·37	NS
Soil types × mite species × extraction methods	4	1·4510		

+, Significant at 10% level of probability.
*, Significant at 5% level of probability.
NS, not significant.

Table 4. *Results of analysis of variance of the numbers of mites delivered by Macfadyen high gradient and Hale flotation extractors from peat and mineral soils*

Source of variation	Degrees of freedom	Mean square	*F*	Significance
Extraction methods	1	58·8195	15·59	***
Soil types	1	92·6856	24·58	***
Mite species/groups within soils	18	55·0939	14·61	***
Extraction methods × soils	1	0·4693	<1	NS
Extraction methods × mite species/groups within soils	18	3·7712		

The data were of fifteen replicates from each soil type, and a square-root transformation was used.
***, Significant at 0·1% level of probability.
NS, not significant.

aunal compositions ($P<0{\cdot}05$). For the five species common to both soil types, the two oils had significantly different numbers of the species considered ($P<0{\cdot}05$), the total umbers of the five species were significantly different ($P<0{\cdot}05$), the extraction methods vere significantly different ($P<0{\cdot}05$), and the soils had a different faunal composition $P<0{\cdot}10$).

A further analysis of variance was then made to include the fifteen replicates for each

extraction method per soil type. A square-root transformation was again used, and the results are given in Table 4. Twenty species or groups were considered in this analysis (sixteen species and four groups). The difference between the extraction methods was highly significant ($P<0{\cdot}001$), and the numbers of the mite species or groups considered within soils were highly significantly different at $P<0{\cdot}001$. For extraction methods, t-tests on the square root of the totals within replicates of all groups and species show that for the peat soil, $t_{28} = 3{\cdot}063$, which is significant at $P<0{\cdot}01$, and for the mineral soil, $t_{28} = 4{\cdot}935$, significant at $P<0{\cdot}001$. Therefore the differences between the total numbers of mites delivered by the two extractors from the two soils tested (Table 2), were, in the main, real.

DISCUSSION

Murphy (1962a, b) has reviewed different types of extractors for recovery of animals from soil, but few comparative tests of the two main types of extractors for soil arthropods, heat and flotation, have been made. A wet (Salt and Hollick flotation) and a dry (Tullgren funnel) method of extraction of soil arthropods were contrasted by El-Kifl (1957), who found that the Tullgren funnel was 'more efficient for extracting Collembola, Hemiptera, mites and psocids than flotation'. Thysanoptera, aphids, beetles, Hymenoptera, spiders, Thysanura and myriapods, however, were extracted better with the flotation method. A comparison of a Tullgren funnel and a modified Salt and Hollick flotation technique (Raw 1955) for the extraction of Acarina from mull and moder woodland soils was made by Satchell & Nelson (1962). They found that there was no significant difference between the mean numbers of mites recovered from samples of the mull soil by the two methods, but on moder the mean number extracted by flotation was 44% greater. The flotation method was much more efficient in extracting Scutacaridae, *Steganacarus magnus* (Nicolet) and hypopi of Astigmata from moder samples. Mean numbers of *Nothrus silvestris* Nicolet and immature forms of *Tectocepheus* species were significantly greater in Tullgren funnel extractions from the moder samples. Again, Wood (1965) has shown that a Tullgren (split funnel) method was superior to a Salt and Hollick flotation method for extracting most species and groups of mites and Collembola, especially weakly sclerotized forms, from a series of soil types, ranging from a mull-like rendzina to brown earths. Six species, two Collembola and four Oribatei, were obtained in greater numbers by the flotation method; and the efficiency of the funnel method for recovery of microarthropods appeared to differ with soil type.

As a result of such work, authors have sometimes incorrectly argued that all flotation methods are superior to all heat extractors for certain groups of soil arthropods, thus causing misunderstanding and confusion. These comparisons were made for extractors which differed considerably in design, procedure and sampling from the Macfadyen and Hale methods compared in the present experiments. The present experiments show that the total number of any arthropod group delivered by any method depends upon the soil which is being studied, size and number of sample units, and the faunal composition of the soil. No universal extraction method exists. As Macfadyen (1962) has pointed out the sampling and extraction methods to be used in a research project must be selected according to the type of problem, e.g. exploratory work, community or trophic studies.

There are differences for extraction of mites and Collembola in the Hale flotation apparatus. Hale (1964) found that for Collembola in peat samples the flotation method 'has an efficiency of extraction which was similar to the high gradient cylinder'. Two species of Collembola were extracted in significantly greater numbers by flotation than

by heat. For mites, in the present study, twice as many were recovered from similar peat samples using the Macfadyen heat extractor as with the Hale flotation device; and 3¼ times as great a total number of mites were recovered from samples of mineral soil by the heat extractor as by flotation. These differences were significant at $P<0{\cdot}01$ and $P<0{\cdot}001$ respectively. The result for mites in the mineral soil is to be expected, as the Hale flotation method was developed primarily for peat.

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SUMMARY

Numbers are given of various Acarina extracted from peat and mineral soils, using a flotation method developed by Hale (1964) for Collembola. Comparing the Hale flotation method with the high gradient extractor (Macfadyen 1961) it is estimated that for the recovery of Acarina the latter is twice (or 200%) as efficient with the peat soil used, and 3¼ times (325%) as efficient with the mineral soil used in the experiments. These differences were significant at $P<0{\cdot}01$ for peat, and at $P<0{\cdot}001$ for mineral soil.

REFERENCES

El-Kifl, A. H. (1957). Comparison between a wet and a dry method for extraction of soil arthropod fauna. *Bull. Soc. ent. Égypte*, **41**, 525–6.

Hale, W. G. (1964). A flotation method for extracting Collembola from organic soils. *J. Anim. Ecol.* **33**, 363–9.

Ladell, W. R. S. (1936). A new apparatus for separating insects and other arthropods from the soil. *Ann. appl. Biol.* **23**, 862–79.

Macfadyen, A. (1961). Improved funnel-type extractors for soil arthropods. *J. Anim. Ecol.* **30**, 171–84.

Macfadyen, A. (1962). Soil arthropod sampling. *Advances in Ecological Research* (Ed. by J. B. Cragg), vol. 1, pp. 1–34. London.

Murphy, P. W. (1962a). Extraction methods for soil animals. I. Dynamic methods with particular reference to funnel processes. *Progress in Soil Zoology* (Ed. by P. W. Murphy), pp. 75–114. London.

Murphy, P. W. (1962b). Extraction methods for soil animals. II. Mechanical methods. *Progress in Soil Zoology* (Ed. by P. W. Murphy), pp. 115–55. London.

Raw, F. (1955). A flotation extraction process for soil micro-arthropods. *Soil Zoology* (Ed. by D. K. McE. Kevan), pp. 341–6. London.

Salt, G. & Hollick, F. S. J. (1944). Studies of wireworm populations. I. A census of wireworms in pasture. *Ann. appl. Biol.* **31**, 52–64.

Satchell, J. E. & Nelson, J. M. (1962). A comparison of the Tullgren-funnel and flotation methods of extracting Acarina from woodland soil. *Progress in Soil Zoology* (Ed. by P. W. Murphy), pp. 212–16. London.

Wood, T. G. (1965). Comparison of a funnel and a flotation method for extracting Acari and Collembola from moorland soils. *Pedobiologia*, **5**, 131–9.

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Rev. Écol. Biol. Sol, 1968, T. V, 3, p. 515 à 521.

Population density and biomass of earthworms in some Uganda soils

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INTRODUCTION

Ecological studies on earthworms in tropical soils of Africa are few and mostly confined to West Africa. BATES (1960) made observations on the casting activity of *Hippopera nigeriae* (Taylor) in lowland rain forest soil near Ibadan, Nigeria. MADGE (1965), who also worked on a Nigerian lowland rain forest soil, has given estimates of the populations and fresh weight biomasses of *Hyperiodrilus africanus* (Beddard). Mention must be made of recent studies in Egypt (EL-DUWEINI & GHABBOUR, 1965) on earthworm ecology, but these fall outside the tropics.

In East Africa, taxonomic studies on earthworms collected by various expeditions have been made by BEDDARD, BENHAM, COGNETTI DE MARTIIS, MICHAELSEN and STEPHENSON (in STEPHENSON, 1930, 1933); but there has been no ecological study on terrestrial earthworms, although some observations have been made on the swampworms which are abundant in waterlogged habitats (WASAWO & VISSER, 1959). Consequently, in conjunction with research on the micro-organisms, nematodes and microarthropods of the soils of Kabanyolo University Farm (BANAGE & VISSER, 1967 a ; BLOCK, in press), a survey of the earthworm fauna was made from December 1964 to February 1966. The aim of the investigation was to provide basic information on the numbers, biomasses and species distribution of earthworms in these soils.

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STUDY AREA

Kabanyolo University Farm has an area of 340 acres (137.6 ha) on a site about 12 miles (19 km) north of Kampala and at an altitude of 3950 ft. (1204 m). Parts of the Farm have been cultivated and grazed since 1953 when it was purchased by Makerere University College. General descriptions of the area are given in BANAGE & VISSER (1967 b) and BLOCK (in press). The mean annual rainfall of 49·68 in. (1245-1727 mm) has a bimodal distribution with the main peaks occurring in March — May and October — December. January — February is the more pronounced dry season of the two. The soils range from red latosols on the central ridge of the Farm, through sandy loams on the slopes, to clays and silts in the valleys to the east and west.

A range of habitats with different soils, management régimes and plant cover to include: swamp forest, bush, elephant grass, coffee plantation, banana plantation, pasture and arable fields was chosen for examination. The bush, banana and pasture sites were sampled on eight occasions, the arable site on four and the other sites on two occasions only.

METHODS

A means of expelling earthworms from soils in the field was required for this survey, as hand sorting proved extremely tedious for the number and size of samples involved. A large number of small worms were found in these soils, and as hand sorting tends to underestimate these in a population (RAW, 1960), a vermifuge was used. A solution of potassium permanganate (7 g/gallon of water) applied to 4 ft² (DAWSON, BOYNS & SHORROCK, 1938) expelled far fewer earthworms than the formalin solution of RAW (1959). Formalin (25 ml of 40 % formaldehyde solution/gallon of water) was therefore selected as a vermifuge.

The disadvantages of the wet methods of sampling for earthworms are twofold: the deeper living and aestivating worms do not react to the solution applied to the soil surface, and the efficiency in expelling worms depends on the dampness of the soil being sampled. The latter factor is of particular importance in tropical soils which can become extremely dry during some seasons. The results given here are, therefore, estimates of the active, subsurface populations at the time of sampling and not of the total populations.

In the field, quadrats of 4 ft² (0.37 m²) area were randomly selected, pegged out and cleared of growing plants and surface litter. One gallon (4.54 l.) of the vermifuge solution was applied to each quadrat with a watering can followed by a second application after 20 minutes. The expelled worms were collected into 5 % formalin solution. At each quadrat there were 3-4 collectors, working for a total of about 40 minutes. On each occasion a sample consisted of five quadrats at each site, except for the first two sampling occasions (December 1964 and January 1965) when only two quadrats were taken at each site.

RESULTS

EXPULSION OF EARTHWORMS.

On all sites, except the swamp forest, the proportion of earthworms expelled by the first application of the vermifuge was usually over 75 % of the total collected. On the swamp forest site such a small number of

earthworms was found (total of 11 for all occasions), that the proportion expelled by the first application (36 %) cannot be regarded as significant. For the pasture, the proportion of the total worms expelled by the first application of the formalin solution, on each sampling occasion, ranged from 77 % (May) to 96 % (April). The range for the bush site was 55 % (May) to 100 % (October) and that for the banana soil was 18 % (July) to 87 % (April). Very few worms were collected with the initial formalin application on the banana and bush sites, when the soils were dry and there had been very little rainfall for the preceding three or four weeks, e.g. on 28 May and 23 July 1965. On the other hand, on 27 April and 21 October 1965, when the soils were moist after fairly heavy rainfall in the preceding weeks (average of 1.5 in. or 38.1 mm/week), large numbers of worms were collected on these two sites, with the first formalin application. Apart from soil moisture increasing the efficiency of the vermifuge for expelling worms from these soils, this suggests that the worms were either aestivating, or too deep in the soil to be affected by the irritant solution during the dry periods.

In an attempt to locate the earthworms in the dry season, and to observe their condition and position in the soil, the following experiment was performed. On 2 February 1965, at the banana and the elephant grass sites, the surface soil from a 4 ft^2 quadrat was dug out to a depth of 9 in. (22.9 cm) and hand sorted for earthworms, after which it was spread out on a polythene sheet and subjected to two applications of the vermifuge in the normal way. The floor of the soil pit in the quadrat was similarly treated with vermifuge. The total sampling depth of both these operations was about 2 ft (0.61 m). In the banana soil six earthworms, five of which were aestivating, were found by hand sorting the surface soil. The five worms were lying singly, tightly coiled upon themselves, in smooth-walled, hardened soil chambers. All the specimens found thus were clitellate. In the elephant grass soil six active specimens were recovered with formalin solution from the top 9 in. of soil in the quadrat, but these might have been aroused from aestivation by the disturbance of the soil. No worms were found in the floor of the soil pit on either site suggesting that there had been no downward migration beyond 9 in.

Qualitative composition of the fauna.

Over 60 % of the earthworms collected on the bush and banana sites were clitellate and therefore identifiable. Although over 1,000 worms were collected from pasture soil, only 26 % of them were identifiable. At present, no explanation can be offered for the predominance of non-clitellate worms in this population. However, the pasture was only established in 1961, after a period of arable cultivation, and the population could have been still in an immature state in 1965. Mr. R. W. Sims of the British Museum (Natural History) has identified the worms as far as possible to generic level. Table 1 gives a preliminary list of the genera with the numbers of each genus recorded from each site, together with data for a *Eucalyptus* and *Acacia* woodland on Makerere Hill, Kampala, for comparison. Specific identifications and descriptions will be published elsewhere.

A total of five genera, probably comprising nine species, was found in the Kabanyolo soils, with an additional genus *(Eminoscolex)* comprising two

TABLE 1

List of earthworm genera identified from the Kabanyolo collections and from a *Eucalyptus* and *Acacia* woodland on Makerere Hill

	Kabanyolo University Farm			*Makerere Hill*
	Bush	Banana plantation	Pasture	*Eucalyptus* and *Acacia* woodland
Family *Acanthodrilidae* Subfamily *Ocnerodrilinae*				
Gordiodrilus sp. 1.	21	82	10	—
Gordiodrilus sp. 2.	1	—	—	—
? Ocnerodrilus sp.	30	—	—	—
Pygmaeodrilus sp.	—	3	—	15
Subfamily *Octochaetinae*				
Dichogaster sp. 1.	14	12	28	—
Dichogaster sp. 2.	12	181	76	—
Dichogaster sp. 3.	7	—	—	9
Family *Eudrilidae* Subfamily *Eudrilinae*				
Eminoscolex sp. 1.	—	—	—	87
Eminoscolex sp. 2.	—	—	—	6
Polytoreutus sp. 1.	2	8	1	—
Polytoreutus sp. 2.	—	—	—	3
Number of species	(7)	(5)	(4)	(5)
Number of genera	(4)	(4)	(3)	(4)
Total number of earthworms collected.	122	1099	186	
Total number of identifiable (clitellate) specimens	87	286	115	
Identifiable (clitellate) specimens as percentage of total collected	71	26	62	

species, on Makerere Hill. Of the three sites sampled most extensively at Kabanyolo, bush had seven species contained in four genera, whilst pasture had four species in three genera. The members of the subfamily Ocnerodrilinae are usually associated with marshy habitats (SIMS, pers. comm.) and it is interesting to record them from much drier sites at Kabanyolo. The octochaetine genus *Dichogaster* is characteristic of the savanna grasslands and areas of cultivation in tropical Africa. It was a very common genus on the three Kabanyolo sites. Little is known of the habitats of the Eudrilinae which, with the exception of *Polytoreutus* sp. 1, were found only in the Makerere woodland soil.

POPULATION AND BIOMASS ESTIMATES.

Estimates of the earthworm population and wet weight biomass for each of the Kabanyolo sites are given in Table 2. The recorded biomass is

the actual weight of earthworms obtained after preservation for 4-5 hours in 5 % formalin solution. As RAW (1962) has shown that the weight of worms after preservation in this solution is about 25 % less than their actual fresh weight, this has been allowed for in converting recorded weight to estimated fresh weight.

TABLE 2

Numbers and biomasses of earthworms from seven sites at Kabanyolo University Farm (December 1964 to February 1966)

	1964 Dec.	1965 Jan.	1965 Feb.	1965 Apr.	1965 May	1965 July	1965 Oct.	1966 Feb.	Total number of quadrats	Mean of all samples
Swamp forest										
A	14.8	0.0	—	—	—	—	—	—		7.40
B	0.46	0.0	—	—	—	—	—	—	(4)	0.23
C	0.57	0.0	—	—	—	—	—	—		0.30
Bush										
A	25.6	0.0	0.0	30.7	10.8	—	2.1	22.1		13.04
B	0.44	0.0	0.0	1.47	2.26	—	0.03	0.51	(29)	0.67
C	0.55	0.0	0.0	1.84	2.82	—	0.04	0.64		0.84
Elephant grass										
A	76.7	0.0	—	—	—	—	—	—		38.35
B	0.86	0.0	—	—	—	—	—	—	(4)	0.43
C	1.07	0.0	—	—	—	—	—	—		0.54
Banana plantation										
A	207.3	18.8	17.2	193.2	180.3	17.8	99.0	80.7		101.79
B	9.39	0.34	3.76	3.55	7.78	0.14	2.18	1.95	(34)	3.64
C	11.74	0.42	4.70	4.44	9.72	0.17	2.72	2.44		4.55
Coffee plantation										
A	53.8	0.0	—	—	—	—	—	—		26.9
B	0.89	0.0	—	—	—	—	—	—	(4)	0.44
C	1.11	0.0	—	—	—	—	—	—		0.55
Pasture										
A	44.4	0.0	0.0	83.4	16.7	0.0	—	4.8		21.32
B	9.19	0.0	0.0	2.93	1.83	0.0	—	0.19	(29)	2.02
C	11.49	0.0	0.0	3.66	2.30	0.0	—	0.24		2.52
Arable										
A	33.6	0.0	—	0.0	—	—	—	0.0		8.40
B	0.21	0.0	—	0.0	—	—	—	0.0	(14)	0.05
C	0.26	0.0	—	0.0	—	—	—	0.0		0.06

Key: A = Population/m²
B = Recorded biomass/m²
C = Estimated fresh weight biomass/m²
— = Not sampled

The banana plantation soil supported the largest number of earthworms (mean population of 101.79 individuals/m^2) and also the largest estimated fresh weight biomass (mean of 4.55 g/m^2). The next largest mean populations were found in soil under elephant grass and coffee, but these samples contained high proportions of small, immature (non-clitellate) worms and the estimated biomass for each of these sites is about 0.5 g/m^2. The second largest biomass (mean of 2.52 g/m^2) was estimated for the pasture site, which supported about 1/5 of the mean earthworm population of the banana plantation soil. Even during the severe dry season, the soil underneath the bananas was always moist due to the mulch of leaves and old pseudostems. This is probably a very important factor in the maintenance of the earthworm population in the upper soil layers throughout the year.

Seasonally, fewer earthworms and smaller biomasses were found in the banana soil during the dry period in January and February 1965, and none at all in pasture and bush soils. In April and May the populations increased on these sites, but the fresh weight biomass in the banana soil did not show any significant increase between February and April due to a large number of immature worms being present. However, the fresh weight biomass on this site doubled between April and May 1965. The largest single population estimate was 207.3 earthworms/m^2 with a fresh weight biomass of 11.74 g/m^2, which was on the banana site on 9 December 1964. A comparable fresh weight biomass to this, 11.49 g/m^2, was estimated for the pasture on the same date, but in this case the population was much smaller, namely 44.4 earthworms/m^2.

A comparison of the total numbers and biomasses of earthworms at Kabanyolo with those estimated by MADGE (1965) for *Hyperiodrilus africanus* (Beddard) in tropical rain forest soil at Ibadan, Nigeria, shows that his mean population of 34.2/m^2 is within the range of Kabanyolo estimate of 7.40-101.79/m^2. In terms of biomass, *H. africanus* had a mean fresh weight of 10.2 g/m^2 which is over twice the maximum fresh weight biomass for all species estimated for Kabanyolo (4.55 g/m^2 for the banana soil). Most of the estimates of earthworm numbers and weights given in SATCHELL (1967) for temperate soils are in excess of those at Kabanyolo, showing that these tropical soils have a relatively impoverished earthworm fauna.

ACKNOWLEDGMENTS

We acknowledge gratefully the encouragement in the early part of this study given by Dr. Margaret A. KEAY, Head of the Department of Agricultural Biology at Makerere; the generous help of Mr. R. W. SIMS of the British Museum (Natural History) in identifying the earthworms and of the technical staff of the Department in field work. We are also grateful for finance from both the Rockefeller Foundation and Makerere University College.

SUMMARY

1. A survey of the earthworms of seven sites at Kabanyolo University Farm, near Kampala, Uganda, was made using the formalin method of RAW (1959).

2. Mean estimates of earthworm numbers ranged from 7.40/m² in swamp forest soil to 101.79/m² in banana plantation soil. Mean estimates of earthworm biomasses ranged from 0.06 g/m² in arable soil to 4.55 g/m² in soil under bananas.

3. Seasonal differences in numbers and biomass on three extensively sampled sites (bush, banana plantation and pasture) are discussed, and the efficiency of the formalin method for these tropical soils is examined.

4. Over 60 % of the earthworms collected from the bush and banana plantation soils were clitellate, as compared with only 26 % of those from the pasture.

5. A total of five genera, probably comprising nine species, have been identified from Kabanyolo soils. The relative abundance of the genera on three sites are compared with collections from a *Eucalyptus* and *Acacia* woodland site, 12 miles (19 km) away on Makerere Hill.

References

Banage (W. B.) & Visser (S. A.), 1967 a. — Micro-organisms and nematodes from a virgin bush site in Uganda. *Progress in Soil Biology* (Ed. by O. Graff & J. E. Satchell), 93-101. Amsterdam.

Banage (W. B.) & Visser (S. A.), 1967 b. — Soil moisture and temperature levels and fluctuations in one year in a Uganda soil catena. *E. Afr. agric. For. J.* **32**: 450-455.

Bates (J. A. R.), 1960. — Studies on a Nigerian forest soil. I. The distribution of organic matter in the profile and in various soil fractions. *J. Soil Sci.* **11**: 246-256.

Block (W.), (In press). — Microarthropods in some Uganda soils.

Dawson (M. B.), Boyns (B. M.) & Shorrock (R. W.), 1938. — Potassium permanganate in green keeping. *J. Bd Greenkeep. Res.* **5**: 258-268.

El-Duweini (A. K.) & Ghabbour (S. I.), 1965. — Population density and biomass of earthworms in different types of Egyptian soils. *J. appl. Ecol.* **2**: 271-288.

Madge (D. S.), 1965. — Leaf fall and litter disappearance in a tropical forest. *Pedobiologia*, **5**: 273-288.

Raw (F.), 1959. — Estimating earthworm populations by using formalin. *Nature, Lond.* **184**: 1661-1662.

Raw (F.), 1960. — Earthworm population studies: a comparison of sampling methods. *Nature, Lond.* **187**: 257.

Raw (F.), 1962. — Studies of earthworm populations in orchards. I. Leaf burial in apple orchards. *Ann. appl. Biol.* **50**: 389-404.

Satchell (J. E.), 1967. — Lumbricidae. *Soil Biology* (Ed. by A. Burges & F. Raw), 259-322. London.

Stephenson (J. L.), 1930. — *The Oligochaeta.* Oxford.

Stephenson (J. L.), 1933. — Reports on the scientific results of an expedition to the south-western highlands of Tanganyika Territory. IV. Oligochaeta. *Bull. Mus. comp. Zool. Harv.* **75**: 225-247.

Wasawo (D. P. S.) & Visser (S. A.), 1959. — Swampworms and tussock mounds in the swamps of Teso, Uganda. *E. Afr. agric. For. J.* **25**: 86-90.

Micro-arthropods in some Uganda soils

W. Block

In proceedings of a UNESCO/IBP Symposium on Methods of Study in Soil Ecology (ed. J. Phillipson) p. 195–202. UNESCO, Paris. (1970).

Quantitative studies of micro-arthropods in tropical soils are limited; in East Africa only those of Salt (1952, 1955) and Burnett (1965) are known. The present survey covered the Acari and Collembola of cultivated and uncultivated soils of a mixed farm near Kampala (Uganda).

STUDY AREA

Kabanyolo farm lies 19 km NNE. of the capital Kampala (0°28′ N., 32°37′ E.) and is about 53 km north of the equator. Compared to the surrounding peasant holdings it is large, being 138 ha in extent. The land is

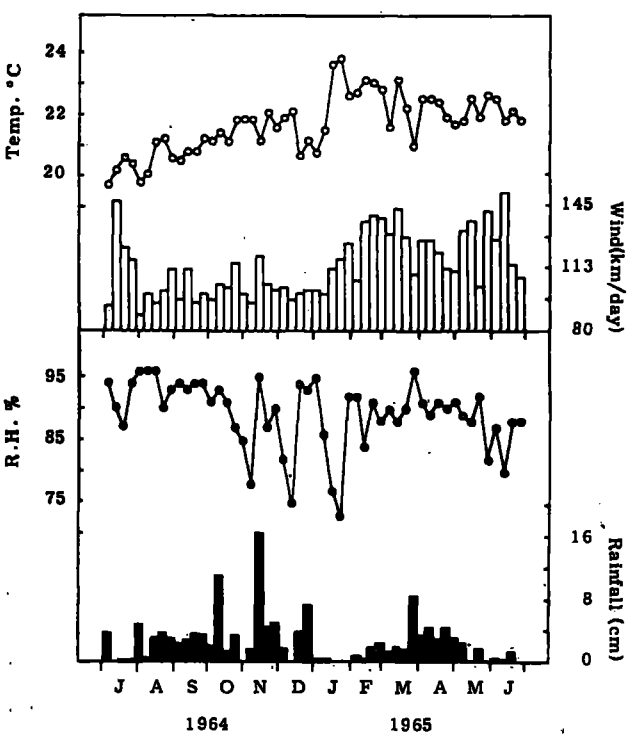

FIG. 1. Meteorological data from Kabanyolo farm, near Kampala (Uganda), for the study year, 1 July 1964 to 30 June 1965. The data are plotted as seven-day averages except for total rainfall.

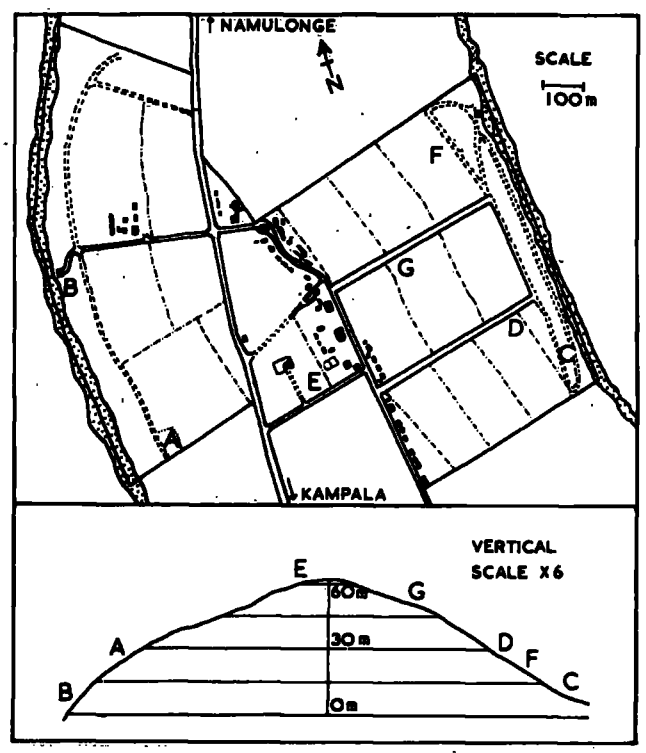

FIG. 2. Plan of Kabanyolo farm showing the field layout and sample sites, and a section showing the positions of the sample sites. A. Bush. B. Swamp forest. C. Elephant grass. D. Banana. E. Coffee. F. Pasture. G. Arable soil.

FIG. 3. Kabanyolo farm. Bush sample site.

FIG. 4. Kabanyolo farm. Swamp-forest sample site.

at 1,204 m above sea level and this should be borne in mind in a consideration of the climatic data for the study period, which are summarized in Figure 1. There is a bi-modal rainfall pattern with a main peak in April-May and a lesser peak in October-November. Figure 2 is a plan of the farm with a section showing the positions of the sample sites.

The soils grade from shallow red latosols (pH 5.5-6.0) on the ridge to deep loams overlying blue clays (pH 4.5-5.2) in the swamps. The sample sites are thus situated on a transect from a valley swamp over an increasingly dry and impoverished ridge with thin soils, and descending again to a valley swamp with deep and relatively rich soils. The difference in altitude of ridge and swamp is about 61 m, and this topography is typical of southern Buganda.

Seven sites were chosen for study, taking into consideration the soil, vegetation and cultural practices and these are described briefly below. Data on soil organic matter and microbiology of the bush site are given in Banage and Visser (1967).

Bush. (Fig. 3.) This is an area of natural bush, which is ungrazed though occasionally burnt in the dry season (January-February); it is on the west slope. The soil

is a deep sandy loam and the vegetation grows to a height of 1.8 m or more during the rains. The grasses, *Pennisetum purpureum* Schumach, *Hyparrhenia* spp., *Panicum maximum* Jacq. and *Imperata cylindrica* (L.), are dominant, but various shrubs (*Acanthus* sp., *Pseudarthria hookeri* Wright & Walk.-Arn. and *Lantana camara* L.) are also found. Very little plant litter is found on the soil surface in any season.

Swamp forest. (Fig. 4.) This is a wet area fringing a papyrus swamp with loam soil overlying heavy clay and situated at the bottom of the west slope of the farm. It is a mixed forest of *Macaranga schweinfurthii* Pax. and *Alchornea floribunda* Muell. Arg., with occasional wild date palms (*Phoenix reclinata* Jacq.) and *Erythrina excelsa* Baker. The dominant herb species are *Dracaena steudneri* Schwein. ex Engl. and *Impatiens niamniamensis* Gilg. There is abundant leaf litter on the forest floor.

Elephant grass. (Fig. 5.) This is situated on the east slope of the farm which is covered entirely by *Pennisetum purpureum* Schumach growing to a height of about 4.6 m. The soil is a clay loam with abundant grass litter on the surface; the site is steep and terraced.

Banana plantation. (Fig. 6.) This is also on the east slope and the area was cleared from bush in 1957. The site is terraced along the contour, and the soil is mulched with old leaves and pseudostems of banana.

Coffee plantation. (Fig. 7.) This is situated on the western brow of the ridge and has a shallow soil mulched with coffee husks. The plantation is of Rubusta coffee (*Coffea canephora* Pierre ex Froehner) and was laid out in 1957.

Pasture. (Fig. 8.) This is part of a 40 ha arable-ley block on the east slope of the farm, which was cleared from bush in 1956. The plant cover is a mixture of *Chloris gayana* Kunth. and *Panicum maximum* Jacq. and this is grazed heavily by cattle.

Arable soil. (Fig. 9.) This is part of the arable-ley block also, and the site is regularly cultivated with two crops per year. It was sampled when under maize (*Zea mays* L.) sorghum (*Sorghum vulgare* Pers.).

METHODS

Samples, each consisting of 10 soil cores, were collected at random from each site on three occasions: at the end of the second rains (24 December 1964), in the dry season (17 February 1965) and at the beginning of the main rains (25 March 1965). Each core was 10 square centimetres in surface area and 3 cm deep. Previously, deeper sampling had shown that less than 10 per cent of the Acari and Collembola were present below 3 cm. The arthropods were extracted from the cores using the flotation technique of Raw (1955), though ligneous material in the pasture samples caused considerable difficulty. Extracted animals were identified and counted. The extraction efficiency was calculated to be about 87 per cent for Acari and Collembola from these soils.

FIG. 5. Kabanyolo farm. Elephant-grass sample site.

RESULTS

Table 1 shows for the seven sites the mean populations of Acari, Collembola and total Arthropoda. The latter term includes all the arthropods collected. Total arthropods were most abundant in swamp forest soil, and smallest numbers were found in arable soil. The largest numbers of Acari occurred in the coffee plantation and the smallest in arable area. Most Collembola

TABLE 1. Populations of soil Collembola and Acari and total Arthropoda (in thousands per square metre) of seven sites at Kabanyolo farm. The data are the means and standard errors of 30 soil cores

Site	Collembola	Acari	Total Arthropoda
Bush	2.20 ± 0.48	14.40 ± 1.18	19.71 ± 1.54
Swamp forest	3.43 ± 0.60	12.20 ± 1.51	24.16 ± 3.08
Elephant grass	1.67 ± 0.24	12.97 ± 2.63	21.50 ± 2.97
Banana plantation	1.80 ± 0.37	6.87 ± 0.88	18.06 ± 4.36
Coffee plantation	2.13 ± 0.52	16.13 ± 3.38	20.02 ± 3.59
Pasture	0.53 ± 0.13	4.00 ± 0.43	7.52 ± 0.73
Arable soil	0.37 ± 0.13	3.40 ± 0.50	4.00 ± 0.54

FIG. 6. Kabanyolo farm. Banana-plantation sample site.

FIG. 7. Kabanyolo farm. Coffee-plantation sample site.

occurred in the swamp forest and the smallest numbers in arable and pasture soils, but generally the Collembola populations were very much smaller than the Acari on all the sites examined. Protura and Symphyla were not recovered from these soils using this extraction technique, although small numbers of Diplura were recovered from some sites.

Table 2 shows the break-down of the Acari data into groups. The Cryptostigmata comprised over 50 per cent of all Acari on all the sites except elephant grass and the coffee plantation. On these two sites the Cryptostigmata were partly replaced by the Astigmata, which formed 48 per cent of all Acari in the coffee plantation soil. The largest number (33 per cent of the total Acari) of mesostigmatid mites was found in the swamp forest, where most Collembola occurred. In the banana-plantation soil, this group was 42 per cent of the total Acari.

The data for all sites and the three sampling dates are shown in Figure 10. Square-root transformation of these data followed by analyses of variance were made to ascertain if the differences suggested in Figure 10 were significant. Table 3 shows the results of these

FIG. 8. Kabanyolo farm. Pasture sample site.

FIG. 9. Kabanyolo farm. Arable sample site.

analyses. Highly significant differences ($P < 0.001$) between sites are shown for all groups except the Prostigmata. This group had significantly different populations on the three sampling dates.

DISCUSSION

A comparison of the results of the present study and other East African work shows that there are great variations in the numbers of Acari and Collembola (which form the bulk of micro-arthropods) in soils under different crops and natural vegetation. Estimates of Acari populations range from 3,400 per square metre (arable soil, Kabanyolo farm) to 44,620 per square metre (pasture soil at Kawanda Research Station, Uganda; Salt 1952). Population estimates for Collembola are generally smaller, and range from 370 per square metre (arable soil, Kabanyolo farm) to 29,970 per square metre (elephant grass soil at Kawanda Research Station, Uganda; Salt 1955).

TABLE 2. Soil Acari populations (in thousands per square metre) of seven sites at Kabanyolo farm. The data are the means and standard errors of 30 soil cores, and the percentages of each sub-order of the total Acari are given

Site	Cryptostigmata	Mesostigmata	Prostigmata	Astigmata	Total Acari
Bush	9.63 ± 0.80	3.83 ± 0.52	0.47 ± 0.13	0.47 ± 0.19	14.40 ± 1.18
%	66.9	26.5	3.3	3.3	
Swamp forest	7.47 ± 0.91	4.07 ± 0.64	0.43 ± 0.21	0.23 ± 0.15	12.20 ± 1.51
%	61.2	33.4	3.5	1.9	
Elephant grass	6.13 ± 0.80	3.47 ± 0.47	0.60 ± 0.22	2.76 ± 1.93	12.97 ± 2.63
%	47.3	26.8	4.6	21.3	
Banana plantation	3.53 ± 0.59	2.90 ± 0.44	0.20 ± 0.07	0.23 ± 0.12	6.87 ± 0.88
%	51.4	42.3	2.9	3.4	
Coffee plantation	4.90 ± 0.67	3.17 ± 0.49	0.33 ± 0.10	7.73 ± 2.61	16.13 ± 3.38
%	30.4	19.7	2.0	47.9	
Pasture	2.67 ± 0.35	0.90 ± 0.21	0.43 ± 0.18	0.0	4.00 ± 0.43
%	66.8	22.5	10.7		
Arable Soil	2.17 ± 0.42	1.10 ± 0.20	0.07 ± 0.04	0.07 ± 0.04	3.40 ± 0.50
%	63.8	32.2	2.0	2.0	

TABLE 3. Results of the analyses of variance of the transformed data of individual counts of soil Acari, Collembola and total Arthropoda of seven sites at Kabanyolo farm

Source of variation	Degrees of freedom	Mean square	F	Significance
		Cryptostigmata		
Sites	6	12.4679	20.17	***[4]
Dates	2	1.9715	3.19	*[2]
Sites × dates	12	2.6965	4.36	***
		Mesostigmata		
Sites	6	6.4984	11.60	***
Dates	2	0.7456	1.33	NS[5]
Sites × dates	12	1.8448	3.29	***
		Prostigmata		
Sites	6	0.4101	1.81	+[1]
Dates	2	3.6288	16.05	***
Sites × dates	12	0.5479	2.42	**[3]
		Astigmata		
Sites	6	13.1948	15.84	***
Dates	2	1.3461	1.62	NS
Sites × dates	12	4.7765	5.73	***
		Total Acarina		
Sites	6	19.9222	16.36	***
Dates	2	1.6446	1.35	NS
Sites × dates	12	4.7048	3.86	***
		Collembola		
Sites	6	5.7652	9.30	***
Dates	2	1.0388	1.68	NS
Sites × dates	12	1.5775	2.54	**
		Total Arthropoda		
Sites	6	31.9734	17.83	***
Dates	2	0.8102	<1	
Sites × dates	12	6.7840	3.78	***

1. + Significant at 10 per cent level of probability.
2. * Significant at 5 per cent level of probability.
3. ** Significant at 1 per cent level of probability.
4. *** Significant at 0.1 per cent level of probability.
5. NS Not significant.

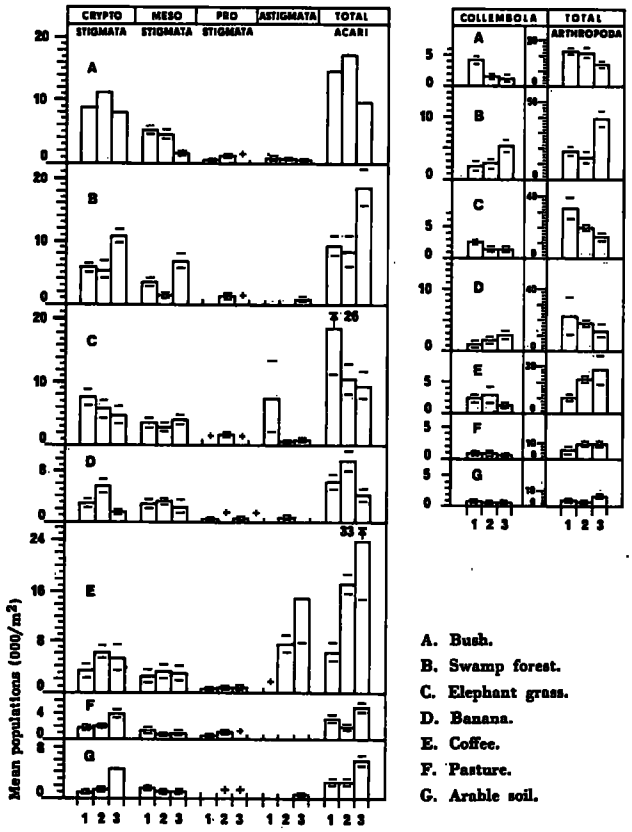

FIG. 10. Population estimates for soil Acari, Collembola and total Arthropoda of seven sites at Kabanyolo farm. The populations are the means (in thousands per square metre), with the standard errors, of the numbers extracted from 10 soil cores per site on each sampling occasion. Sampling dates: 1 = 24 December 1964, 2 = 17 February 1965 and 3 = 25 March 1965. The symbol + indicates that the population mean was less than 100 individuals per square metre.

The sample sites at Kabanyolo form a transect from a valley swamp with a deep soil, rich in minerals and organic matter, through progressively leached soils to the very shallow impoverished soil, low in organic matter and minerals, on the ridge top. The coffee-plantation site is nearest to the top of the ridge. In temperate zones the abundance of micro-arthropods generally reflects changes in soil organic matter, minerals, moisture or temperature. Under tropical conditions at Kabanyolo, although the mean number of micro-arthropods in the rich soil of the swamp forest is relatively high (15,630 per square metre), the largest population of micro-arthropods is found in the poor soil of the coffee plantation (18,260 per square metre). This suggests that artificially applied mulch and naturally occurring leaf litter on the surface of the soil have a direct effect on the abundance of micro-arthropods in the soil below. Belfield (1967) has shown the importance of soil moisture for arthropods in the tropics. However, the bush site, which has a deep and fairly rich soil with very little surface litter, supports the second largest micro-arthropod population found on the farm (16,600 per square metre).

The pasture and arable sites are both situated about half way down the slope in the transect, and both are regularly cultivated, using normal farm machinery. There is no litter on the soil surface and these sites have the smallest numbers of micro-arthropods. The bush site excepted, mulch or natural leaf litter appears to override any effects of soil impoverishment on the numbers of micro-arthropods for the sites examined. The bush site has not been cultivated for at least 12 years, but the coffee trees have been growing for 8 years, suggesting that a lack of cultivation (or an undisturbed soil) is as important as an insulating cover of organic material for the maintenance of large populations of micro-arthropods under these tropical conditions.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the help and encouragement of Dr. Margaret A. Keay, Reader and Head of the Department of Agricultural Biology at Makereer University College. Thanks are due also to Dr. R. C. Campbell and the ARC Statistics Group at Cambridge for statistical assistance, and to the Research Grants Committee at Makerere for finance and to Mr. Peter Halfpenny who traced the figures.

Résumé

Microarthropodes dans quelques sols en Ouganda (William Block)

Les estimations de nombres d'*Acari* et de *Collembola* sont données pour sept endroits à la ferme Kabanyola, près de Kampala (Ouganda).

Les acariens sont les plus abondants dans le sol cultivé en café ($16\,130 \pm 3\,380/m^2$) et sont les moins abondants dans le sol arable ($3\,400 \pm 50/m^2$). Les populations de *Collembolens* sont beaucoup plus petites, entre $3\,430 \pm 60/m^2$ dans le sol des forêts humides et $370 \pm 130/m^2$ dans le sol arable.

Les analyses de variation des données transformées montrent qu'il y a des différences significatives entre les endroits pour le total *Acari*, *Cryptostigmata*, *Mesostigmata*, *Astigmata* et *Collembola*.

Les différences de la faune entre les endroits à Kabanyola sont discutées en relation avec les sols, la matière organique et la culture.

Discussion

M. J. Hadley. I return to that old bugbear: extraction efficiency. There are two main ways of measuring this for small arthropods. One is to compare the number of animals obtained from similar soil samples in different types of extraction apparatus. This gives a relative efficiency and was the basis of Dr. Edward's paper. The second type of efficiency measurement is to determine the "absolute" efficiency by introducing a known number of animals into a sterilized soil sample and counting the number of these after extraction. Your figure of 87 per cent for micro-arthropods in Uganda presumably refers to the latter measurement, namely absolute efficiency. What do you think of the validity of this type of measurement? I think that gross overestimates of extraction efficiency are given by the use of these artificial soil samples.

W. Block. I confirm that my extraction efficiency estimate was obtained by inserting animals into sterile soil cores. I believe that comparative extraction methods which give estimates of relative efficiency to be the best. Unfortunately, other types of extractors were not available for comparison

in Uganda, and my figure should only be regarded as an approximate one.

A. MACFADYEN. Dr. Coleman also gave an estimate of extraction efficiency. Please will he let us know how this was arrived at?

D. COLEMAN. Our extractor's efficiency was measured by a third method: examining soil cores after extraction by spreading them out under a dissecting microscope and counting the animals remaining. This avoids the artificiality objected to by Dr. Hadley.

V. G. MARSHALL. The Astigmata are not normally found in large numbers in northern temperate soils. You recovered many Astigmata in some sites in Uganda. Were these members of a single species or were there many species involved? A second question, did you get termites in your samples?

W. BLOCK. I do not entirely agree with the speaker's first point, as large numbers of Astigmata, usually of one species, have been found in certain areas in Britain. I have found this group in quite large numbers in peat and mineral soils of the Moorhouse National Nature Reserve in Westmorland. With reference to the Uganda observations, the material which was collected probably belongs to 8 or 9 species.

Answering your second question, a few worker individuals were found in some of the soil cores; but my core size was small and so they would not be collected in large numbers.

M. S. GHILAROV. Have you observed so-called "suspended soils" on twigs of trees in mixed forest you have investigated? Have you compared your data with that recorded by Maldague in the Congo?

W. BLOCK. The answer is no to your first question and yes to the second. Generally my figures for micro-arthropods are lower than those of Maldague.

Bibliography / Bibliographie

BANAGE, W. B.; VISSER, S. A. 1967. Micro-organisms and nematodes from a virgin bush site in Uganda. In: O. Graff and J. E. Satchell (ed.), *Progress in soil biology*, p. 93-101. Amsterdam, North Holland Publishing Co.

BELFIELD, W. 1967. The effects of overhead watering on the meiofauna in a West African pasture. In: O. Graff and J. E. Satchell (ed.), *Progress in soil biology*, p. 192-210. Amsterdam, North Holland Publishing Co.

BURNETT, G. F. 1965. *The effect of some cultural practices and insecticide applications on the soil arthropod fauna at Arusha Chini*. 13 p. (Tropical Pesticides Research Institute Miscellaneous Report no. 519.)

RAW, F. 1955. A flotation extraction process for soil microarthropods. In: D. K. McE. Kevan (ed.), *Soil zoology*, p. 341-346. London, Butterworths.

SALT, G. 1952. The arthropod population of the soil in some East African pastures. *Bull. ent. Res.*, vol. 43, p. 203-220.

——. 1955. The arthropod population of soil under elephant grass in Uganda. *Bull. ent. Res.*, vol. 46, p. 539-545.

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Oxygen uptake in an Antarctic collembole *Cryptopygus antarcticus*

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Tilbrook, P. J. and Block, W. 1972. Oxygen uptake in an Antarctic collembole, *Cryptopygus antarcticus*. – Oikos 23: 313–317. Copenhagen.

The relationship between length and weight was investigated for the Antarctic springtail, *Cryptopygus antarcticus* Willem. The range of individuals from juvenile to adult was divided arbitrarily into five size classes, whose lengths ranged from 440–1,990 µm, and live weights from 2.2–119.5 µg. Measurements of oxygen consumption of individuals were made using a Cartesian Diver micro-respirometer at +2°, +6° and +10°C, and mean rates were calculated for each size class at each experimental temperature. These varied from 10.52–75.91 µl × 10^{-4}/individual and hr at +2°C, 41.40–78.04 at + 6°C, and 120.81–136.60 at +10°C. These respiration data are discussed in relation to live weight and temperature, and to other work on temperate and Antarctic collembola.

P. J. Tilbrook, British Antarctic Survey Biological Unit, Monks Wood Experimental Station, Abbots Ripton, Huntingdon, U.K., and Dr. W. Block, Department of Zoology, Leicester University, Leicester LE1 7RH, U.K.

Исследовали зависимость между длиной и весом у коллембол *Cryptopygus antarcticus* Коллемболы разных возрастов от неполовозрелых до взрослых форм произвольно разделялись на 5 размерных классов. Их длина варьировала в перделах от 440 до 1,990 мм, а живой вес–от 2,2 до 119,5 мм. Измерения дыхания проводили с помощью микрореспирометра при +2, +6 и +10°C. Для каждого класса определена средняя скорость потребления кислорода при разных температурах. Эти данные варьируют в пределах 10,52–75,91 млх 10^{-4}/экз./час при 2°C, 41,40–78,04 при 6°C и 120,81–136,60 – при 10°C. Обсуждаются корреляции интенсивности дыхания, живого веса и температуры, сравниваются данные, полученные на коллемболах из Антарктики и других областей.

Manuscript accepted May 1972

1. Introduction

It has often been stated that the Antarctic terrestrial ecosystem is a simple one – a reference to the paucity of species present in the biota. While it is recognised that this simplicity is only relative and that many of the groups represented are little known and present many problems to detailed study, the Antarctic would nevertheless appear to offer a good opportunity for a total ecosystem analysis. To this end, a number of terrestrial reference sites are being established by the British Antarctic Survey for intensive long-term study with a view to assembling an energy flow model for each. The first two sites have been set up at Signy Island, in the South Orkney Islands, which is typical of the Maritime Antarctic zone (Holdgate 1967). These are representative of wet and dry moss communities.

One of the major factors required for an energy flow study is population respiration and ideally this should be measured for all the component species. The terrestrial arthropods of the Antarctic consist almost entirely of Acari and Collembola, and these are the best known, both taxonomically and ecologically, of all the land invertebrates. Furthermore, techniques are available for the measurement of their respiration rates experimentally. Consequently, for an initial study of their respiration, the collembolan *Cryptopygus antarcticus* Willem (Isotomidae) was selected as it has been shown to be one of the most important arthropods in the Maritime Antarctic (Tilbrook 1967 a and b). It is found in almost all terrestrial habitats in this zone, and frequently exhibits a high relative abundance, comprising 70–90 per cent of the arthropod fauna in the majority of moss communities. The biology of *C. antarcticus* has been documented by Tilbrook (1970), and a study of its population dynamics in a mixed bryophyte community at Signy Island was carried out during 1962–63 (Tilbrook unpubl.). The results of preliminary respiration measurements for *C. antarcticus* are given in this paper.

2. Methods

The specimens used for this study were taken from samples of moss and lichen which were collected on Signy Island by O. H. S. Darling in March 1970, and transported to England in polythene containers stored at +4°C. The material was kept at +6°C at the British Antarctic Survey's Zoological Section at Monks Wood Experimental Station before being transferred to Leicester University where the respirometry was carried out. There the containers were kept in a constant temperature room, together with the respirometer and electromicrobalance so that any treatment thereafter took place at a room temperature within 1°C of the experimental temperature. At least one week was allowed for acclimatisation.

Measurements of oxygen consumption were made upon individual animals by means of a Cartesian Diver micro-respirometer (Linderstrøm-Lang 1943, Holter 1943). Stoppered divers were used and full operational details can be found in Zeuthen (1964). Divers in the range 2.84–28.65 µl gas volume were used in these experiments and measurements were made on individual collemboles in the weight range 3.50–127.75 µg. An equilibration time period of at least one hour was allowed between placing the diver into the flotation chamber of the respirometer and the commencement of readings. Readings were made at 30-min intervals and each experiment was continued for 3–6 hr. At the end of the experiment, each individual was preserved separately in 75 per cent alcohol and later its total body length was measured accurately under a magnification of ×16.

It was hoped to measure the respiration rates of a series of individuals representing the complete weight range at each temperature, but unfortunately this was not possible. Due to previous experience of the difficulties of culturing this species, and the desirability of keeping disturbance and handling to a minimum, it was felt that specimens should only be taken from the stock culture immediately prior to the experiment. Consequently, presorting was not carried out, and the extremes of the size range were not always available. Furthermore, the smaller individuals were more difficult to handle and more susceptible to damage. Initially animals were weighed alive before loading into the divers, but later in the work there was some doubt as to the accuracy of the electromicrobalance, particularly when weighing the smallest individuals. Consequently only reliable weights were used to determine a length-weight relationship. As live weights were not available for some of the later experimental animals, and since body length was considered the more accurate measurement, weights were taken from the derived curve in all cases when calculating the weight specific oxygen consumption.

3. Length-weight relationship

The 36 reliable weight measurements were used to derive a curve of body weight against total body length. On the assumption that the two variates conformed to the simple allometry relationship $W = \alpha L^{\beta}$ of Huxley (1924), a logarithmic transformation was applied to both variates to obtain linearity. Fig. 1 indicates that a linear model is adequate to represent the relationship between $\log_e W$ and $\log_e L$. There is a greater variation in $\log_e W$ corresponding to smaller values of $\log_e L$. It was decided therefore that use of a weighted analysis, with weights inversely proportional to variance, would be more efficient.

If it is assumed that a specimen of length L has a weight W with mean $= \exp.\ \{\alpha + \beta\ (\log_e L - L^*)\}$

where $L^* = \sum_{i=1}^{n} \log_e L_i / n$, and constant variance σ^2

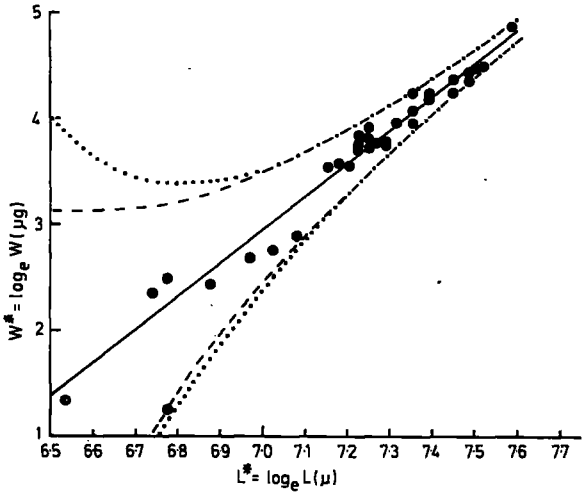

Fig. 1. Relationship between weight ($\log_e W$) and length ($\log_e L$) in *Cryptopygus antarcticus*. The fitted line is shown along with the approximate 95% confidence limits. The ..... line is based on 'statistical differentials', and the line -------- is based on d^2. See text.

then, using the method of 'statistical differentials' (Johnson and Leone 1964), the variance of the transformed variate $\log_e W$ is approximately given by

$$\frac{\sigma^2}{[\varepsilon(W)]^2} = \frac{\sigma^2}{\exp\{2[\alpha + \beta(\log_e L - L^*)]\}}$$

The estimation of the parameters of the linear regression model by the weighted least squares procedure required iterative calculations. The resulting prediction line and the approximate 95% confidence limits based on the assumption of normally distributed errors after the logarithmic transformation are shown in Figs. 1 and 2. The apparently unsatisfactory upper limit for small values of L is thought to arise from too low a weighting being given to smaller individuals, partly because of relatively few observations in this region, and partly because of the inexact assumed variance of $\log_e W$.

An alternative approach is to rely on empirically derived estimates of variance from the data. The procedure employed was to fit an ordinary Least Squares straight line to the plot of $\log_e W$ against $\log_e L$, to calculate the deviation d of the observed $\log_e W$ values from the fitted value and assume that d^2 is a first approximation to the variance. By plotting the values of d^2 against $\log_e L$ the trend in the variance in shown and a smooth line drawn through the points can be used to give an improved estimate of the variance of $\log_e W$ for a given $\log_e L$. The analysis using the reciprocals of these estimates of variance as weights gave improved estimates of the parameters of the linear regression, which by repeated application may be determined to any desired degree of accuracy. With the present data, however, one iteration is considered sufficient.

The prediction equation obtained by this approach is

$$\log_e W = 4.202 + 3.119\,(\log_e L - 7.407)$$
$$\text{or} \quad W = 6.1894 L^{3.119} \times 10^{-9}$$

This produces the fitted line and the approximate 95% confidence limits shown on Figs. 1 and 2.

Using this relationship the weights of all specimens used in the respiration experiments have been estimated from their body length measurements.

4. Oxygen uptake and live weight

For an assessment of the respiratory metabolism of a species it is essential to know the age structure of the population. Collembolan growth is by a series of moults, which continue throughout life, even after the attainment of maximum size, but the number of instars occurring before both sexual maturity and maximum size are reached, varies between species. Attempts to differentiate between instars of *C. antarcticus* on the basis of body length, were unsuccessful (Tilbrook 1970). Therefore, during the analysis of samples taken for the population study the material was divided into five equal but arbitrary size classes using body length. The five size classes with their corresponding weight ranges, which have been derived from Fig. 2, are given in Tab. 1. A live weight has been obtained for each size class using the mid-point of each length range in Fig. 2.

A total of 75 measurements of oxygen uptake were made on individuals of *C. antarcticus* at three temperatures: 35 measurements at +2°C, 26 measurements at +6°C, and 14 measurements at +10°C. On a whole animal basis there is not a clear relationship between oxygen uptake and live weight in this species, but on a weight specific oxygen uptake basis a pattern is evident. Fig. 3 shows the relationship between live weight and weight specific oxygen uptake for individuals of *C. antarcticus* at +2°, +6° and +10°C on a double log scale. Regression lines have been fitted for each temperature. The data at +2°C exhibit considerable variability re-

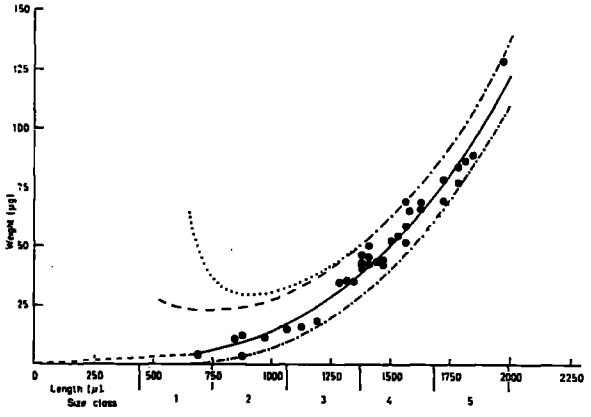

Fig. 2. Relationship between weight and length in *Cryptopygus antarcticus*. The fitted line is shown along with the approximate 95% confidence limits. The ..... line is based on 'statistical differentials', and the line -------- is based on d^2. See text.

Tab. 1. Body length and live weight ranges for each of the five size classes in *Cryptopygus antarcticus*. The live weights have been derived from the mid-point of the body length range for each size class.

Size class	Body length range, µm	Live weight range, µg	Live weight, µg
I.....	440–750	2.2–6.0	3.0
II.....	750–1,060	6.0–16.8	10.2
III.....	1,060–1,370	16.8–37.7	25.7
IV.....	1,370–1,680	37.7–70.7	52.5
V.....	1,680–1,990	70.7–119.5	92.8

sulting in a poor correlation coefficient. This may be due to the difficulties encountered in maintaining a constant low temperature during the respiration experiments. The slopes of the regression lines may also be affected by the paucity of respiration data for individuals of size classes I and II, as these small animals were scarce in the cultures.

As would be expected there is a decrease in weight specific oxygen consumption with increasing body weight at each of the three experimental temperatures. Differences of metabolic rate for individual animals between the three temperatures are more pronounced for the smaller individuals, and these differences diminish with increasing body size.

From Fig. 3 it is possible to derive mean oxygen uptake rates for each of the five size classes, both on a whole animal and a weight specific basis. These are given in Tab. 2. The whole animal respiration rate has been calculated from the derived weight specific rate and the mean live weight of each size class. It can be seen that for whole animals the oxygen consumption increases steadily through the five size classes at +2°C, whereas this effect is not so pronounced at +6°C, and at +10°C there is little increase. Considered on a weight specific basis, however, there is a very marked decrease in oxygen consumption with increasing live weight at each of the three temperatures. The decrease is greatest at +10°C and +6°C. Such a decrease is to be expected because, as the animal grows and increases in live weight, there will be a corresponding reduction in metabolic rate per unit weight.

5. Oxygen uptake and temperature

From the data in Tab. 2 the relationship between oxygen uptake and temperature can be derived and is shown on a whole animal basis in Fig. 4. Over the experimental temperature range there is a general increase in respiration rate for each size class. On both a weight specific and a whole animal basis, however, the metabolic rate of the smaller individuals appears to be more affected by change in temperature.

From the whole animal data a Q_{10} has been calculated for each size class over the experimental temperature range (+ 2 to + 10°C). The Q_{10} estimates are, size class I (21.14), II (9.17), III (4.90), IV (3.00) and V (2.08). The values for size classes I and II are clearly high, and because of the paucity of data for these small individuals, they must be treated with caution. The Q_{10}s

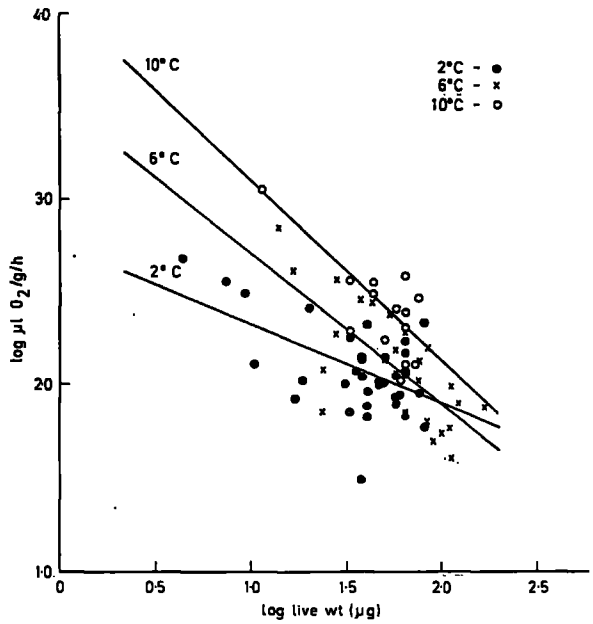

Fig. 3. Relationship between weight specific oxygen consumption and live weight in *Cryptopygus antarcticus* at three temperatures. The coefficients for the linear regression at each temperature are:
+2°C — a = −0.43, b = 2.75, r = 0.56
+6°C — a = −0.82, b = 3.53, r = 0.73
+10°C — a = −0.88, b = 3.89, r = 0.73

Tab. 2. Relationship between live weight and oxygen uptake per individual animal and per µg live weight at three temperatures in *Cryptopygus antarcticus*.
A – oxygen uptake per individual animal (µl × 10^{-4} O_2/ind and hr).
B – oxygen uptake per µg live weight (µl × 10^{-4} O_2/µg and hr).

Size class	Live weight, µg	+2°C		+6°C		+10°C	
		A	B	A	B	A	B
I.....	3.0	10.52	3.51	41.40	13.80	120.81	40.27
II.....	10.2	21.31	2.09	51.59	5.06	125.46	12.30
III.....	25.7	36.31	1.41	61.37	2.39	129.40	5.03
IV.....	52.5	54.86	1.04	69.67	1.33	132.19	2.52
V.....	92.8	75.91	0.82	78.04	0.84	136.60	1.47

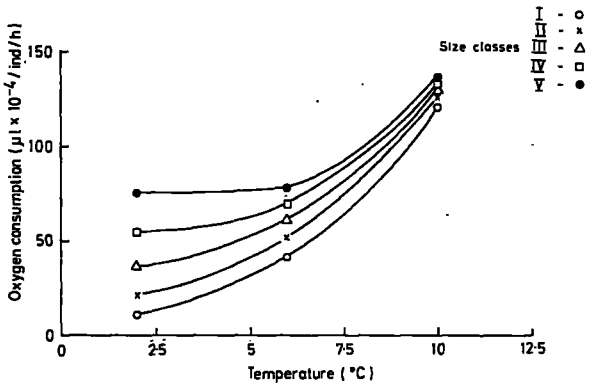

Fig. 4. Oxygen consumption (µl × 10^{-4}/individual and hr) and temperature (°C) for five size classes of *Cryptopygus antarcticus*.

for classes III, IV and V are similar to those obtained for other soil Collembola: 1.9–2.7 (Zinkler 1966), 3.5–4.0 (Healey 1967). The published data for Q_{10} in these studies, however, are either just for adults or are mean estimates for several life stages. No comparative figures are available for the early instars.

5. Discussion

Very little is known of the respiration rates of soil Collembola although measurements have been made, or are quoted by, Healey (1967), Zinkler (1966), Berthet (1964), and Strong et al. (1970). The approximate nature of some of the data given, however, together with the broad variation in both experimental temperatures and weight of animals, makes any detailed comparison difficult, even with the aid of Krogh's curve or a Q_{10} coefficient. Nevertheless, these studies indicate that the respiration rate of *C. antarcticus* is high, particularly in the immature stages, suggesting some degree of cold adaptation. The only other data available for an Antarctic collembolan are those given in general form by Strong et al. (1970) for *Isotoma klovstadi*, and these indicate even higher metabolic rates at low temperatures. The weight is not stated for this species but adults are probably in the region of 100 µg and at −4°C their oxygen consumption averaged 400 µl/g and hr. This compares with 82 µl/g and hr for adult *C. antarcticus* (mean weight 92.8 µg) at +2°C and 545µl/g and hr for another isotomid, *Isotoma viridis* (weight 718.0 µg) at −18°C (Zinkler 1966).

Before the question of cold adaptation can be clarified or the respiration rates applied to field populations further data are required, particularly for the smaller life stages. This work is in progress at Signy Island in the Antarctic, using fresh animals collected direct from the field and measured at current field temperatures.

7. Acknowledgements

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References

BERTHET, P. 1964. L'activité des Oribatides (Acari: Oribatei) d'une Chênaie. – Mem. Inst. Roy. Sci. Nat. Belg. 152: 1–152.

HEALEY, I. N. 1967. The population metabolism of *Onychiurus procampatus* Gisin (Collembola). – In: Progress in Soil Biology, eds. O. Graff and J. E. Satchell. North-Holland Publishing Company, Amsterdam, pp. 127–134.

HOLDGATE, M. W. 1967. The Antarctic Ecosystem. – Phil. Trans. R. Soc. Ser. B. 252: 363–383.

HOLTER, H. 1943. Technique of the Cartesian Diver. – C. r. Lab. Carlsberg Ser. Chim. 24: 399–478.

HUXLEY, J. S. 1924. Constant differential growth ratios and their significance. – Nature, Lond. 114: 895–896.

JOHNSON, N. L. and LEONE, F. C. 1964. Statistics and experimental design in Engineering and the Physical Sciences. Vol. 2 – Wiley, New York. 399 pp.

LINDERSTRØM-LANG, K. U. 1943. On the theory of the Cartesian Diver microrespirometer. – C. r. Lab. Carlsberg Ser. Chim. 24: 333–398.

STRONG, F. E., DUNKLE, R. L. and DUNN, R. L. 1970. Low-temperature physiology of Antarctic arthropods. – Antarct. J. 5: 123.

TILBROOK, P. J. 1967a. The terrestrial invertebrate fauna of the Maritime Antarctic. – Phil. Trans. R. Soc. Ser. B. 252: 261–278.

– 1967b. Arthropod ecology in the Maritime Antarctic. – Antarct. Res. Ser. 10: 331–356.

– 1970. The biology of *Cryptopygus antarcticus*. – In: Antarctic Ecology, ed. M. W. Holdgate. Vol. 2, Academic Press, London, pp. 908–918.

ZEUTHEN, E. 1964. Microgasometric Methods: Cartesian Divers. – In: 2nd Int. Congr. Histo- and Cyto-chemistry, eds. T. H. Schiebler, A. G. E. Pearse and H. H. Wolff, Wiley, New York, pp. 70–80.

ZINKLER, D. 1966. Vergleichende untersuchungen zur atmungsphysiologie von Collembolen (Apterygota) und anderen Bodenkleinarthropoden. – Z. vergl. Physiol. 52: 99–144.

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Respiration studies on the Antarctic collembolan Cryptopygus antarcticus

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Analyses are presented of 190 measurements of individual respiration rate for the complete size range of *Cryptopygus antarcticus* Willem. A Cartesian Diver micro-respirometer was used at Signy Island (Maritime Antarctic) during the austral summer 1971/72. Oxygen consumption per individual increased linearly with live weight on a log basis at 0°, 5° and 10°C. The 5° and 10°C regression lines differed significantly and the weight exponent b varied from 0.669 to 0.825. Mean oxygen uptake rates for 5 size classes ranged from 0.671 to 22.610 µl $\times$ 10^{-3} O_2 ind^{-1} h^{-1}, and from 95.66 to 469.20 µl O_2 g^{-1} h^{-1} over the temperature range studied. Juveniles showed least change in rate, and adults the maximum change, over 0° to 10°C. Egg respiration was 0.306 ul $\times$ 10^{-3} O_2 h^{-1} at 5°C. Data are compared with other Antarctic Collembola, and temperate species. Comparison of respiration rates with cultured, acclimated animals showed considerable differences. Cultured juveniles have much higher rates, especially above 5°C, than field animals. Population metabolism is estimated for a typical habitat and cold adaptation is discussed.

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Сравнивали результаты измерений интенсивности дыхания у 190 особей всех размерных групп *Cryptopygus antarcticus* Willem. Измерния проводились с помощью Картезианского поплавка на острове Сайни в Антарктике в течение южного лета 1971–72 гг. Потребление кислорода возрастало в прямой линейной зависимости от веса при 0, 5 и 10°C. Линии регрессии при 5 и 10°C значительно различались, и экспонента веса b колебалась в пределах 0,669–0,825. Средние данные потребления кислорода для пяти размерных классов колебались от 0,671 до 22,610 млх 10^{-3} O_2/ экз. /$час^{-1}$ и от 95,66 до 469,20 мл O_2/ $г^{-1}$ /$час^{-1}$ в пределах изученной температурной шкалы. У ювенильных особей наблюдались минимальные колебания, а у взрослых – наибольшие, в пределах от 0 до 10°. Дыхание яиц составляло 0,306 мл х 10^{-3} O_2 /$час^{-1}$ при 5°C. Сравнивались данные, полученные на других видах Антарктических коллембол и видах из зоны умеренного климата. Сравнения интенсивности дыхания с акклиматизированными животными в культурах показали существенные различия. У животных в культурах интенсивность дыхания гораздо выше, особенно при температуре выше 5°C, чем у животных из естественных условий. Обсуждается уровень метаболизма популяции определенный в типичном местообитании, и адаптации к холодному климату.

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1. Introduction

The terrestrial arthropods of the Maritime Antarctic consist almost entirely of Collembola and Acari. There is a lack of information on the physiology of all such micro-arthropods living in extreme cold environments. Preliminary data were given by Tilbrook and Block (1972) for respiration rates of *Cryptopygus antarcticus* Willem at 2°, 6° and 10°C measured with a Cartesian Diver micro-respirometer. Rates varied from 1.052 – 7.591 µl × 10^{-3} O_2 ind^{-1} h^{-1} at 42°C to 12.081 – 13.660 µl × 10^{-3} O_2 ind^{-1} h^{-1} at 10°C. These measurements were made at Leicester University using individuals maintained in culture at a temperature of 5 ± 1.0°C and acclimated to the experimental temperature.

As the effects of long term culture upon respiration rate were not known, the present programme was undertaken at Signy Island, South Orkney Islands, during the southern summer (December–March) 1971/72. Measurements of respiration rates of animals from the complete size range (1–125 µg live wt) were made at various temperatures covering as far as possible their normal environmental range. These data enable an investigation of the relation of oxygen uptake to both live weight and temperature, and a comparison with rates from acclimated, cultured animals. In addition these data may be applied to field populations to derive an estimate of population metabolism, and they can be used to study cold adaptation in this species.

Cryptopygus antarcticus Willem (1902), is the commonest collembolan in the Maritime Antarctic (Tilbrook 1967 a, 1970). It has a circumpolar distribution, being found on the Antarctic Peninsula, South Shetland Islands, South Orkney Islands, South Georgia, South Sandwich Islands, Bouvetøya, Kerguelen, Heard and Macquarie Islands. The species is not only numerically the dominant arthropod in many areas but, because of its activity and biomass, it is probably one of the most important components of the terrestrial ecosystem. The biology of *C. antarcticus* has been detailed (Tilbrook 1970), and the Signy Island sites have been described (Tilbrook 1973).

2. Methods

Two Cartesian Diver micro-respirometers were established in a constant temperature room at the station on Signy Island. The room temperature was controlled to ±1.5°C. An experimental temperature control for the respirometer waterbath of ±0.01°C was achieved using a Hetofrig portable liquid flow cooler (CA 3) and a Heto ultrathermostat (Type 01E923/225). Each respirometer had a capacity of 7 chambers, thus enabling 14 measurements to be made simultaneously. Stoppered divers (Zeuthen 1964) were used throughout the study with gas volumes in the range 1.90–22.45 µl. Diver calibration was by direct measurement of the gas bubble with a micro-syringe.

Respiratory measurements were made on single animals collected from the field immediately prior to the experiment. For the majority of these collections, field temperatures were measured using a Grant thermistor thermometer Model S. In most experiments respiration rates were measured within 5°C of the field temperature. Animals were collected in samples of mosses and lichens in the field between 0900–0945, hand sorted from the samples in the constant temperature room, and individuals were loaded directly into the divers. An equilibration period of 30–75 min was allowed after the divers had been placed in the flotation chambers, before readings commenced. Readings were made at intervals of 30–40 min over 4–6 h.

The behaviour of *C. antarcticus* in the diver was observed as far as possible at each reading of equilibrium pressure. After a brief exploratory period following loading, individuals remained relatively quiescent during the course of the experiment. Therefore, measurements were generally made of the resting metabolic rate of each animal.

At the end of each experiment, animals were preserved separately in 75% ethanol. Later, each individual was cleared in Nesbitt's solution at 70°C, which also relaxed the body and ensured that it reverted to its normal state. Total body length was measured under a microscope at ×16 magnification, and this was used to derive the live weight (Tilbrook and Block 1972) using the relationship

$$W = 6.1894\ L^{3.119} \times 10^{-9}$$

where W = live weight (µg) and L = length (µm). Individual cleared specimens were then mounted in Hoyer's medium, with the furcula pointing forwards, and examined under phase contrast at magnifications up to ×600 to determine their sex. The structure and setation of the genital aperture were found to be reliable sexual characters in this species.

The three experimental temperatures used were 0°C, 5°C and 10°C. Individuals representing the complete size range of *C. antarcticus* were measured in the respiration experiments. In the absence of any characters on which to separate the instar stages, the field population had been divided previously into 5 equal size classes on the basis of body length (Tilbrook and Block 1972). As far as possible, at least 10 respiration measurements were made at each temperature for each size class. The smallest animal was 469.5 µm in length with a live weight of 1.33 µg, and the largest was 2128.4 µm long with a live weight of 148.54 µg. Eight measurements were made on egg respiration at 5°C. The eggs were collected from fresh cultures of adult *C. antarcticus* set up overnight at 5°C. Between 6–14 ova of the same age were placed in divers (V_g: 2.52–15.60 µl) using a fine brush. The mean respiratory rate per egg was calculated from each batch.

Graphs were plotted of the equilibrium pressure readings with time for each animal. Linear regressions were

Tab. 1. Distribution of respiration measurements for *Cryptopygus antarcticus* with size class, live weight and temperature at Signy Island.

Size class/ stage	Body length range (µm)	Live wt range (µg)	°C 0	5	10	Total
Ova*			–	(8)	–	(8)
....	< 750	2.2–6.0	9	12	9	30
I ...	750–1060	6.0–16.8	7	10	9	26
II...	1060–1370	16.8–37.7	9	10	14	33
V...	1370–1680	37.7–70.7	9	13	12	34
/....	> 1680	70.7–119.5	19	29	19	67
Total determinations			53	74	63	190

* Determinations for eggs are not included in totals.

tted to these data on return to the UK. Oxygen uptake ates were calculated using the formula

$$VO_2 = \frac{\Delta EP \cdot V_g \cdot 273}{P_0 \cdot T}$$

here VO_2 = volume of oxygen consumed (µl h^{-1}), EP = change in equilibrium pressure (mm h^{-1}), V_g = as volume of diver (µl), T = temperature (°K), and $_0$ = normal pressure (10000 mm Brodie's fluid).

A total of 190 measurements of respiration rate was ade for post ovum *C. antarcticus*, and the number of terminations for each size class, eggs and at each mperature are given in Tab. 1.

Results

1. Respiration rate and live weight

xygen consumption (µl × 10^{-3} O_2 ind^{-1} h^{-1}) is otted against live weight (µg) for each individual easured at each of the 3 temperatures (Fig. 1). Linear gressions have been fitted to these data, and the result- g equations and correlation coefficients are given in b. 2. At each temperature there is a steady increase in piratory rate with live weight, but the 5° and 10°C gression lines cross at 4.5 µg.

b. 2. Linear regressions (y = a + bx), correlation coefents (r) and number of observations (n) for $\log_{10}$ reration rate (y) on $\log_{10}$ live wt (x) for *Cryptopygus antarcs* at 3 temperatures. Regressions are given for respiratory es per individual and per g live wt per h.

	n	a	b	r (P < 0.001 throughout)
× 10^{-3} O_2 ind^{-1} h^{-1}				
.....	53	−0.5335	0.7533	+0.8974
.....	74	−0.1701	0.6692	+0.9084
.....	63	−0.2687	0.8249	+0.9681
O_2 g^{-1} h^{-1}				
.....	53	2.4668	−0.2470	−0.5549
.....	74	2.8291	−0.3305	−0.7310
.....	63	2.7313	−0.1751	−0.6344

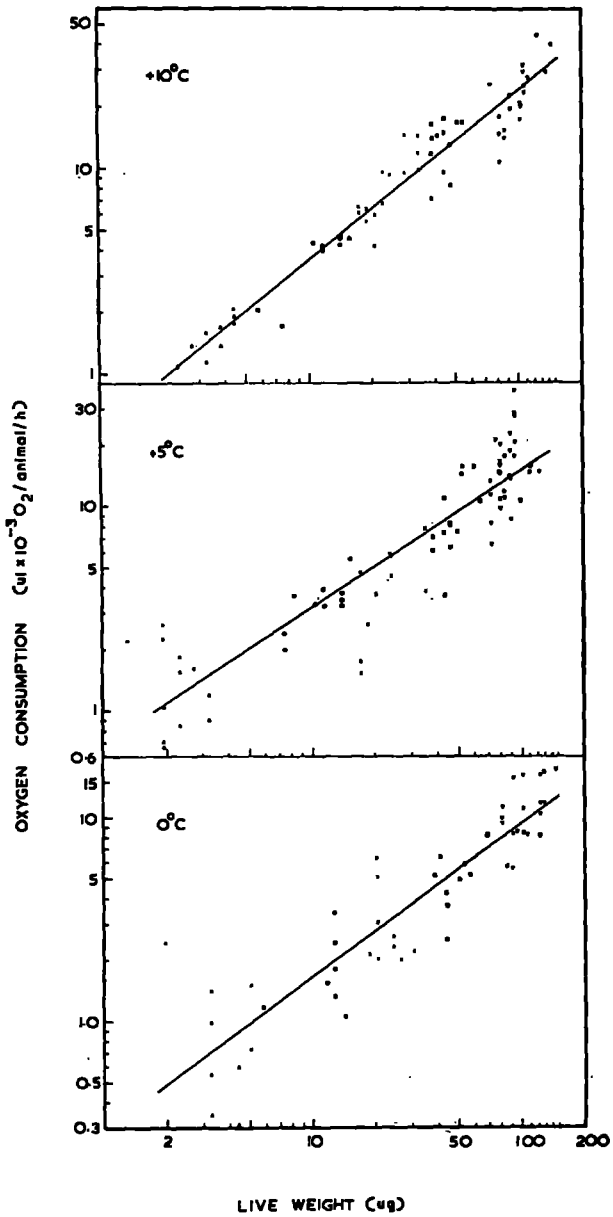

Fig. 1. Oxygen consumption (µl × 10^{-3} O_2 ind^{-1} h^{-1}) as a function of live weight (µg) for *Cryptopygus antarcticus* at 0°, 5° and 10°C. Data are plotted on a double log scale, and individual measurements with the fitted linear regression line are shown for each temperature. ▲ = size class I, ● = size class II, × = size class III, ■ = size class IV, and ▼ = size class V.

The relationship between the 3 regression equations was examined by the method of Ostle (1963), which tests the hypothesis that a single regression line can adequately describe the relationships at the 3 temperatures. The overall regression equation for respiratory rate (y) on live weight (x) is $\log_{10} y = 0.7299 \log_{10} x - 0.2829$. The analysis shows that the 3 regression lines are

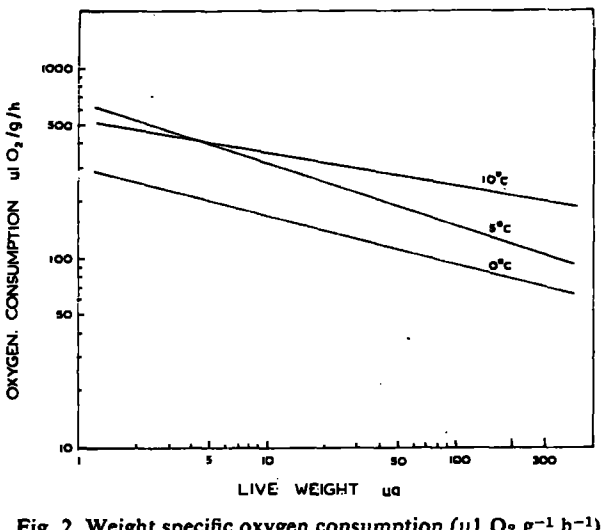

Fig. 2. Weight specific oxygen consumption ($\mu l\ O_2\ g^{-1}\ h^{-1}$) as a function of live weight for *Cryptopygus antarcticus* at 0°, 5° and 10°C. Data are plotted on a double $\log_{10}$ scale and the linear regression line is shown for each temperature.

not homogeneous; the slopes within temperatures, the linearity of temperature means, and the within- and between-temperature slopes all differ significantly. Since all components achieve significance it is not justifiable to describe the complete data for all temperatures by a single regression line. The slopes of the lines were then compared statistically, and the difference between the 5° and 10°C regression lines was very significant ($P < 0.001$).

The individual weight specific respiratory rates were analysed similarly (Fig. 2). The linear regressions and correlation coefficients (Tab. 2) confirm a significant negative relationship between weight specific respiration rate and live weight.

From the foregoing regression equations, mean rates of oxygen uptake per individual and per g have been calculated (Tab. 3) using a live weight value derived for each size class (Tilbrook and Block 1972), and these rates will be used in subsequent analyses. This method has been used, rather than taking the mean value of the individual measurements for each size class, as it avoids any bias due to an uneven distribution of body weights within the relatively small size class samples.

The striking features of these respiration data are the significant differences between the 5° and 10°C regression lines, and their intersection at a live weight of 4.5 µg. Size class I individuals, therefore, have their maximum respiratory rate at 5°C. Although the position of these lines may be influenced by the respiration rates for the larger individuals, it seems more likely to result from a temperature response by the smaller individuals. Either their respiration rate is particularly high at 5°C or depressed at 10°C. As there is no significant difference between the slopes of the 0° and 10°C regression lines, the former seems to be more likely.

Tab. 3. Mean oxygen consumption rates per individual and per g live wt for 5 size classes of *Cryptopygus antarcticus* a 3 temperatures.

Size class	I	II	III	IVb	V
Live weight µg	3.0	10.2	25.7	52.5	92.8
$\mu l \times 10^{-3}\ O_2\ ind^{-1}\ h^{-1}$					
0°C	0.671	1.684	3.378	5.785	8.884
5°C	1.410	3.197	5.934	9.572	14.010
10°C	1.333	3.658	7.840	14.140	22.610
$\mu l\ O_2\ g^{-1}\ h^{-1}$					
0°C	223.3	165.1	131.4	110.1	95.6
5°C	469.2	313.2	230.7	182.2	150.9
10°C	444.3	358.6	305.1	269.2	243.7

The mean summer temperature (December–March) i the upper layers of the moss from which the experi mental animals were collected, is approximately 3° (Chabers 1966). Although diel temperature fluctuation in such habitats are often broad (15°C, Longton an Holdgate 1967) and rapid, there may be a seasonal adap tation of respiratory rate to the mean summer tempera ture. If so, the measurements at 10°C have been made a an above average summer temperature, and the resul suggeststhat the smaller individuals are better able t utilize the relatively long periods of equable summer tem perature (3–5°C), perhaps to enable more rapid growt

Considering further the exponent b in the equatio $y = a \cdot x^b$, where y = oxygen consumption, x = li wt, and a and b are constants for any particular temper ture; b varies, over the temperature range 0° to 10° from 0.669 to 0.823 with a mean value of 0.749. Thu oxygen consumption of *C. antarcticus* increases by power of the live weight; indicating that respiration proportional to surface area. It accords very well wi the mean value for b of 0.74 calculated by Zinkler (196 for 8 species of arthropleone Collembola at 18°C. Th correlates with the mode of respiration in most arthi pleone Collembola, which is by gaseous diffusi through the cuticle. However, a much lower b val (0.503) is given for *Onychiurus procampatus* Gisin 15°C (Healey 1967 a). These are the only data publish for the exponent b in the Ametabola, but many figu have been reported for other insects. Edwards (19 gives a b values of 1.0 for the Holometabola, and a ran of 0.67–0.75 in the Hemimetabola. Thus the Collembo so far investigated fall within the range for hemime bolous insects. Berthet (1964) calculated a similar me value (b = 0.72) for 16 species of Oribatidae.

3.2. Respiration rate and temperature

Each of the 5 size classes reacts in a characteristic, different way in respect of respiratory rate to temperatu Respiratory rates derived from the regressions of re ration on live weight (Tab. 3) were used to study effects of temperature upon metabolism of *C. antarcti* Fig. 3 A shows the respiration rate per individual

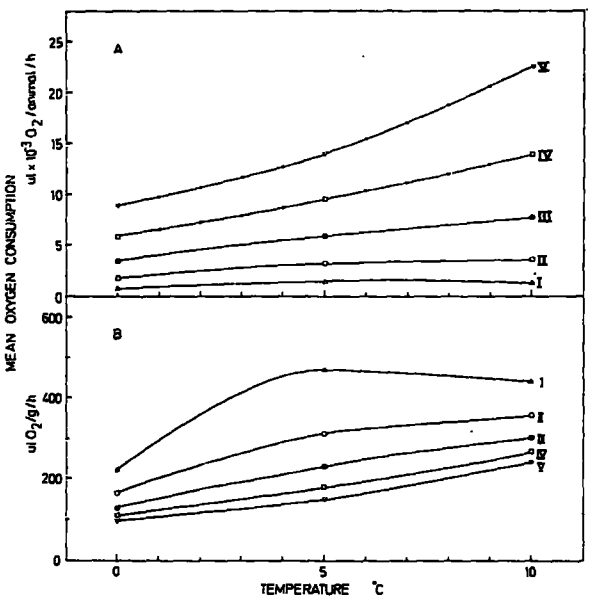

Fig. 3. Effect of temperature on mean oxygen consumption of each of the 5 size classes (I to V) of *Cryptopygus antarcticus*.
A: µl × 10^{-3} O_2 ind^{-1} h^{-1}. Respiratory rates which have been calculated using the Krogh-Jørgensen function are shown at 1°C intervals for size classes IV and V.
B: µl O_2 g^{-1} h^{-1}.

ach size class plotted against the three experimental emperatures. Size class III alone approaches linearity. ize classes I and II exhibit the least change, and IV and ' show the maximum change over the temperature ange. There is a much greater range of respiratory ates between size classes at 10° than at 0°C. Although ° to 10°C is representative of the range of summer emperatures experienced in the maritime Antarctic abitats of this species, the overall duration of exposure) temperatures around 10°C is probably small.

Fig. 3 B demonstrates the relationship between the eight specific respiratory rate and temperature for each ze class. Again, size class III individuals show an alost linear relationship of weight specific respiration ith increasing temperature in the range studied. Unlike e whole animal data, size classes IV and V show the nallest increase with temperature over the experimental nge, and I and II exhibit the greatest increase, particarly between 0° and 5°C. The range of weight specific spiratory rates for the five size classes at each temperure is largest at 5°C and least at 0°C.

In order to calculate respiratory rates at intermediate nperatures within the experimental range for the mputation of population metabolism, a Krogh-Jørnsen function was applied to the data for size classes and V. The data for size classes I, II and II were not alysed in this way as they were not exponential.

The function, derived by Krogh (1914) and Jørgensen 16), is based on the exponential relationship of respiratory rate (v) to temperature (t) using three constants (a, b and c), where $v = a + bc^t$. Determinations of respiratory rate are required at 3 different temperatures such that $t_1 - t_2 = t_2 - t_3$. For *C. antarcticus*, the derived constants for the Krogh-Jørgensen function were

Size class IV $v = 1.320 + 7.568 \times 1.109^t$
Size class V $v = -12.578 + 18.360 \times 1.038^t$

These constants were used to calculate the respiratory rate for individuals of size classes IV and V at 1°C intervals from the mean respiration rates at 0°, 5° and 10°C. The results have been plotted in Fig. 3 A.

The temperature coefficient (Q_{10}) has been calculated for each of the 5 size classes of *C. antarcticus* using the mean respiratory rate per individual (Tab. 3) for the temperature ranges: 0–5°C, 5–10°C, and 0–10°C (Tab.4). The Q_{10} for size class I individuals over the temperature range 5–10°C was not calculated as the mean figures indicate a slight reduction in respiration rate. The temperature coefficients fall within the normal range reported for Collembola (Zinkler 1966, Healey 1967 a) and for soil Acari (Berthet 1964, Webb 1969). They differ markedly, however, in the smaller size classes, from those reported earlier for *C. antarcticus* (Tilbrook and Block 1972), but it was stressed in this preliminary work that insufficient data were available for the smaller individuals. The Q_{10}s are higher over the lower part compared with the upper part of the temperature range. Whereas Q_{10} values decrease with increasing size class over 0° to 5°C, this is reversed for 5° to 10°C. Size class V individuals show the least change in temperature coefficient. Juvenile *C. antarcticus* have a greater capacity to respond to a rise in temperature below 5°C than larger individuals.

Zinkler (1966) gave Q_{10} values varying from 2.07 to 2.92 for 5 species of Collembola measured in the temperature range 8°–18°C, and Healey (1967a) estimated the Q_{10} for *O. procampatus* to be 3.5–4.0 at temperatures around 15°C. Q_{10}s have been calculated from Zinkler's data for the respiration rates of adult *Isotoma saltans* (Nicolet) and *Isotoma hiemalis* (Schött), two Collembola from high montane habitats. For *I. saltans*, the Q_{10} (−2° to 3°C) is 4.18 and for *I. hiemalis* the Q_{10}s are

Tab. 4. Temperature coefficients (Q_{10}s) calculated for the temperature ranges 0° to 5°C, 5° to 10°C, and 0° to 10°C for each of the 5 size classes of *Cryptopygus antarcticus* using the mean respiration rate per individual per hour (Tab. 4).

Temperature range		0°–5°C	5°–10°C	0°–10°C
Size class	I	4.42	–	1.99
	II	3.60	1.31	2.17
	III	3.09	1.74	2.32
	IV	2.74	2.18	2.44
	V	2.49	2.60	2.54

Q_{10} (−2° to 3°C) = 3.05
Q_{10} (3° to 8°C) = 3.98
Q_{10} (−2° to 8°C) = 3.49

These values are all higher than the Q_{10}s calculated for size class V *C. antarcticus* over similar temperature ranges, although *I. hiemalis* is somewhat larger. Both species investigated by Zinkler were measured in groups of 10–13 individuals, which may have caused greater activity. Therefore, the results are not directly comparable with those of resting metabolic rate in *C. antarcticus*.

From the respiratory data given for *C. antarcticus* by Dunkle and Strong (1972) it has been calculated that the Q_{10}s are 13.78 (0–10°C) and 1.49 (10–20°C). The former value is very high compared with the present study, but again, it may reflect active metabolic rate as 10 adults were used for each determination. It is therefore difficult to compare the temperature coefficients derived from the two studies. Zinkler (1966) has suggested that the active metabolic rate of Collembola is at least twice that when resting.

For a second but larger Antarctic species, *Isotoma klovstadi* Carpenter, adult Q_{10} values were calculated from the respiration data given by Strong et al. (1970)

Q_{10} (−4° to 18°C) = 3.00
Q_{10} (−4° to 22°C) = 1.48

A direct comparison with *C. antarcticus* is precluded by the much wider temperature ranges.

Respiration rates for *C. antarcticus* at the three experimental temperatures were further compared with the variable field collection temperatures. For the respirometric determinations at 0°C, the range of field collection temperatures was small (−0.9° to 1.0°C). No field collection temperatures were recorded for animals measured at 5°C. For the 10°C determinations there was a much greater range of field collection temperatures (1.0–5.5°C).

The difference between each individual measurement of respiration rate and the appropriate regression line (Fig. 1) was calculated at 0° and 10°C. The divergence was compared with field collection temperature. At 0°C, there was a much narrower range of divergence when the field collection temperature was 0°C, than when it was −0.9°C or 1.0°C. The greatest range of divergence was detected in animals which were collected at a field temperature of 0.75°C. There were twice as many positive as there were negative divergences for animals collected below 0°C. This indicates that the respiration rates measured for these animals were more frequently lower than expected rates from the overall regression line. The converse was true for animals collected at field temperatures above 0°C. However, at 10°C no such pattern emerged from the results, although this may be partly due to the lack of data for animals collected at temperatures higher than the experimental one. For both experimental temperatures, no significant effect of field collection temperature on respiration rate of size class V animals could be detected by multiple regression analysis. Therefore, these preliminary observations merely suggest that the field collection temperature may influence the measured respiration rate in these animals.

3.3. Respiration rate and sex

It is not known precisely when, in the life cycle, the genital characters develop, but from the extensive collections of *C. antarcticus* from Signy Island, it was possible to distinguish the sex of some size class II animals. It is important to remember that the animals have been grouped according to size rather than age or developmental stage. Whilst acceptable for the computation of population metabolism, this method makes analysis of the respiration data on the basis of sex very difficult. The arbitrary size class groupings will mask any tendency for individuals of one sex to be heavier than those of the other at the same age. Consequently, the sex ratio of size class IV individuals from the present respiration experiments is 1:1.0. It is known that the female grows to a larger size than the male in this species (Tilbrook 1970), and this feature accounts for the sex ratio of 1:2.72 for size class V individuals.

Comparing the respiration rates of each sex for animals of the same size (i.e. within size classes III and IV) there is no significant difference. In size class V, with females consistently and significantly heavier than males probably due to egg production, it was expected that at all experimental temperatures a significant difference in respiration rate would be found. This is not apparent from the present data. Healey (1966) reported indications of a difference in respiratory level between the sexes of *Onychiurus procampatus*, but he gave no data. More information is required, particularly on a seasonal and developmental basis, before a definitive statement can be made on the influence of sex on respiration rate in *C. antarcticus*, but it would seem from the present study that it has little effect.

3.4. Respiration rate of eggs

The mean respiratory rate per egg was 0.306 ± 0.031 μl $\times 10^{-3} O_2$ h^{-1} for *C. antarcticus*. This is approximately 1/5 of the respiration rate for a size class I animal and 1/46 of the rate of a size class V individual at the same temperature. No published data exists on the respiration of collembolan eggs.

4. Discussion

In this discussion only Collembola will be considered in detail. The other common soil micro-arthropod group, the Acari, will be mentioned only briefly as there is a current lack of respiratory data on Antarctic species and because many Acari have a large proportion of the

body weight (in the Cryptostigmata, 45–80%) taken up by metabolically inert exoskeleton.

4.1. Comparison with other Antarctic Collembola

The results presented in this paper are the most comprehensive available on collembolan respiration in the Antarctic. Some preliminary data are reported by Strong et al. (1970) for *I. klovstadi* from CapeHallett Station, Victoria Land; and by Dunkle and Strong (1972) for *C. antarcticus* at Palmer Station, Antarctic Peninsula (Tab. 5). In both cases, measurements were made with an electrolytic respirometer sensitive to 0.01 µl O_2 uptake (after Heusner 1970). Both studies included only adult individuals and these were bulked in groups of 10.

It is difficult to make precise comparisons between the respiration rates of *C. antarcticus* and *I. klovstadi* because of the paucity of data for the latter species. However, with a similar adult live weight (up to 100 µg), its weight specific respiratory rate at −4°C is approximately four times greater than the mean of size classes IV and V for *C. antarcticus* at 0°C at Signy Island. The maximum metabolic rate of *I. klovstadi* was found at 18°C, with a reduction in rate at 20°C. No such decrease in rate was recorded for *C. antarcticus* by Dunkle and Strong (1972) though the rate of increase dropped considerably above 15°C.

A comparison of the two sets of data for *C. antarcticus* from Signy Island and Palmer Station (Tab. 5) shows that only at 0°C is there good agreement. At Signy Island, the mean respiration rate for size classes IV and V at 0°C is 102.88 µl O_2 g^{-1} h^{-1} compared with 12 µl O_2 g^{-1} h^{-1} at the same temperature for adults from Palmer Station. At 5° and 10°C the Signy Island values are considerably lower than those measured at Palmer Station. However, the animals measured at Palmer Station, referred to as adults, are stated to have an average live weight of 260 µg which is more than twice as heavy as the size class V individuals from Signy Island. Although this species has a variable size range throughout its geographical distribution (Tilbrook 1970), it is known from collections made in the vicinity of Palmer Station (Tilbrook 1967a, b), that the largest individuals in this area fall within the Signy Island size class V. These weight differences may partly account for the different respiratory rates in the two studies.

4.2. Comparison of field and cultured specimens of C. antarcticus

A comparison of the respiratory data obtained from fresh animals collected from the field at Signy Island, and from animals returned to the U.K. in culture at constant temperature and subsequently measured at Leicester University (Tilbrook and Block 1972) may indicate the effects of constant temperature upon metabolism of *C. antarcticus*. Furthermore, this will have implications for future physiological work on cultured Collembola from Antarctica.

Results from field and cultured animals are compared on the basis of mean weight specific respiratory rate for each size class against live weight, plotted on a double logarithmic scale (Fig. 4). There is good agreement between the slope and position of the lines for 2°C cultured individuals and 0°C field animals. At 5° and 6°, and 10°C however, both position and slope differ markedly. Fig. 5 shows the respiratory data for field and cultured animals plotted on an individual rate basis against temperature. Rates are similar at the lower end of the temperature range studied, but with increasing temperature, field animals show a general divergence of response between size classes, whereas the rates from cultured individuals converge. The main cause of this feature is the very small increase in respiration rate with temperature shown by field animals of size classes I, II and III compared with cultured animals.

Tab. 5. Comparison of the respiration rates of Antarctic and Alpine Collembola.

Species	°C	Mean respiration rate µl O_2 g^{-1} h^{-1}		Reference
Cryptopygus antarcticus	0	112		Dunkle and Strong (1972)
	5	462		
	10	1544		
	15	2217		
	20	2306		
		Mean	Range	
Cryptopygus antarcticus	0	115.112	(223.3–95.6)	Present study
	5	269.240	(469.2–150.9)	
	10	324.180	(444.3–243.7)	
Protoma klovstadi	−4	400		Strong et al. (1970)
	18	4500		
	22	1100		
Protoma saltans	−2	111		Zinkler (1966)
	3	227		
Protoma hiemalis	−2	115		Zinkler (1966)
	3	201		
	8	401		

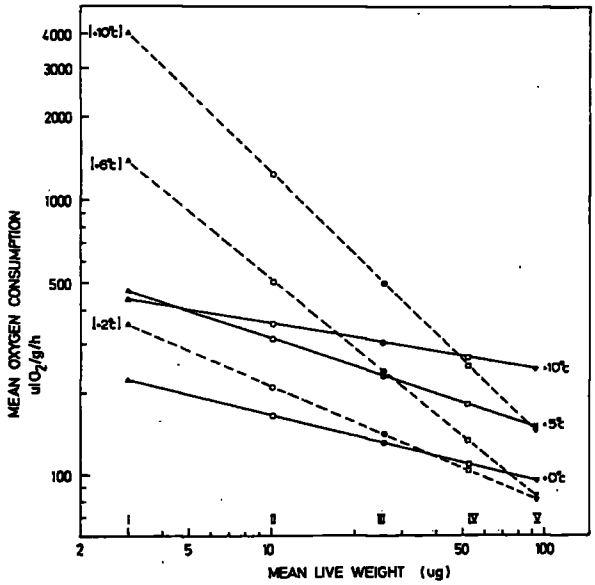

Fig. 4. Comparison of the relation between mean oxygen consumption (μl O_2 g^{-1} h^{-1}) and mean live wt (μg) for field (—) and cultured (---) individuals of *Cryptopygus antarcticus*. Data are plotted on a double $\log_{10}$ scale. △ = size class I, ○ = size class II, ● = size class III, □ = size class IV, and ▽ = size class V.

From these data it is concluded that juvenile *C. antarcticus* are most affected by long-term culture under the conditions adopted (temperature of 5 ± 1.0°C, with a 7 d period for acclimation at a new temperature before respirometric determinations were made). Once again, the limitations of the earlier work, in terms of reliability of data for the smaller size classes, should be stressed. Nevertheless, this comparison suggests that there is a significant difference between respiration data obtained from cultured and fresh animals, and it further stresses the desirability of working with fresh material or, at least, of knowing precisely the thermal history of the experimental animals so that these effects can be taken into account.

4.3. Comparison with temperate species of Collembola

There is a paucity of respiratory data for temperate collembolan species. Healey (1966), working with *O. procampatus*, reported that at 15°C the juvenile (10 μg live weight) respiration rate was 1/3 that of the adult (100 μg live weight) rate, which was 32 μl × 10^{-3} O_2 ind^{-1} h^{-1}. The adult rate for *O. procampatus* is very similar to that calculated using a Q_{10} of 2.54 (Tab. 4) for adult *C. antarcticus* at 15°C (35.585 μl × 10^{-3} O_2 ind^{-1} h^{-1}). The juvenile rates of the two species, however, are different. That calculated for *C. antarcticus* using a Q_{10} of 1.99 is 2.805 μl × 10^{-3} O_2 ind^{-1} h^{-1}, which is much lower than *O. procampatus* at the same temperature.

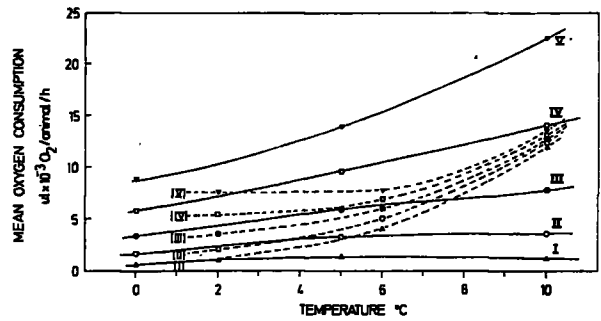

Fig. 5. Comparison of the relation between mean oxygen consumption (μl × 10^{-3} O_2 ind^{-1} h^{-1}) and temperature (°C) for field (—) and cultured (---) individuals of *Cryptopygus antarcticus*. Data are plotted for each of the 5 size classes.

The most relevant contribution on respiratory rates of temperate Collembola is undoubtedly that of Zinkler (1966). Amongst the 13 species which he studied were 2 cold stenothermal forms: *I. saltans* – the "glacier flea", which is deep black-blue in colour and inhabits snow and ice-covered areas in the Austrian Alps; and *I. hiemalis*, which is most active on old snow layers in spring in the Harz Mountains. *I. saltans* approximates most closely to *C. antarcticus*, the adults being 1.9 mm in length and 83–89 μg in live weight. *I. hiemalis* is much larger (2.0–2.5 mm in length) and heavier (200–230 μg live wt).

Zinkler's respiration measurements were made on groups of 10–13 animals with a Warburg respirometer at 3 temperatures (−2°, 3°, and 8°C) related to field habitat conditions. The weight specific respiratory rates for these 2 species are compared with the available data for Antarctic springtails in Tab. 5. Compared to the Signy Island data for *C. antarcticus*, both the *I. saltans* and *I. hiemalis* respiratory rates are of the same order of magnitude, taking into account the slightly different temperatures of measurement.

4.4. Cold adaptation in C. antarcticus

The present study has shown that individuals of *C. antarcticus* have measurable respiration rates at 0°C. Results of respirometric determinations below 0° have been given for *I. saltans* and *I. hiemalis* at −2° (Zinkler 1966) and for *I. klovstadi* at −4°C (Strong et al. 1970). There is evidence, therefore, that stenothermal springtails are metabolically active at very low temperatures. Observations on the activity of individual *C. antarcticus* in a cold cell with a stereo-microscope showed that this species exhibits locomotory activity below 0°C, and it can withstand temperatures at least as low as −23°C (Tilbrook 1970). The extreme low winter temperature in some of its habitats on Signy Island is approximately −25°C. Janetschek (1967) reports that in *Gomphiocephalus hodgsoni* Carpenter from South Victoria Land, cold death occurs between −20

and −28°C. As with most invertebrates, however, the point at which cold stupor occurs in this species is probably dependant on the speed of cooling. *I. klovstadi* in North Victoria Land, is very resistant to low temperatures (Pryor 1962). Adults survived for one month at −16°C, and cold death occurred between −50° and −60°C, temperatures which are not usually encountered in their soil micro-habitats.

No respiratory data have been published for temperate Collembola species at 0°C, but by comparison with the data of 13 species considered by Zinkler (1966), *C. antarcticus* generally has a higher metabolic rate at lower temperatures, which suggests some degree of cold adaptation. Temperate exceptions are the 2 alpine-montane species whose rates have already been shown to be similar to those found for *C. antarcticus* at 0° and 5°C. It is perhaps surprising that metabolic rates of the Antarctic *C. antarcticus* and the alpine *I. saltans* and *I. hiemalis* do not differ more than they do, considering the more severe environmental temperatures of Signy Island. The alpine species are subjected to a much wider annual temperature range with particularly high summer temperatures.

The smaller soil arthropods, chiefly Collembola and Acari, appear to be little affected by severe cold. They have been reported to overwinter in all life stages in polar and tundra habitats (Agrell 1941, Hammer 1944, Block 1965, 1966, Tilbrook 1967b). Populations of larger soil arthropods often suffer heavy winter mortality, e.g. Coleoptera (Bro Larsen 1944), and Tipulidae Coulson 1962). For overwintering Collembola, soil moisture must be important, as they will be inactivated in wet soil when it freezes, whereas in dry soil, Collembola may be able to remain active in the air spaces if they are cold resistant. In such micro-habitats under these temperature conditions, relative humidity will be much reduced, but so also will evaporation from the cuticle surface, so Collembola may well not suffer undue desiccation.

For *C. antarcticus*, the crucial periods of the year are probably the beginning and end of the Antarctic summer. At the start of this period large volumes of free water from melting snow and ice may often flood their habitats. This may be partly the cause of the raft-like aggregations of thousands of individuals of this species, which can be seen on fresh water pools during the summer months in the Maritime Antarctic. Flooding of some habitats may result in a much reduced oxygen tension. The effect of this on metabolic rate is largely unknown, although Zinkler (1966) found that *Tetracentophora bielanensis* (Waga) can withstand oxygen concentrations down to 6% before showing any reduction in respiratory rate. *I. saltans* showed greatest sensitivity to increased CO_2 concentrations (5%) when compared with several other species. This can be explained by the fact that this species lives in snow and ice conditions which strongly absorb CO_2 gas for most of the year, and hence it exhibits a high degree of sensitivity to this gas. Similar physiological adaptations may occur in Antarctic springtails which inhabit cold environments.

At the onset of the austral winter, *C. antarcticus* again experiences severe environmental conditions, especially temperature, in its habitat. High winds blow off freshly deposited snow from the substrate surface, thereby exposing organisms in the upper layers to the lowered temperatures prevalent at this time (−15° to −20°C). Once a snow cover is established, the moss turf is insulated and temperature fluctuations are reduced, and do not show the extreme minima of the air temperature. During 1962/63 at Signy Island, Tilbrook (1967b) studied the physical environment of 3 adjoining plant communities where *C. antarcticus* was the dominant microarthropod. The 3 communities were described as a lichen encrusted moss zone, a *Polytrichum – Dicranum* (now *Chorisodontium*) zone and a *Pohlia* zone. He observed that snow depths varied from 20 to 80 cm on the 3 zones, and the lowest temperature recorded (−10°C) was in the lichen encrusted zone, which had the thinnest snow cover (approx. 5 cm) in July 1962. It was evident, therefore, that at this site *C. antarcticus* was not normally subject to field temperatures which cause cold death.

O. procampatus continued to grow and breed in frozen soil under snow cover on a moorland site in Britain during an extremely cold winter (1962/63) (Healey 1967b). There was a significant increase in population density between December and January. In this species, feeding and defaecation were observed in culture at temperatures down to −4°C, and activity was maintained to −6°C, provided the temperature decline was 1°C or less per day. A sudden cooling led to inactivation at 5°C. This suggests that in temperate Collembola, at least, a period of acclimation is required to produce cold resistance, and inactivation may be caused by a sudden sharp frost. Studies of *C. antarcticus* are now required to determine if a similar system operates in a springtail exposed to a more extreme cold stenothermic environment.

4.5. Population metabolism of C. antarcticus

Preliminary estimates have been made of the total population metabolism of *C. antarcticus* from the data given in this paper. Lacking a detailed knowledge of the size class structure of the population at the Signy Island site, only crude estimates can be made. Certain limitations have been imposed. The calculation of metabolism has been restricted to the summer months, and a mean habitat temperature of 3°C has been used to represent this period.

The mean summer (November 1962 – March 1963 inclusive) population of *C. antarcticus* for the Signy Island site with 3 contrasting plant communities (Tilbrook 1967b) was 15218 m^{-2}. Using this mean summer population figure, 2 estimates of population metabolism

have been made using the mean respiration rates per individual at 5° C (from Tab. 3) for size classes I and V. This gives estimates of the maximum and minimum levels of population respiration, assuming the population to be composed of one or the other of these size classes. The calculated values range from 15.449 to 153.507 ml O_2 m^{-2} summer month.

There are very few estimates of population metabolism for Collembola, but Healey (1966) gave a range of from 10 to 129 ml O_2 m^{-2} $month^{-1}$ for *O. procampatus* living in *Pteridium* moorland in South Wales, UK. The range is very similar to that for *C. antarcticus* although Healey's values were calculated from population data covering a complete year. The total population metabolism for *C. antarcticus* at Signy Island for the 5 month summer period is calculated to be in the region of 77.246 to 767.535 ml O_2 m^{-2}. Assuming that these summer values will approximate to the total annual population respiration, due to very low respiratory rates at mostly sub-zero winter temperatures, they compare favourably with the total annual population respiration of 548 ml O_2 m^{-2} computed for *O. procampatus*. On the basis of 4.8 cal ml^{-1} O_2 these totals become

C. antarcticus	0.371 to 3.684 kcal m^{-2} yr^{-1}
O. procampatus	2.630 kcal m^{-2} yr^{-1}

Both these estimates are low compared with the data available for the total annual population metabolism of all Collembola in a site. Healey calculated that *O. procampatus* contributed only 22% of the total Collembola respiration on his moorland site; the total being 12.0 kcal m^{-2} yr^{-1}.

For temperate woodland Collembola, Bornebusch (1930) provided data which, when recalculated by Macfadyen (1963), showed a range of 45.8–168.0 kcal m^{-2} yr^{-1}. For Pennine moorland Collembola populations, values of 4.1–15.1 kcal m^{-2} yr^{-1} were calculated by Macfadyen from data given in Cragg (1961). In a grazed meadow ecosystem, total Collembola metabolism was estimated to be 152.6 kcal m^{-2} yr^{-1} (Macfadyen 1964). In general, therefore, the very crude estimates of annual population metabolism for *C. antarcticus* at Signy Island are extremely small compared to the other available data. However, as *C. antarcticus* is numerically the dominant arthropod on the Signy Island site studied, the figures probably represent the maximum level of energy utilisation in metabolic activity by a secondary producer on this type of site under Maritime Antarctic conditions.

It has been shown that factors such as live weight and temperature have an appreciable influence on the respiration of the Antarctic collembole, *C. antarcticus*. Because of these effects, precise measurements of oxygen consumption on individual, and preferably fresh animals, under controlled conditions must be used for the determination of the production of these small arthropods.

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References

AGRELL, I. 1941. Zur Ökologie der Collembolen. Untersuchungen im Schwedisch Lappland. – Opusc. ent. Suppl. 3: 1–236.

BERTHET, P. 1964. L'activité des Oribatides (Acari: Oribatei) d'une Chênaie. – Mém. Inst. r. Sci. nat. Belg. 152: 1–152.

BLOCK, W. 1965. The life histories of *Platynothrus peltifer* (Koch 1839) and *Damaeus clavipes* (Hermann 1804) (Acarina: Cryptostigmata) in soils of Pennine moorland. – Acarologia 7: 735–743.

– 1966. Seasonal fluctuations and distribution of mite populations in moorland soils, with a note on biomass. – J. Anim. Ecol. 35: 487–503.

BORNEBUSCH, C. H. 1930. The fauna of forest soil. – Forst. ForsVaes. Danm. 11: 1–256.

BRO LARSEN, E. 1944. The influence of the severe winter of 1939–42 on the soil fauna of Tipperne. – Oikos 1: 184–207.

CHAMBERS, M. J. G. 1966. Investigations of patterned ground at Signy Island, South Orkney Islands: II. Temperature regimes in the active layer. – Bull. Br. Antarct. Surv. 10: 71–83.

COULSON, J. C. 1962. The biology of *Tipula subnodicornis* Zetterstedt, with comparative observations on *Tipula paludosa* Meigen. – J. Anim. Ecol. 31: 1–21.

CRAGG, J. B. 1961. Some aspects of the ecology of moorland animals. – J. Anim. Ecol. 30: 205–234.

DUNKLE, R. and STRONG, F. 1972. A digital electrolytic micro-respirometer. – Ann. ent. Soc. Am. 65: 705–710.

EDWARDS, G. A. 1953. Respiratory Metabolism. – In: Roeder, K. D. (ed.). Insect Physiology, Wiley, London.

HAMMER, M. 1944. Studies on the oribatids and Collembola of Greenland. – Meddr Grønland 141: 1–210.

HEALEY, I. N. 1966. The population metabolism of *Onychiurus procampatus* Gisin (Collembola). – In: Graff, O. and Satchell, J. E. (ed.). Progress in Soil Biology. North-Holland Publishing, Amsterdam.

– 1967a. The energy flow through a population of soil Collembola. – In: Petrusewicz, K. (ed.). Secondary Productivity of Terrestrial Ecosystems, Polish Academy of Sciences, Warsaw.

– 1967b. An ecological study of temperatures in a Welsh moorland soil, 1962–63. – J. Anim. Ecol. 36: 425–43.

– 1970. Long term numerical recording of very small oxygen consumptions under sterile conditions. – Respir. Physiol. 10: 132–150.

JANETSCHEK, H. 1967. Growth and maturity of the springtail, *Gomphiocephalus hodgsoni* Carpenter, from South Victoria Land and Ross Island. – Antarct. Res. Ser. 10: 295–305.

JØRGENSEN, N. R. 1916. Undersøgelse over Frequensflade og Korrelation. – Copenhagen.

KROGH, A. 1914. The quantitative relation between temperature and standard metabolism in animals. – Int. Z. phys.-chem. Biol. 1: 491–508.

LONGTON, R. E. and HOLDGATE, M. W. 1967. Temperatu

relationships of Antarctic vegetation. – Phil. Trans. R. Soc. B. 252: 237–250.
MACFADYEN, A. 1963. The contribution of the microfauna to total soil metabolism. – In: Doeksen, J. and van der Drift, J. (ed.). Soil organisms. North-Holland Publishing Amsterdam.
– 1964. Energy flow in ecosystems and its exploitation by grazing. – In: Crisp, D. J. (ed.). Grazing in terrestrial and marine environments, Blackwell, Oxford.
OSTLE, B. R. 1963. Statistics in research. – Iowa State University Press, Iowa.
PRYOR, M. E. 1962. Some environmental features of Hallett Station, Antarctica, with special reference to soil arthropods. – Pacif. Insects 4: 681–728.
STRONG, F. E., DUNKLE, R. L. and DUNN, R. L. 1970. Low-temperature physiology of Antarctic arthropods. – Antarct. J. US. 5: 123.
TILBROOK, P. J. 1967a. The terrestrial invertebrate fauna of the Maritime Antarctic. – Phil. Trans. R. Soc. B. 252: 261–278.
– 1967b. Arthropod ecology in the Maritime Antarctic. – Antarct. Res. Series 10: 331–356.
– 1970. The biology of *Cryptopygus antarcticus*. – In: Holdgate, M. W. (ed.). Antarctic ecology. Academic Press, London, Vol. 2.
– 1973. The Signy Island terrestrial reference sites: I. An introduction. – Bull. Br. Antarct. Surv. 33 and 34: 65–76.
– and BLOCK, W. 1972. Oxygen uptake in an Antarctic collembole, *Cryptopygus antarcticus*. – Oikos 23: 313–317.
WEBB, N. R. 1969. Temperature and respiratory metabolism in a species of soil mite. – In: Evans, G. O. (ed.). Proceedings of 2nd International Congress of Acarology. Hungarian Academy of Sciences, Budapest.
WILLEM, V. 1902. Collemboles. – In: Rapports Scientifiques de la Commission de la Belgique; Zoologie: Expedition Antarctique Belge, Resultats du voyage du S. Y. Belgica en 1897: 98–99.
ZEUTHEN, E. 1964. Microgasometric methods: Cartesian Divers. – In: Schiebler, T. H., Pearse, A. G. E. and Wolff, H. H. (ed.). 2nd International Congress of Histo- and Cyto-Chemistry. Wiley, New York.
ZINKLER, D. 1966. Vergleichende untersuchungen zur atmungsphysiologie von Collembolen (Apterygota) und anderen Bodenkleinarthropoden. – Z. vergl. Physiol. 52: 99–144.

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OXYGEN CONSUMPTION OF THE TERRESTRIAL MITE *ALASKOZETES ANTARCTICUS* (ACARI: CRYPTOSTIGMATA)

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SUMMARY

Analysis of 148 measurements of individual respiration rate showed that although respiration was linearly related to live weight on a double $\log_{10}$ scale, there were significant differences between rates at 0°, +5° and +10 °C. Proto- and deutonymphal metabolic rates were higher than other stages, especially at +10 °C. Q_{10} values ranged from 2·07 to 3·83 over 0° to +10 °C. Equations relating individual respiratory rate to live weight and temperature for *A. antarcticus*, and metabolic rate to temperature for 10 species of Antarctic terrestrial invertebrates were developed. Comparison with temperate data indicated considerable cold adaptation in the Antarctic species with 3–5 times increased metabolism. It was calculated that 78–82% of the energy assimilated may be used in respiration by *A. antarcticus*.

INTRODUCTION

The maritime Antarctic affords a unique opportunity for the environmental physiologist to study the effects of low temperatures on terrestrial arthropods. The terrestrial arthropods there consist almost entirely of Acari and Collembola, and although respiration rates have been measured for the collembolan, *Cryptopygus antarcticus* Willem (Tilbrook & Block, 1972; Block & Tilbrook, 1975), there is little information on the physiology of the terrestrial mites. Accordingly, the present study of oxygen consumption of a common cryptostigmatid mite was undertaken at Signy Island, South Orkney Islands, during the southern summer in 1971–2.

Alaskozetes antarcticus (Michael) of the family Podacaridae is endemic to the Antarctic and Sub-Antarctic regions, and is one of the most southern over-wintering land animals at almost 78° latitude (Wallwork, 1967). There are two distinct subspecies: *A. antarcticus antarcticus* and *A. antarcticus intermedius*. This study was concentrated on the former subspecies, which is widely distributed throughout the Antarctic Peninsula area. The habitats of *A. antarcticus* are varied, from inter-tidal debris, penguin guano, seal wallows, and bird nests to the undersides of loose rocks, bones, crustose lichens and algae, especially *Prasiola crispa* (Lightf.) Menegh.

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(Gressitt, 1967; Strong, 1967; Tilbrook, 1967; Wallwork, 1973). It occurs often in dense aggregations which may include all stages from egg to adult. Aggregations are present throughout the year, and development, moulting and maturation occur within them. *A. antarcticus* is a scavenger feeding on detritus, mostly of vertebrate origin. It is one of the largest Antarctic terrestrial arthropods, but the adult is only *ca.* 1 mm in body length, and all stages are slow moving.

The objectives of the present study were to investigate the influence of body weight and temperature upon the oxygen consumption of a range of individual mites representing the post-embryonic life stages of *A. antarcticus*. In addition, data were collected on the variations in metabolism due to sex and breeding condition of the adult. This project was complementary to a long-term ecosystem research programme of two terrestrial sites at Signy Island, which is being undertaken by the British Antarctic Survey (Tilbrook, 1973).

METHODS

Great care was taken to ensure that collected animals were maintained and studied at temperatures representative of their summer habitat conditions (December–March).

Samples of live mites for respirometry were collected daily by hand from habitats close to the B.A.S. Research Station on Signy Island. Field temperatures were measured at the time of collection by a Grant Model S thermistor thermometer. The experimental temperatures were 0°, +5° and +10 °C, and as far as possible the measurements of oxygen uptake were made within 5° of the field temperature. Once collected, the mites were handled entirely in a cold room at the experimental temperature. The mites were sorted and identified to their various life stages under a ×16 stereomicroscope and then weighed individually on a Beckmann electromicrobalance (LM 500) sensitive to 0·1 μg. The micro-respirometer used was a Cartesian Diver (Linderstrøm-Lang, 1943; Holter, 1943), and stoppered divers were utilized (Zeuthen, 1964) with gas volumes in the range 1·90–33·25 μl. The respirometer had a capacity for 14 measurements at one time, and was also in the controlled temperature room. The respirometer water-bath temperature was controlled to ±0·01 °C.

Mites were placed singly in the divers, and at least 30 min was allowed for equilibration after loading into the respirometer. Respiratory measurements were made over 5–6 h, and the individual activity of the mite was recorded. Following this the animals were removed, killed in 75% ethyl alcohol, mounted in 80% lactic acid on slides and examined. Confirmation of life stage by the setation of the anal and genital areas in the adults, and the genital papillae in the juveniles (Wallwork, 1962) was then made, along with observations on sex, egg number, and gut contents. Calculations of individual and weight-specific oxygen consumption rates of *A. antarcticus* were as described for *C. antarcticus* in Block & Tilbrook (1975), except that individual live-weight measurements, rather than estimated values, were used for the weight-specific rates.

RESULTS

Oxygen consumption and live weight

The mean individual live weights of each life stage of *A. antarcticus*, which were calculated from the material used for the respirometric measurements, are given in

Table 1. *Mean live weights* (μg) *of individuals of each life stage of* Alaskozetes antarcticus *used for respiratory measurements at Signy Island. The mean weight* ± S.E. *and the number of individuals* (n) *weighed are also given. Significant differences between the mean weights of life stages are indicated below* (*NS: not significant*)

Life stage	Mean live weight ± S.E. (μg)	*n*
Larva	13·29 ± 0·73	34
Protonymph	25·99 ± 1·10	30
Deutonymph	46·08 ± 2·43	47
Tritonymph	126·65 ± 6·04	28
Adult male	156·97 ± 4·94	40
Adult female (gravid and non-gravid)	187·67 ± 8·75	33
Adult female (gravid)	196·21 ± 10·99	23
Adult female (non-gravid)	168·02 ± 12·56	10

Significance: Larva – protonymph, NS; Protonymph – deutonymph, $P < 0{\cdot}001$; Deutonymph – tritonymph, $P < 0{\cdot}001$; Tritonymph – adult male, NS; Tritonymph – adult female (gravid and non-gravid), $P < 0{\cdot}01$; Adult male – adult female (gravid), $P < 0{\cdot}01$; Adult male – adult female (non-gravid), NS.

Table 1. There was a steady live-weight increase from the larval to the deutonymphal stage, each being approximately double the weight of the previous stage. The largest weight increase (almost 3 ×) occurred between the deuto- and the tritonymph. The adult female was significantly heavier (mean live weight of both gravid and non-gravid individuals) than the tritonymph ($P < 0{\cdot}01$).

Both gravid and non-gravid females separately were generally heavier than the males, and the mean weight of the combined gravid and non-gravid females was significantly different ($P < 0{\cdot}01$) from the male. Within each life stage, there were no significant differences in live weight of material used at each temperature.

$\log_{10}$ oxygen consumption rate ($\times 10^{-3}$ μl O_2 ind^{-1} h^{-1}) was plotted against $\log_{10}$ live weight (μg) for each animal measured at each of the three experimental temperatures (Fig. 1). Linear regressions were fitted to these data, and the resulting equations and correlation coefficients are shown in Table 2. There was a steady increase in respiration rate with increasing live weight at each temperature. The regression lines for +5° and +10 °C were almost parallel, indicating that the relationship of $\log_{10}$ oxygen consumption to $\log_{10}$ live weight was similar at these two temperatures. At 0 °C, however, the regression line diverged from those of +5° and +10 °C over the upper portion.

To investigate this further, the homogeneity of the three regressions was examined using the method of Ostle (1963). This tests whether the combined data can be represented by a single regression line. The overall regression equation for respiration rate ($\dot{V}_{O_2}$) on live weight (W) for the three temperatures combined was $\log_{10} \dot{V}_{O_2} = 0{\cdot}9500 \log_{10} W - 0{\cdot}7791$. The analysis and variance ratio tests (Table 3) showed that the three lines were not homogeneous ($P < 0{\cdot}001$) and could not be represented by a single regression. However, the slopes of the lines were not significantly different, and the failure of the overall regression equation resulted from between-temperature differences. Further, the mean respiration rate at each temperature ($P < 0{\cdot}01$) and the within and between temperature slopes ($P < 0{\cdot}001$) were significantly different. Therefore, the relationship of respiration to weight in *A. antarcticus* was similar at the

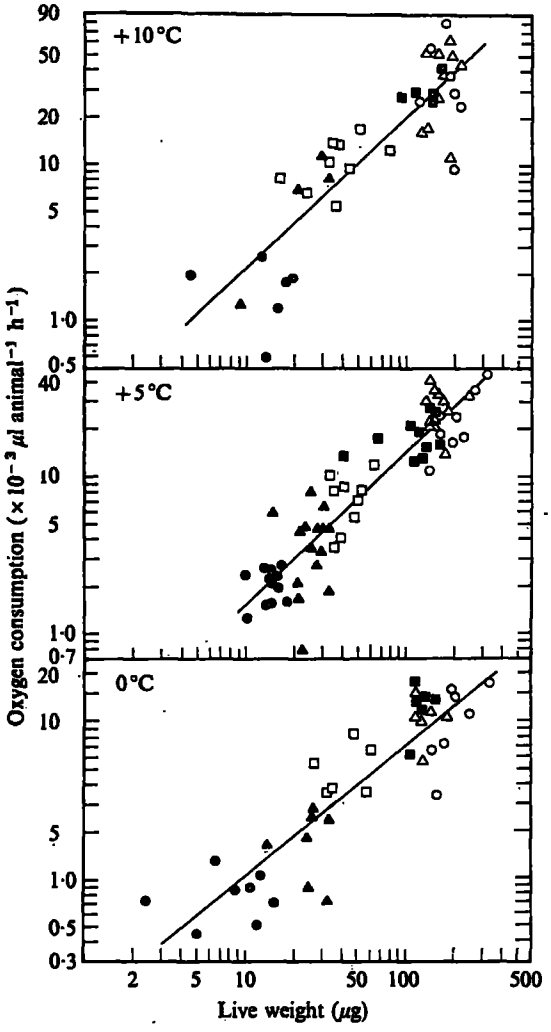

Fig. 1. Oxygen consumption as a function of live weight at 0°, +5° and +10 °C for *Alaskozetes antarcticus*. Data are plotted on $\log_{10}$ scales, and individual measurements with the fitted linear regression line are shown for each temperature. ●, Larva; ▲, protonymph; □, deutonymph; ■, tritonymph; △, adult male; ○, adult female.

three temperatures, but significant differences in respiration rate were detected between temperatures.

Examination of the individual weight-specific respiration rates compared to live weight shows that there was only a very slight negative correlation (Table 2, Fig. 2). The correlation coefficients for each temperature were not significantly different from zero. Therefore weight-specific respiration rate was not correlated with live weight at these temperatures in *A. antarcticus*.

These results contrast with those for the Antarctic collembolan, *C. antarcticus*, reported by Block & Tilbrook (1975). For this species, the +5 °C regression line of individual respiration rate against live weight was significantly different from those of 0° and +10 °C. It was concluded that the smaller, immature individuals had a

Table 2. *Linear regression equations of oxygen consumption* ($\log_{10}$y) *on live weight* ($\log_{10}$x: μg) *for* Alaskozetes antarcticus *at* 0°, +5° *and* +10 °C. *The number of determinations* (n) *and the correlation coefficient* (r) (P < 0·001 *throughout*) *are also given*

Temperature (°C)	*n*	*a*	*b* ± S.E.	*r*
× 10^{-3} μl O_2 ind^{-1} h^{-1}				
0	40	−0·811	+0·830 ± 0·068	+0·893
+5	66	−0·789	+0·971 ± 0·052	+0·919
+10	42	−0·642	+0·976 ± 0·089	+0·866
μl O_2 g^{-1} live wt h^{-1}				
0	40	+2·188	−0·169 ± 0·068	−0·375
+5	66	+2·211	−0·029 ± 0·052	−0·070
+10	42	+2·358	−0·024 ± 0·089	−0·042

Table 3. *Summary of tests for homogeneity of linear regressions of* $\log_{10}$ *oxygen consumption* (y: × 10^{-3} μl O_2 ind^{-1} h^{-1}, *on* $\log_{10}$ *live weight* (x: μg) *for* Alaskozetes antarcticus (D.F. = *degrees of freedom;* S.S. = *sum of squares;* M.S. = *mean of squares*)

Source of variation	D.F.		Residuals S.S	Residuals D.F.	Residuals M.S.
Temperature (°C)					
0	39		1·9713	38	0·0518
+5	65		2·2328	64	0·0348
+10	41		2·8426	40	0·0710
Sum of residuals:	—	S_1 =	7·0468	142	0·0496
Within temperatures	145		7·1973	144	0·0499
Increase in sum of residuals:	—	S_2 =	0·1505	2	0·0752
Between temperatures	2	S_3 =	0·3734	1	0·3734
Total	147	S_T =	10·9193	146	0·0747
	$S_T-(S_1+S_2+S_3)$ =	S_4 =	3·3485	1	3·3485

1. Test for homogeneity:
$$VR = ((S_T-S_1)/4)/(S_1/142) = 19{\cdot}5107;\ \text{D.F. } 4, 142;\ P < 0{\cdot}001.$$
2. Test for identity of slope within temperatures:
$$VR = (S_2/2)/(S_1/142) = 1{\cdot}5167;\ \text{D.F. } 2, 142;\ \text{NS}.$$
3. Test for linearity of temperature means:
$$VR = (S_3/1)/(S_1+S_2)/144 = 7{\cdot}4713;\ \text{D.F. } 1, 144;\ P < 0{\cdot}01.$$
4. Test for identity of within and between temperature slopes:
$$VR = (S_4/1)/(S_1+S_2)/144 = 66{\cdot}9953;\ \text{D.F. } 1, 144;\ P < 0{\cdot}001.$$

significantly higher metabolic rate at +5 °C, which may be a seasonal adaptation to summer temperatures in the region of +3° to +5 °C. *A. antarcticus* at 0 °C exhibited a different metabolism–weight relationship from that at +5° and +10 °C, but this was not significant. The metabolism of *A. antarcticus* in respect to live weight was not affected by a rise in temperature to +10 °C, which was above the summer norm.

Considering the weight exponent b in the relationship $\log_{10}\dot{V}_{O_2} = a+b\ \log_{10}W$ (where $\dot{V}_{O_2}$: respiration rate, and W: live weight) for *A. antarcticus* (Table 2,) b varied from 0·830 to 0·976 with a mean of 0·927 over the 10 °C temperature range. These values are generally higher than those found for terrestrial mites. Berthet (1964) determined that b = 0·72 for 16 species of temperate oribatids, and gave a range of b values: 1·372 (0 °C), 0·123 (+5 °C), 0·459 (+10 °C) and 0·722 (+15 °C) for the adult

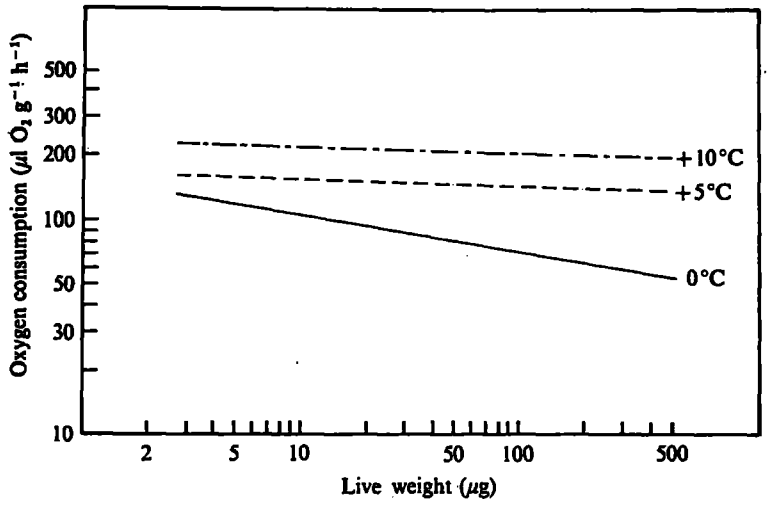

Fig. 2. Weight-specific oxygen consumption as a function of live weight at 0°, +5° and +10 °C for *Alaskozetes antarcticus*. Log_{10} scales are used, and the linear regression line calculated on individual measurements is shown for each temperature.

mite *Steganacarus magnus* Nicolet. The coefficients of the slope of the lines at +10 °C and +15 °C did not differ significantly, and both these groups taken together gave a value of 0·630. These results were partially explained by Berthet in that the correlation coefficient between log_{10} oxygen consumption and log_{10} live weight was highly significant at all temperatures except + 5 °C, and also that the variability of oxygen uptake determinations was greatest at 0 °C, presumably due to decreased sensitivity of the diver. For four species of phthiracarid mites, comprising 44 individuals (mostly adults), Wood & Lawton (1973) determined a weight exponent b of 0·539 at +10 °C. In three oribatid species (all life stages) the value of b ranged from 0·511 to 0·697. For a further 12 species of Cryptostigmata covering 92 individual adults, b was 0·572 at the same temperature. They considered that, after weight, activity was the most important factor influencing mite respiration. However, the results for *A. antarcticus* were obtained on resting animals and the effect of activity on metabolism can largely be excluded. Webb (1975) calculated a mean b value of 0·686 for all life stages of *S. magnus* at +18 °C. He concluded also that two regression lines adequately represented the relationship between respiratory rate and live weight: one for adults ($\ln \dot{V}_{O_2} = 0{\cdot}909 \ln W - 1{\cdot}819$) and another for juveniles ($\ln V_{O_2} = 0{\cdot}561 \ln W - 0{\cdot}201$). Weight therefore, has a major influence upon metabolism of the micro-arthropods studied, but it is not a constant effect either within or between species at differing temperatures within their normal range. This may be due to the varying degree of chitinization of the exoskeleton between individuals and species. Amongst the mites and Collembola, *A. antarcticus* has the largest weight exponents so far determined.

Oxygen consumption during development

In order to examine differences in oxygen uptake between individual life stages of *A. antarcticus* more closely, the mean respiration rates for each stage at each temperature (Table 4) were calculated from the individual data in Fig. 1. Mean oxygen consump-

Table 4. *Mean oxygen consumption rates of each life stage of* Alaskozetes antarcticus *at* 0°, +5° *and* +10 °C. *Mean data individual*$^{-1}$ *and g*$^{-1}$ *with the* S.E. *of the mean and the number of determinations* (n) *are shown*

Life stage	Oxygen consumption					
	0 °C		+5 °C		+10 °C	
× 10^{-3} µl O_2 ind^{-1} h^{-1}	(Mean ± S.E.)	*n*	(Mean ± S.E.)	*n*	(Mean ± S.E.)	*n*
Larva	0·819 ± 0·098	8	2·138 ± 0·128	12	2·853 ± 0·974	8
Protonymph	1·803 ± 0·296	7	3·922 ± 0·502	15	6·910 ± 2·087	4
Deutonymph	5·182 ± 0·790	6	7·473 ± 0·914	9	10·737 ± 1·119	10
Tritonymph	12·777 ± 1·580	6	17·967 ± 1·649	10	30·561 ± 2·754	5
Adult male	10·373 ± 1·200	6	27·905 ± 2·148	12	37·284 ± 5·790	10
Adult female	10·870 ± 2·015	7	23·765 ± 3·877	8	37·148 ± 8·985	7
µl O_2 g^{-1} h^{-1}						
Larva	120·721 ± 32·011	8	148·415 ± 11·775	12	159·904 ± 58·720	6
Protonymph	74·395 ± 13·395	7	158·134 ± 24·617	15	275·450 ± 52·724	4
Deutonymph	126·820 ± 20·976	6	172·203 ± 22·424	9	303·782 ± 33·775	10
Tritonymph	102·841 ± 13·131	6	171·522 ± 23·115	10	235·157 ± 21·803	5
Adult male	78·308 ± 11·495	6	175·003 ± 16·222	12	224·985 ± 34·301	10
Adult female	50·873 ± 7·419	7	109·969 ± 9·918	8	225·195 ± 57·383	7

tion per individual increased steadily with mean live weight of the juvenile stages at each temperature (Fig. 3*a*). The mean adult male respiration rate decreased slightly below the tritonymphal rate at 0 °C but increased above it at +5 °C, and also at +10 °C where it continued the juvenile trend. There was much more variability in the results for males at +10 °C than at +5° and 0 °C. A similar situation was seen for the mean female respiratory rate over the three experimental temperatures, except that at +5 °C the female rate continued the juvenile trend and did not increase as in the male.

Marked differences between the juvenile stages occurred in mean weight-specific respiration rates (Fig. 3*b*), both within and between temperatures. At 0 °C the mean protonymphal rate was depressed compared to both the larval and deutonymphal rates. Thereafter, there was a steady decrease in metabolic rate with increasing live weight, with the adult female having the lowest rate. At +5 °C there were no significant differences between the juvenile stages; but the adult male rate was distinctly increased compared to the female level. At +10 °C metabolic rate increased greatly from the larval to deutonymphal stage, thereafter a steady decline ensued, with no significant differences between the tritonymph and adult male and female. The results stress the considerable differences in oxygen consumption between the various life stages and these are further complicated by differing metabolic responses to the experimental temperatures.

There are few published data on respiration rates throughout development in terrestrial mites. In *Nothrus silvestris* Nicolet, the protonymphal stage had a high rate (213·1 µl O_2 g^{-1} h^{-1}) compared with other juvenile stages and adults (range 119·2–185·8 µl O_2 g^{-1} h^{-1}) at +10 °C (Webb, 1969). The deutonymphs of *Nothrus palustris* C. L. Koch and *Parachipteria willmanni* Hammer had significantly higher respiration rates than the protonymph at +10 °C (Wood & Lawton, 1973). Again, the deutonymphal metabolic rate of *S. magnus* at +18 °C was considerably higher than that of the other nymphal stages, but so also was larval metabolism (Webb, 1975). It seems that there are differences both between species and between temperatures in this respect

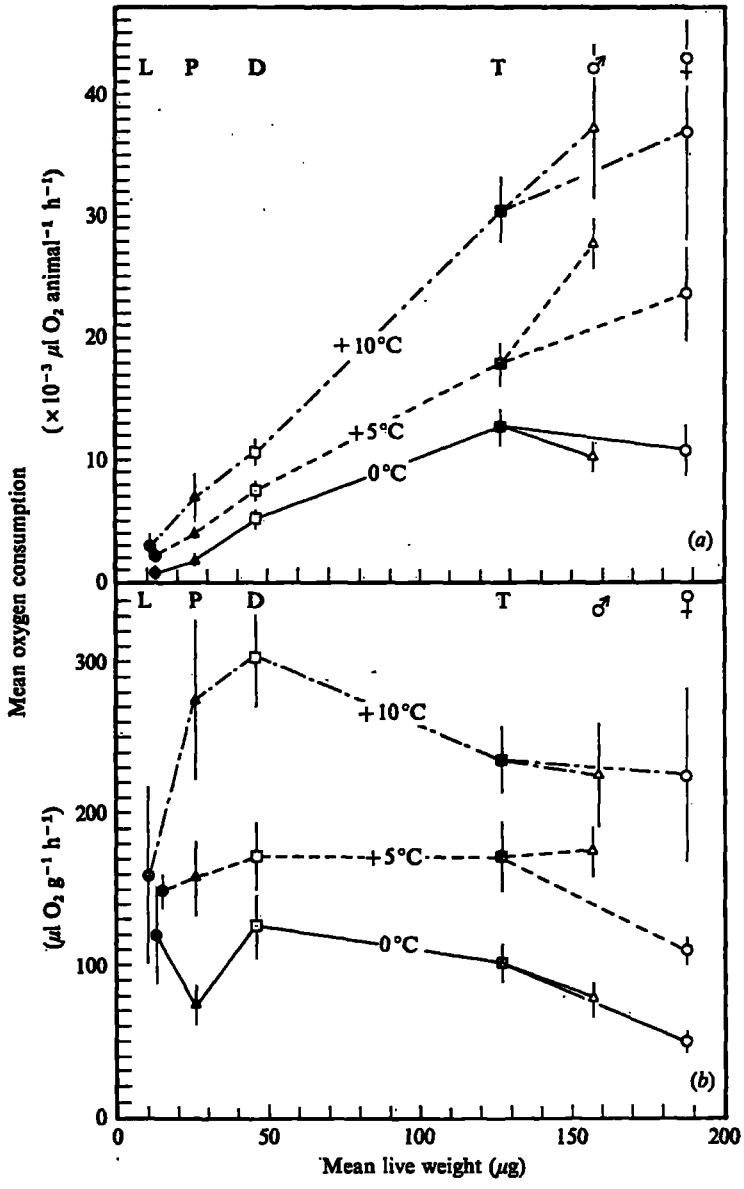

Fig. 3. Mean (±S.E.) oxygen consumption rate plotted against mean live weight for each life stage of *Alaskozetes antarcticus* at 0°, +5° and +10 °C. (*a*) Mean oxygen consumption per animal; (*b*) mean oxygen consumption per g live weight. ●, Larva; ▲, protonymph; □, deutonymph; ■, tritonymph; △, adult male; ○, adult female.

for the five mite species for which there are data. In *A. antarcticus* the proto- and deutonymphs show the greatest metabolic response at +10 °C.

The sex ratio of the weighed individuals (see Table 1) was 1 female:1·21 male. There were no significant differences in oxygen uptake per individual and per g for male and female *A. antarcticus* at each of the three temperatures studied. Further comparisons of the mean respiration rates of male and gravid female did not reveal any

Table 5. *Respiration rates individual*$^{-1}$ *and* g^{-1} *of gravid and non-gravid female* Alaskozetes antarcticus *at the three experimental temperatures. The mean* ± S.E. *and* (n) *are given*

Respiration rates	Temperature (°C)	Adult females	
		Gravid	Non-gravid
$\times 10^{-3}$ μl O_2 ind^{-1} h^{-1}	0	9·833 ± 2·645 (5)	13·462 ± 2·437 (2)
	+5	27·368 ± 5·368 (5)	17·759 ± 3·922 (3)
	+10	37·148 ± 8·984 (7)	Not measured
μl O_2 g^{-1} h^{-1}	0	46·185 ± 7·876 (5)	62·593 ± 18·528 (2)
	+5	108·832 ± 12·246 (5)	111·863 ± 20·379 (3)
	+10	225·195 ± 57·382 (7)	Not measured

differences. This was surprising in view of the fact that the female was heavier (Table 1) and a large proportion (77 %) of the females were carrying eggs. The mean number of eggs was 4·3 per gravid female, and it is interesting to note that gravid females only occurred in the samples from 27 January onwards. These results are similar to *C. antarcticus* (Block & Tilbrook, 1975), in which the effect of sex on respiratory rate was not detected at the same temperatures.

Table 5 shows a further breakdown of the respiration data for adult females into gravid and non-gravid components at each experimental temperature. No data were obtained for non-gravid female *A. antarcticus* at +10 °C, and thus the comparison is restricted to the two lower temperatures. The gravid female rate was higher than that of the non-gravid female at +5 °C on an individual basis, but a multiple regression analysis of oxygen consumption of the adult female on live weight and number of eggs and prelarvae failed to confirm this difference. For mean weight-specific oxygen uptake the gravid rate was lower than the non-gravid female at both 0° and +5 °C. Thus there was a slight reduction in metabolic rate due to an increase in the female weight component (Table 1).

In *N. silvestris*, Webb (1969) found that gravid females showed a 25 % increase in weight-specific oxygen uptake compared to non-breeding adults (non-gravid females and males). In *S. magnus* the egg content of the female was more important than live weight or number of prelarvae in its effect upon respiratory rate at +10 °C (Webb, 1975). Wood & Lawton (1973) studying a range of oribatid mites, recorded that in five out of seven species, the gravid female was heavier than the non-breeding adults (i.e. males and non-gravid females) and usually exhibited higher respiratory rates than these at +10 °C. However, significant differences were only established between individual rates for *Ceratoppia bipilis* (Hermann) and *S. magnus*, and between weight-specific rates for *Damaeus onustus* C. L. Koch and *S. magnus*. These trends are similar to those found in *A. antarcticus*.

Oxygen consumption and temperature

Fig. 4(*a*) shows the mean individual oxygen consumption plotted against temperature for each life stage of *A. antarcticus*. For all stages there is a steady increase of respiration rate with temperature over the experimental range. There is a separation into two groups in this respect: one consisting of larva, protonymph and deutonymph, and the other of tritonymph, adult male and female. This may be a reflexion of an

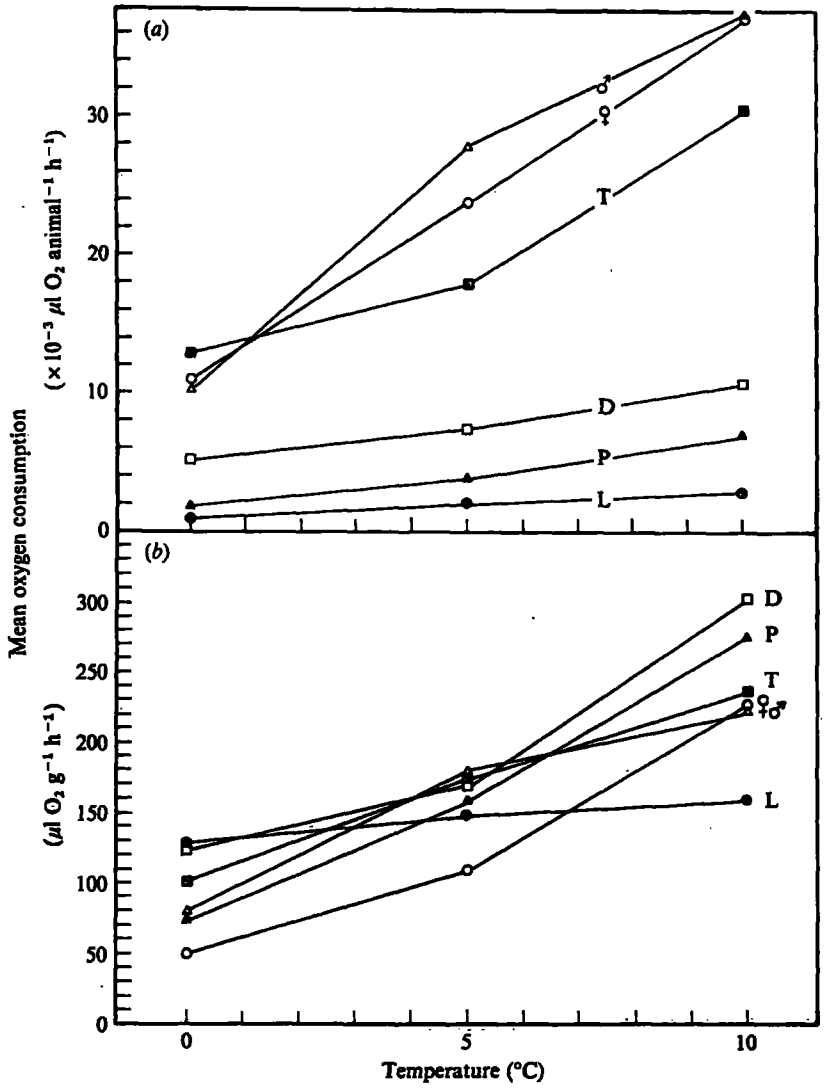

Fig. 4. Mean oxygen consumption rates of each life stage of *Alaskozetes antarcticus* as a function of temperature. (*a*) Mean oxygen consumption per animal; (*b*) mean oxygen consumption per g live weight. ●, Larva; ▲, protonymph; □, deutonymph; ■, tritonymph; △, adult male; ○, adult female.

increased individual metabolism from early in the tritonymphal instar, which occurred at all three temperatures, due to an increase in activity. The range of oxygen consumption values over all life stages is small at 0 °C, greatly increased at +5 °C, and largest at +10 °C. At +5° and +10 °C the order of increasing metabolism follows the developmental cycle, but at 0 °C, the tritonymph has a higher level than the adult male and female. At +5 °C the oxygen consumption of the male exceeds that of the female, whereas they are similar at 0° and +10 °C. A more uniform pattern for all stages emerges when the weight-specific respiration rate and temperature relationship

Table 6. *Temperature coefficients* (Q_{10}) *over three temperature ranges for each life stage of* Alaskozetes antarcticus *calculated from respiration rates per individual*

	Q_{10}		
Life stage	0–5 °C	5–10 °C	0–10 °C
Larva	5·22	1·78	3·48
Protonymph	4·73	3·10	3·83
Deutonymph	2·08	2·06	2·07
Tritonymph	1·98	2·89	2·39
Adult male	7·23	1·78	3·59
Adult female	4·78	2·44	3·42

is examined (Fig. 4*b*). The larval stage showed the least increase of metabolism (g^{-1} h^{-1}) from 0° to +10 °C.

Q_{10} values were calculated for each instar of *A. antarcticus* for the temperature ranges 0° to +5 °C, +5° to +10 °C and 0° to +10 °C, using the mean respiratory rate $animal^{-1}$ (Table 6). Over the full 0° to 10 °C range, there was only a small variation in temperature response from a Q_{10} of 2·07 (deutonymph) to 3·83 (protonymph). If Q_{10} values for the component temperature ranges are examined, more striking differences are apparent. Between 0° and +5 °C, Q_{10} varied greatly from 1·98 (tritonymph) to 7·23 (adult male), and between +5 °C and +10 °C it varied only slightly from 1·78 (larva) to 3·10 (protonymph). The deuto- and tritonymph stages exhibited least change in Q_{10}, whereas the adult male showed most change over the ranges examined. It is concluded that environmental temperature changes within the normal summer range for *A. antarcticus* at Signy Island elicit a complex series of metabolic response patterns, which may be associated with activity of the mites. Again, as for the collembolan, *C. antarcticus* (Block & Tilbrook, 1975), there are very marked changes in Q_{10} above and below +5 °C. Diurnal temperature fluctuations in summer in the habitats of *A. antarcticus* in the maritime Antarctic are probably large (−5° to +16 °C; Chambers, 1966), but at Signy Island the mean summer temperature is in the range −0·5° to +9 °C. The total exposure time of the individual to temperatures around +10 °C in summer is probably small. This may account for the increased variability in respiration levels especially of the adults (Fig. 3*a*) and juveniles (Fig. 3*b*) at +10 °C. The results suggest, therefore, that there may be metabolic adaptation to summer temperatures in *A. antarcticus*.

Few calculations of Q_{10} have been made for Acari. For 16 species of oribatid mites, Berthet (1964) found a Q_{10} range of 3·5–5·7 with a mean of 4·0 from 0° to +15 °C. A Q_{10} of 2·65 was calculated for *N. silvestris* for the temperature range +10° to +20 °C (Webb, 1969), and similarly a Q_{10} of 2·03 for *S. magnus* over the range +11° to +25 °C (Webb, 1975). These were all adults of temperate species, but they have some similarity with the Q_{10} values for the various stages of *A. antarcticus* over 0° to +10 °C (Table 6). The larva, protonymph, adult male and female of *A. antarcticus* have higher temperature coefficients than Webb's species, but lower than Berthet's species. The Q_{10} values of these instars of *A. antarcticus* approach Berthet's mean for adult mites over a similar span of temperature. Compared with a Q_{10} range of 1·99–2·54 for *C. antarcticus* (Block & Tilbrook, 1975) over the same temperature interval, Q_{10} values for *A. antarcticus* are generally higher. It is expected that cold-adapted arthropods will

exhibit a greater response to changing temperature than temperate species, and this is confirmed by *A. antarcticus*. This is also true for male blowflies (Tribe & Bowler, 1968) in which standard metabolism is temperature dependent over the range 10°–30 °C, but not for many marine invertebrates (Newell & Pye, 1971). In *Littorina littorea* (L.) standard respiratory rate is almost independent of temperature, but the active rate is markedly temperature dependent and the point beyond which a decline occurs varies seasonally. The mechanisms of metabolism–temperature interaction are little understood at present, and current research on *A. antarcticus* is directed towards this end.

An attempt was made to determine if the environmental temperature at the time of collection of the mites from the field influenced their respiration rate as measured in the divers. A multiple regression equation between respiration ($\log_{10}\dot{V}_{O_2}$: $\times 10^{-3}$ μl O_2 ind^{-1} h^{-1}), live weight ($\log_{10}W$: μg) and field collection temperature (T: °C) was calculated on the individual data at each experimental temperature. The experimental temperatures, mean field collection temperatures (FCT) and the regression equations were:

$$0\ ^\circ C\ (FCT: +4{\cdot}91\ ^\circ C); \dot{V}_{O_2} = -0{\cdot}8916 + 0{\cdot}8050W + 0{\cdot}0251T\ (NS)$$
$$+5\ ^\circ C\ (FCT: +2{\cdot}57\ ^\circ C); \dot{V}_{O_2} = -0{\cdot}6083 + 0{\cdot}9003W - 0{\cdot}0227T\ (P < 0{\cdot}05)$$
$$+10\ ^\circ C\ (FCT: +5{\cdot}59\ ^\circ C); \dot{V}_{O_2} = -0{\cdot}7930 + 0{\cdot}9998W + 0{\cdot}0194T\ (NS)$$

By testing the regression sums of squares of FCT derived from a comparison of the multiple (above) and linear regressions (Table 2) against the residual sums of squares it was found that FCT only had a significant ($P < 0{\cdot}05$) effect on respiration rate at +5 °C. This contrasts with *C. antarcticus* where a similar effect was detected at 0 °C.

DISCUSSION

The results of the present study showed that the relationship between oxygen consumption rate and live weight remained constant in *A. antarcticus* over the temperature range 0° to +10 °C. Significant differences in respiration level were detected between these temperatures. This is in contrast to a similar study of the collembolan *C. antarcticus* (Block & Tilbrook, 1975). Comparative data for other species suggest that weight is the major influence on metabolism in micro-arthropods, but this is not constant within or between species and it may vary with temperature. This is probably caused by the varying degree of sclerotization of the different life stages and species for which data exist.

The influence of temperature on oxygen consumption of *A. antarcticus* was also important. In terms of individual respiration and temperature, there were two life-stage groups, one consisting of larva, proto- and deutonymph with low rates, and the other composed of tritonymph, adult males and females with high rates. The early instars (proto- and deutonymph) exhibited the highest weight-specific respiration rates, particularly at +10 °C. Also, the various life stages showed markedly different temperature responses as indicated by Q_{10}. The effect of temperature changes, which are representative of those occurring in the natural environment, upon cold-adapted species such as *A. antarcticus* require further investigation.

Comparative respiration data for temperate mites have been recorded by Berthet

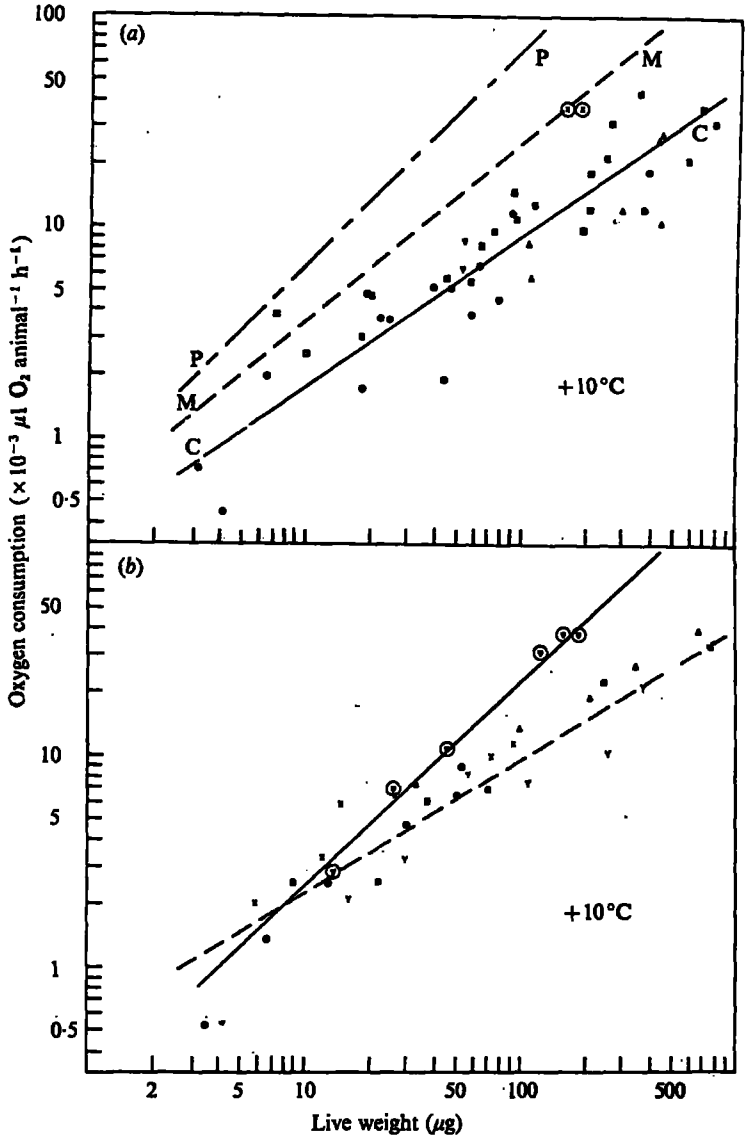

Fig. 5. Comparison of oxygen consumption as a function of live weight at +10 °C for *Alaskozetes antarcticus* and temperate mite species. Double $\log_{10}$ scales are used. (*a*) Individual data for adults of 39 species of Cryptostigmata: ⊗, *Alaskozetes antarcticus* (Present study); ●, 15 species (Berthet, 1964); ▼, 1 species (Webb, 1969); ■, 21 species (Wood & Lawton, 1973); ▲, 1 species (Webb, 1975). Regression lines have been fitted for 39 species of Cryptostigmata (C——C), 22 species of Mesostigmata (Webb, 1970; Wood & Lawton, 1973) (M— —M), and 5 species of Prostigmata (Wood & Lawton, 1973) (P– — –P). (*b*) Data for all life stages of six species of Cryptostigmata: ⊙, *Alaskozetes antarcticus* (Present study); ●, *Nothrus silvestris* (Webb, 1969); ▲, *Damaeus onustus*; ■, *Nothrus palustris*; ×, *Parachipteria willmanni* (Wood & Lawton, 1973); Y, *Steganacarus magnus* (Webb, 1975). Regression lines have been fitted for *A. antarcticus* (——) and five temperate species excluding *A. antarcticus* (– – –).

Table 7. *Regression equations of* $\log_{10}$ *respiration rate* ($\times 10^{-3}$ μl O_2 ind^{-1} h^{-1}) *on* $\log_{10}$ *live weight* (μg) *for six species of oribatid mites at* +10 °C. *The regressions are calculated on the mean rates for post-embryonic life stages of each species, and the number of measurements* (n) *together with the correlation coefficient* (r) *are given* ($P < 0.001$ *throughout*)

Species	Authority	*n*	*a*	*b* ± S.E.	*r*
Alaskozetes antarcticus	Present study	6	−0·598	+0·978 ± 0·0459	+0·996
Nothrus silvestris	Webb, 1969	6	−0·704	+0·930 ± 0·0681	+0·989
Damaeus onustus	Wood & Lawton, 1973	6	+0·099	+0·507 ± 0·0334	+0·991
Nothrus palustris	Wood & Lawton, 1973	5	−0·365	+0·687 ± 0·1185	+0·958
Parachipteria willmanni	Wood & Lawton, 1973	6	−0·066	+0·581 ± 0·1119	+0·933
Steganacarus magnus	Webb, 1975	6	−0·408	+0·643 ± 0·1007	+0·954

(1964), Webb (1969, 1970, 1975) and Wood & Lawton (1973). At 0 °C, adults of four species of oribatids over a similar weight range (calculated from Berthet, 1964) had much lower ($1{\cdot}073 - 5{\cdot}872 \times 10^{-3}$ μl O_2 ind^{-1} h^{-1}) respiration rates than adult *A. antarcticus* (Table 4). Also, at +5 °C, adult *A. antarcticus* showed much higher levels of metabolism, compared to adults of 16 oribatid species (Berthet, 1964) but this difference was not so pronounced at +10 °C. Fig. 5(*a*) is a double $\log_{10}$ plot of all the available respiration data at +10 °C against live weight of adult Cryptostigmata. The equation for the fitted regression line (C) of respiration rate ($\dot{V}_{O_2}$: $\times 10^{-3}$ μl O_2 ind^{-1} h^{-1}) on live weight (W: μg) excluding *A. antarcticus* is $\log_{10} \dot{V}_{O_2} = 0{\cdot}7189 \log_{10} W - 0{\cdot}4643$ ($n = 48$, $r = +0{\cdot}923$, $\text{S.E.}_b = \pm 0{\cdot}044$). Published data for respiration rates at +10 °C of adults of 19 species of Mesostigmata (Webb, 1970; Wood & Lawton, 1973) and adults of five species of Prostigmata (Wood & Lawton, 1973) allow the following equations to be derived on the same basis:

$$\text{Mesostigmata (M): } \log_{10} \dot{V}_{O_2} = 0{\cdot}8502 \log_{10} W - 0{\cdot}2945 \ (n = 22, r = +0{\cdot}891, \text{S.E.}_b = \pm 0{\cdot}097),$$

$$\text{Prostigmata (P): } \log_{10} \dot{V}_{O_2} = 1{\cdot}0382 \log_{10} W - 0{\cdot}2186 \ (n = 5, r = +0{\cdot}978, \text{S.E.}_b = \pm 0{\cdot}127).$$

It is concluded that on the basis of the available data for temperate mites (adults only), the Cryptostigmata have a lower weight exponent (*b*) compared to the other two groups (Fig. 5*a*). Adults of *A. antarcticus* at +10 °C have respiration rates comparable to Mesostigmata of similar weight.

Respiratory data covering all the post-embryonic life stages of individual mites are very limited. Fig. 5(*b*) compares results for six species of Cryptostigmata including *A. antarcticus* for which life-stage data are available at +10 °C. Linear regressions have been fitted for each species, and the regression equations are given in Table 7.

Over the upper part of its weight range, individuals of all life stages of *A. antarcticus* have much higher respiration levels than other species, which suggests some degree of metabolic adaptation in this species. Variation in the regression coefficient occurs

between species, and the *b* value for *N. silvestris* (0·930) approaches that of *A. antarcticus*; the remaining species having lower weight exponents. A general relationship linking oxygen consumption and live weight has been derived for the six oribatid species in Fig. 5(*b*): $\log_{10}\dot{V}_{O_2} = 0{\cdot}6614 \log_{10}W - 0{\cdot}2838$ ($n = 38, r = +0{\cdot}911$, S.E.$_b$ = $\pm 0{\cdot}049$). A similar relationship of $\log_e\dot{V}_{O_2} = 0{\cdot}710 \log_e W - 0{\cdot}606$ has been derived from data covering adults and nymphs of several oribatid mites (Chapman & Webb, 1977). By contrast, analysis of life-stage respiration and weight data for four species of Mesostigmata (Wood & Lawton, 1973) gives the following relationship: $\log_{10}\dot{V}_{O_2} = 0{\cdot}8139 \log_{10}W - 0{\cdot}2083$ ($n = 16$, $r = +0{\cdot}862$, S.E.$_b$ = $\pm 0{\cdot}128$), indicating that live weight has a greater influence on the measured respiration rate over the life cycle in these mites than in the Cryptostigmata.

The present study reports a *b* value ranging from +0·830 (0 °C) to +0·976 (+10 °C) for *A. antarcticus*. This is generally higher than that of other Antarctic invertebrates which have been studied: +0·120 (0 °C) to +0·570 (+10 °C) for cultured *C. antarcticus* (Tilbrook & Block, 1972), +0·669 (+5 °C) to +0·825 (+10 °C) for field *C. antarcticus* (Block & Tilbrook, 1975) and +0·51 (+5° and +10 °C) for the tardigrade *Macrobiotus furciger* J. Murray (Jennings, 1975). Individual respiration is almost directly dependent upon live weight rather than surface area in *A. antarcticus*. Zeuthen (1947) concluded that animals < 1 g in weight do not obey the surface law of $\dot{V}_{O_2} = a\,W^{0{\cdot}67}$, and this is confirmed by examination of the limited micro-arthropod data available. Live weight has been shown to be a major factor affecting individual respiration levels in such arthropods, but its effect varies within the species according to developmental stage and between species over their normal temperature range. Studies of respiration and growth rates together, over a range of field temperatures, in selected arthropods are required to clarify this.

Considering the effect of temperature alone on the respiration of *A. antarcticus*, a regression analysis of the individual data for the three experimental temperatures allows the following equation to be derived: $\log_{10}\dot{V}_{O_2} = 0{\cdot}6180 + 0{\cdot}0520T$ ($n = 148$, $r = +0{\cdot}367$, S.E.$_b$ = $\pm 0{\cdot}011$), where $\dot{V}_{O_2}$: respiration rate ($\times 10^{-3}$ μl O_2 ind^{-1} h^{-1}) and T: temperature (°C). A mean Q_{10} value may be calculated as the antilog of 10 × coefficient *b*, which is 3·31 and this corresponds to the average value for the range of temperature coefficients given in Table 6. However, the weak regression and correlation coefficients confirm that temperature alone does not influence respiration significantly in this species. Berthet (1964) transformed his individual weight data to a standard weight equal to the mean of all the mites used in his respiration experiments. For adult data from 16 species at +5°, +10° and +15 °C he calculated the relationship, $\log_{10}\dot{V}_{O_2} = 1{\cdot}929 + 0{\cdot}055T$ ($n = 48$). The regression coefficient for temperature is not significantly different from that of *A. antarcticus*, but further comparison is precluded because of life-stage differences in the data.

The effects of both live weight and temperature on individual respiration of *A. antarcticus* can be examined by means of a multiple regression, the equation $\log_{10}\dot{V}_{O_2} = -12{\cdot}4663 + 0{\cdot}9237 \log_{10}W + 0{\cdot}04219T$ ($n = 148$) being calculated, where $\dot{V}_{O_2}$: respiration rate ($\times 10^{-3}$ μl O_2 ind^{-1} h^{-1}), W: live weight (μg) and T: temperature (°K). This was further developed in respect of the absolute temperature by analogy with Arrhenius' law to give $\log_{10}\dot{V}_{O_2} = 12{\cdot}4000 + 0{\cdot}9238 \log_{10}W - 0{\cdot}3267T$ ($n = 148$), where $\dot{V}_{O_2}$: respiration rate ($\times 10^{-3}$ μl O_2 ind^{-1} h^{-1}), W: live weight (μg) and

T: $1 \times 10^4/T$ absolute. This general relationship is representative of the active life stages of *A. antarcticus* over the temperature range 0° to +10 °C. This allows a comparison with Berthet's (1964) generalization for adults of several species over the temperature interval +5° to +15 °C, where $\log_{10} \dot{V}_{O_2} = 18{\cdot}059 + 0{\cdot}700 \log_{10} W - 0{\cdot}487T$. It can be seen that weight exerts a greater influence on respiration level in *A. antarcticus* than in the temperate species, and that temperature has a slightly reduced effect on respiration for the Antarctic mite.

In order to compare the equations resulting from the present study with those from Berthet (1964), substitution in the equations was made for an average mite (83·88 μg) calculated from the live weights of all the life stages of *A. antarcticus* together with adults of Berthet's 16 species. Two temperatures, +5° and +10 °C were used which represent the overlap of the two experimental temperature ranges. The calculated respiration rates were:

A. antarcticus	equation +5 °C,	$\dot{V}_{O_2} = 266{\cdot}2 \times 10^{-3}$ μl O_2 ind^{-1} h^{-1}
16 species	equation +5 °C,	$\dot{V}_{O_2} = 77{\cdot}2 \times 10^{-3}$ μl O_2 ind^{-1} h^{-1}
A. antarcticus	equation +10 °C,	$\dot{V}_{O_2} = 429{\cdot}2 \times 10^{-3}$ μl O_2 ind^{-1} h^{-1}
16 species	equation +10 °C,	$\dot{V}_{O_2} = 157{\cdot}4 \times 10^{-3}$ μl O_2 ind^{-1} h^{-1}

The respiration values derived by the *A. antarcticus* equation are 3·45 times greater than those from Berthet's equation at +5 °C and 2·73 times greater at +10 °C. This trend is continued over the complete weight range of all the material at each temperature. Although there are considerable differences, such as life stage and habitat, between the two sets of mites on which the equations are based, it is clear that the Antarctic species has a much higher level of oxygen consumption than temperate species over the range +5° to +10 °C. It is concluded that for *A. antarcticus* there is translation of the metabolism-temperature curve but no rotation (Precht, 1958). It is suggested that this species occupies an intermediate position in respect of its metabolism being partially independent of environmental temperature fluctuations (Hazel & Prosser, 1974), a similar situation to the majority of invertebrate poikilotherms.

The available data on metabolic rate (weight-specific oxygen consumption) and live weight, which have been reported for a range of Antarctic terrestrial invertebrates, are shown in Fig. 6. For *A. antarcticus*, only Marsh (1973) is comparable, and his average value lies within the range of results for the present study at +5 °C. The collembolan *C. antarcticus* is generally smaller in size, and its metabolic rate (μl O_2 g^{-1} h^{-1}) is higher than that of *A. antarcticus*. The other collembolan *Isotoma klovstadi* Carpenter is larger than *C. antarcticus*, but higher metabolic rates have been measured for this species even at −4 °C (Strong, Dunkle & Dunn, 1970). *Gamasellus racovitzai* (Trouessart) (Goddard, 1976*a*), a mesostigmatid mite, although of similar weight to *A. antarcticus*, has a higher metabolism probably due to its greater locomotory activity at low temperatures associated with its predatory role. The Antarctic Prostigmata are amongst the smallest arthropods to be measured with a Cartesian diver microrespirometer, and several of them are very active species. Hence their higher metabolic rates (Goddard, 1976*b*; Block, 1976), compared with other mites and the Collembola.

Considering all the data for Antarctic terrestrial invertebrates, a relationship of metabolic rate to temperature over the range −4° to +22 °C has been derived as:

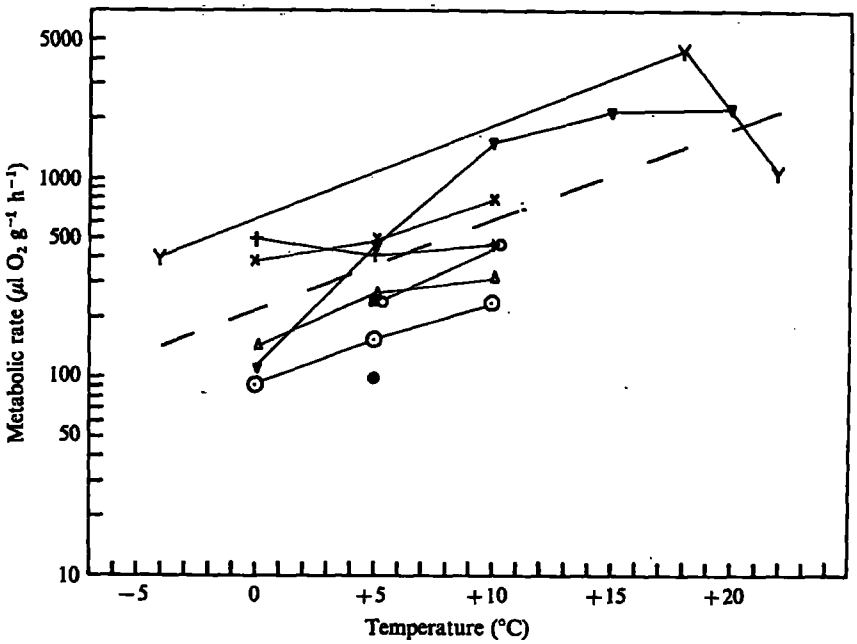

Fig. 6. Metabolic rate as a function of temperature for ten species of Antarctic terrestrial invertebrates. A regression line has been fitted to the combined data (— — —). Data are taken from various sources: ⊙, *Alaskozetes antarcticus* (Present study); ●, *A. antarcticus* (Marsh, 1973); △ *Cryptopygus antarcticus* (Block & Tilbrook, 1975), ▼, *C. antarcticus* (Dunkle & Strong, 1972); ■, *C. antarcticus* (Marsh, 1973); Y, *Isotoma klovstadi* (Strong, Dunkle & Dunn, 1970), ×, *Gamasellus racovitzai* (Goddard, 1976*a*); +, five species of Prostigmata (Goddard, 1976*b*), and ○, *Macrobiotus furciger* (Jennings, 1975).

$\log_{10} \dot{V}_{O_2} = 2{\cdot}2874 + 0{\cdot}0483T$ ($n = 24$, $r = +0{\cdot}732$, S.E.$_b = \pm 0{\cdot}00957$), where $\dot{V}_{O_2}$: metabolic rate (μl O_2 g^{-1} h^{-1}) and T: temperature (°C). The overall Q_{10} calculated from the regression coefficient b is 3·04, which is slightly higher than the majority of values found for temperate micro-arthropods. Comparison of this relationship for Antarctic species with that derived from 109 species of temperate Acari over 0° to +25 °C, where $\log_{10} \dot{V}_{O_2} = 1{\cdot}8227 + 0{\cdot}0363T$ ($n = 109$, $r = +0{\cdot}446$, S.E.$_b = \pm 0{\cdot}00704$), indicates that there is no significant difference between the regression coefficients. Therefore it may be concluded that the metabolic response to temperature of the two groups of Antarctic and temperate terrestrial invertebrates is similar over their normal temperature ranges, but the Antarctic group has a generally elevated level of metabolism. This elevation is 3 to 5 times the metabolic rate of temperate Acari over the range 0° to +20 °C.

It is possible, knowing the respiratory rate of an animal and the calories lost for each unit of oxygen consumed, to calculate the minimum energy required to support metabolism. Using an oxy-calorific equivalent of 4·74 calories ml^{-1} of oxygen consumed (Petrusewicz & Macfadyen, 1970) for an animal feeding on a mixed diet and with an RQ of 0·82, and the respiratory rates of *A. antarcticus* determined at Signy Island (Table 4), it was calculated that from 0·093 (larva at 0 °C) to 4·241 (adult male at +10 °C) μcal ind^{-1} $24\,h^{-1}$ were required for maintenance metabolism. Marsh (1973) using a mean respiration value of $21{\cdot}875 \times 10^{-3}$ μl O_2 ind^{-1} h^{-1} at +5 °C,

an ingestion rate of 0·341 μg dry weight of food 24 h^{-1} and a calorific food equivalent fo 4·7 μcal μg^{-1} determined that 78·2% of the energy assimilated was utilized in respiration for an individual *A. antarcticus* of 81·0 μg weight. Marsh's mean respiration figure at +5 °C falls between the tritonymph and adult values in the present study (Fig. 3*a*), but his mean weight corresponds to midway between the deuto- and tritonymphal stages (Table 1). Notwithstanding these differences, a similar calculation of the proportion of energy used by *A. antarcticus* in maintenance metabolism, based on the Signy Island respiration data at +5 °C and a mean weight of 81·0 μg, gave a value of 82·3%. This is rather higher than Marsh's estimate, but together the two values suggest that the majority of energy assimilated by *A. antarcticus* is used in respiratory metabolism. It is concluded that this is probably a feature of micro-arthropod energetics in habitats with low environmental temperatures, leaving only a small proportion of energy for production of tissues and young. Hence, these animals have slow growth rates and generally long life cycles compared to temperate species (Block, 1965).

There has been little attention paid to metabolic compensation to temperature amongst terrestrial poikilotherms of high latitudes. In studies of arctic insects, Scholander *et al.* (1952) found scant evidence for a relative elevation in respiratory activity at low temperatures. This is in contrast to the results of the present study. Most cold-adapted terrestrial arthropods are probably dependent on exposure to relatively high environmental temperatures, for albeit short periods, for their activity and development. At Signy Island, habitat temperatures in the summer for *A. antarcticus* are mostly in the range −5° to +9·5 °C, when growth and reproduction are maximal. As temperatures fall below 0 °C, a capacity to survive mechanical damage due to freezing rather than to compensate metabolically becomes more important. With the severe winter conditions of its habitat (minimum temperature −20° to −30 °C), *A. antarcticus* must be able to withstand freezing in most of its life stages. Investigations are presently in progress to determine if the capacity to withstand freezing is linked to a facility to supercool, and to elucidate the possible mechanisms involved.

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REFERENCES

BERTHET, P. (1964). L'activité des Oribatides (Acari: Oribatidae) d'une Chênaie. *Mém. Inst. r. Sci. nat. Belg.* **152**, 1–152.

BLOCK, W. (1965). The life histories of *Platynothrus peltifer* (Koch 1839) and *Damaeus clavipes* (Hermann 1804) (Acarina: Cryptostigmata) in soils of Pennine moorland. *Acarologia* **7**, 735–43.

BLOCK, W. (1976). Oxygen uptake by *Nanorchestes antarcticus* (Acari). *Oikos* **27**, 320–3.

BLOCK, W. & TILBROOK, P. J. (1975). Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos* **26**, 15–25.

CHAMBERS, M. J. G. (1966). Investigations of patterned ground at Signy Island, South Orkney Islands: II. Temperature regimes in the active layer. *Bull. Br. Antarct. Surv.* **10**, 71–83.

CHAPMAN, S. B. & WEBB, N. R. (1977). The productivity of a *Calluna* heathland in southern England. In *The Ecology of some British Moors and Montane Grasslands* (ed. O. W. Heal and D. F. Perkins). Springer-Verlag (in the press).

DUNKLE, R. & STRONG, F. E. (1972). A digital electrolytic micro-respirometer. *Ann. ent. Soc. Am.* **65**, 705–10.

GODDARD, D. G. (1976*a*). The Signy Island Terrestrial Reference Sites: VI. Oxygen uptake of *Gamasellus racovitzai* (Trouessart) (Acari: Mesostigmata). *Bull. Br. Antarct. Surv.* **45**, 1–6.

GODDARD, D. G. (1976*b*). The Signy Island Terrestrial Reference Sites: X. Oxygen uptake of some Antarctic prostigmatid mites (Acari: Prostigmata). *Bull. Br. Antarct. Surv.* **45**, 53–7.

GRESSITT. J. L. (1967). Notes on arthropod populations in the Antarctic Peninsula – South Orkney Islands area. *Antarct. Res. Series* **10**, 373–91.

HAZEL, J. R. & PROSSER, C. L. (1974). Molecular mechanisms of temperature compensation in poikilotherms. *Physiol. Rev.* **54**, 620–77.

HOLTER, H. (1943). Technique of the Cartesian Diver. *C. r. Trav. Lab. Carlsberg Ser. Chim.* **24**, 399–478.

JENNINGS, P. G. (1975). The Signy Island Terrestrial Reference Sites: V. Oxygen uptake of *Macrobiotus furciger* J. Murray (Tardigrada). *Bull. Br. Antarct. Surv.* **41** & **42**, 161–8.

LINDERSTRØM-LANG, K. U. (1943). On the theory of the Cartesian Diver micro-respirometer. *C. r. Trav. Lab. Carlsberg Ser. Chim.* **24**, 333–98.

MARSH, J. B. (1973). Radioisotopic determination of the ingestion rates of three species of Antarctic arthropods: *Cryptopygus antarcticus* Willem (Collembola: Isotomidae), *Belgica antarctica* Jacobs (Diptera: Chironomidae) and *Alaskozetes antarcticus* (Micheal) (Cryptostigmata: Podacaridae). M.Sc. thesis, University of California at Davis.

NEWELL, R. C. & PYE, V. I. (1971). Quantitative aspects of the relation between metabolism and temperature in the winkle *Littorina littorea* (L.). *Comp. Biochem. Physiol.* **38B**, 635–50.

OSTLE, B. R. (1963). *Statistics in Research.* Iowa State University Press.

PETRUSEWICZ, K. & MACFADYEN, A. (1970). Productivity of terrestrial animals, I.B.P. Handbook No. 13. Oxford: Blackwells.

PRECHT, H. (1958). Concepts of the temperature adaptation of unchanging reaction systems of cold blooded animals. In *Physiological Adaptation* (ed. C. L. Prosser). *Am. Physiol. Soc.* 50–78.

SCHOLANDER, P. F., FLAGG, W., WALTERS, V. & IRVINE, L. (1953). Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.* **26**, 67–92.

STRONG, J. (1967). Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. *Antarct. Res. Series* **10**, 357–71.

STRONG, F. E., DUNKLE, R. L. & DUNN, R. L. (1970). Low-temperature physiology of Antarctic arthropods. *Antarct. J. U.S.* **5**, 123.

TILBROOK, P. J. (1967). Arthropod ecology in the Maritime Antarctic. *Antarctic Res. Series* **10**, 331–56.

TILBROOK, P. J. (1973). The Signy Island Terrestrial Reference Sites: I. An introduction. *Bull. Br. Antarct. Surv.* **33** & **34**, 65–76.

TILBROOK, P. J. & BLOCK, W. (1972). Oxygen uptake in an Antarctic collembole *Cryptopygus antarcticus*. *Oikos* **23**, 313–17.

TRIBE, M. A. & BOWLER, K. (1968). Temperature dependence of 'standard metabolic rate' in a poikilotherm. *Comp. Biochem. Physiol.* **25**, 427–36.

WALLWORK, J. A. (1962). A redescription of *Notaspis antarctica* Michael, 1903 (Acari: Oribatei). *Pacif. Insects* **4**, (4), 869–80.

WALLWORK, J. A. (1967). Cryptostigmata (oribatid mites). *Antarct. Res. Series* **10**, 105–22.

WALLWORK, J. A. (1973). Zoogeography of some terrestrial micro-Arthropoda in Antarctica. *Biol. Rev.* **48**, 233–59.

WEBB, N. R. (1969). The respiratory metabolism of *Nothrus silvestris* Nicolet (Acari). *Oikos* **20**, 294–9.

WEBB, N. R. (1970). Oxygen consumption and population metabolism of some mesostigmatid mites (Acari: Mesostigmata). *Pedobiologia* **10**, 447–56.

WEBB, N. R. (1975). Respiratory metabolism of *Steganacarus magnus* (Acari). *Oikos* **26**, 43–6.

WOOD, T. G. & LAWTON, J. H. (1973). Experimental studies on the respiratory rates of mites (Acari) from beech-woodland leaf litter. *Oecologia* **12**, 169–91.

ZEUTHEN, E. (1947). Body size and metabolic rate in the animal kingdom. *C. r. Trav. Lab. Carlsberg Ser. Chim.* **26**, 17–165.

ZEUTHEN, E. (1964). *Microgasometric Methods: Cartesian Divers* (pp. 70–80). *2nd Int. Congr. Histo- & Cytochemistry* (ed. T. H. Schiebler, A. G. E. Pearse and H. H. Wolff). New York: Wiley.

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Effects of long-term storage on the oxygen uptake of Cryptopygus antarcticus (Collembola)

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During storage of the collembolan *Cryptopygus antarcticus* Willem at +5°C over 387 d, both respiration and metabolic rates of size class V and IV individuals declined significantly. For pooled data for adults of both size classes this decline was calculated as: $\log_{10} MR = 2.359 - 0.145 \log_{10} T$ (where MR: metabolic rate in $\mu l\ O_2\ g^{-1}\ h^{-1}$ and T: time in d). No differences were detected between the sexes, but a significant difference ($P < 0.05$) in metabolism existed between fresh animals measured at the start of the storage experiment and earlier in the austral summer at Signy Island. The respiration and metabolic rates of the stored individuals were similar to those from earlier measurements made in the UK on individuals which had been subjected to similar treatment. It is suggested that the metabolic decline is an adaptation to constant temperature unrelated to the nutritional conditions. Short- and long-term metabolic adaptation is discussed in relation to studies on mites, nematodes and other invertebrates.

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При содержании коллембол *Cryptopygus antarcticus* Willem при +5°C в течение 387 дней интенсивность дыхания и метаболизма у особей V и IV размерных групп значительно снижалась. Для взрослых особей обеих размерных групп это снижение описывается равенством:

$$\log_{10} MR = 2{,}359 - 0{,}145 \log_{10} T$$

где MR – интенсивность метаболизма в $\mu л_2 0.г^{-1}.час^{-1}$ и T – время в сутках. Половые различия не были обнаружены, но большая разница ($P < 0{,}05$) в интенсивности метаболизма установлена у животных в начале эксперимента и в более ранние сроки летом. Показатели интенсивности дыхания и метаболизма у животных в опыте сходны с ранее полученными данными опытов, проведенных в Вецлкобритании на животных, помещенных в такие же условия. Установлено, что снижение интенсивности метаболизма – адаптация к постоянной температуре и не зависит от условий питания. Обсуждаются кратко- и долгосрочные метаболические адаптации у клещей, нематод и других беспозвоночных.

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Introduction

In recent years an increasing number of studies have been carried out on the oxygen consumption rates of soil organisms. Many of these have been completed with a view to applying the results to field population data to produce estimates of field population or community metabolism. As part of an investigation of the energetics of terrestrial arthropods at Signy Island, South Orkney Islands, the respiration rate of the numerous and widespread collembolan *Cryptopygus antarcticus* Willem was measured. This was first done in the U.K. using material which had been sent back from the Antarctic in culture (Tilbrook and Block 1972). It was not known, however, whether long term storage affected the oxygen uptake of these animals.

It was later possible to undertake a more extensive set of measurements of the respiration rate of the same species using specimens fresh from the field at Signy Island (Block and Tilbrook 1975). Initial comparison of the two sets of data suggested that they were markedly different, the juveniles having the greatest difference, especially at temperatures in the range +5 to +10°C. It was therefore decided to undertake an experiment to examine specifically the relationship of length of storage time at constant temperature to respiration rate. The results of this experiment are reported here.

Methods

On 1 March 1972 pieces of moss turf, composed of *Polytrichum alpestre* Hoppe and *Chorisodontium aciphyllum* (Hook f. et Wils.) were collected from near the British Antarctic Survey research station on Signy Island and taken directly into a constant temperature room at +5°C. Individuals of *C. antarcticus* were removed by teasing the moss apart and tapping out the arthropods onto white paper. Some animals were used immediately for respiration determinations while others were put in culture vessels for measurements on subsequent days.

Two to three hundred individuals were introduced into each of several culture vessels together with a small piece of moss turf. Each culture vessel consisted of a small polythene bottle with a bakelite lid. Plaster of Paris formed a thin film on the walls and about 1.5 cm in depth on the base. This was then moistened with distilled water to saturation point before the introduction of the moss and the experimental animals. In the lid a small hole had been cut and was covered with very fine mesh (75 mesh cm^{-1}) bolting silk. The culture vessels containing live Collembola were stored at 5 ± 1°C during transport to the U.K. and while at Leicester University. On each day selected for further measurements, animals were tapped out of moss from one of the culture vessels and used for respiration determinations. The intervals chosen for measurement of the respiration rate were day 0, 2, 4, 15, 86, 206 and 387. The closeness of the first four experimental days was because it was felt that any significant change in oxygen consumption would be rapid and so likely to occur during the first two weeks.

In order to overcome the variation of respiration rate due to individual size it was necessary to select animals of similar body size. Because of the absence of characters on which the instar stages could be separated, a field population of this species previously had been divided into five equal size classes on the basis of body length (Tilbrook and Block 1972). Size class V individuals were utilised for this experiment as they are the largest (>1680 μm body length; 70.7–119.5 μg live weight) most easy to handle and gave reliable results with the diver volumes (Vg: 4.40–19.20 μl) available. Unfortunately, by day 86 of the experiment the numbers of individuals from size class V were diminishing and on the last two experimental dates (days 206 and 387) no animals from this group were found. On these occasions the largest individuals were used, but these belonged to either size class IV or III.

All respirometric measurements were made at +5°C. This temperature was selected as it is close to the mean summer field temperature experienced by the animals and also it was the temperature at which live material had been stored prior to previous experimental work in the U.K. For measurement of respiration rate, two Cartesian Diver micro-respirometers were used on each occasion. Up to and including day 15, these were set up in a constant temperature room at Signy Island and thereafter two instruments in a temperature controlled room at Leicester University were used. Details of the respirometric technique were given in Block and Tilbrook (1975). Respiratory measurements were made on single animals which were loaded directly into the divers after removal from the culture vessels. An equilibration period of 30–75 min was allowed after the divers had been placed in the respirometer before readings began. Readings were made at intervals of 30–40 min over 4–6 h. Using the two Cartesian Divers it was possible to obtain a maximum of fourteen determinations on each occasion.

At the end of each measurement, animals were preserved separately in 75% alcohol. Later, each individual was cleared in Nesbitt's solution at 70°C, which also relaxed the body and ensured that it reverted to its normal state. Total body length was measured under a microscope at ×16 magnification, and this was used to derive the live weight using the relationship: $W = 6.1894\ L^{3.119} \times 10^{-9}$ where W: live weight (μg) and L: length (μm) (Tilbrook and Block 1972). Later, the sex of individual animals was determined under phase contrast using ×600 magnification.

Results

In discussing the experimental results the terms respiration rate (x 10^{-3} μl O_2 ind^{-1} h^{-1}) and metabolic rate (μl

Tab. 1. Live weight (μg), respiration rate (× 10 μl O_2 ind^{-1} h^{-1}) and metabolic rate (μl O_2 g^{-1} h^{-1}) for size classes III, IV and V of *Cryptopygus antarcticus* on each occasion during the storage experiment. Mean values ±SE and number of measurements (n) are given in each case.

Day	Date	Live weight III	IV	V
1	1 Mar 72	–	66.31 ± 1.97 (2)	87.12 ± 2.53 (12)
2	2 Mar 72	–	–	90.60 ± 3.30 (14)
4	4 Mar 72	–	66.31 ± 1.97 (2)	89.58 ± 4.39 (12)
15	15 Mar 72	–	68.28 ± 0.0 (1)	99.21 ± 5.19 (13)
86	25 May 72	–	58.34 ± 4.25 (3)	94.44 ± 4.65 (7)
206	22 Sept 72	34.73 ± 0.84 (3)	52.73 ± 1.61 (8)	–
387	22 Mar 73	33.05 ± 0.0 (1)	53.40 ± 3.47 (7)	–

O_2 g^{-1} h^{-1}) will be used. Mean respiration and metabolic rates are given in Tab. 1 together with the mean estimated live weight on a size class basis for each occasion during the experiment. It was impossible to allocate each live specimen of *C. antarcticus* accurately to its size class before respirometry, and hence there was a mixture of two size classes on every occasion.

Examination of the mean live weight of all the individuals of each size class used in the experiment (V: 92.19 μg; IV: 60.89 μg) showed that they were not significantly different from those of field fresh animals (V: 92.80 μg; IV: 52.50 μg) (Block and Tilbrook 1975).

The mean live weight of the experimental animals (Tab. 1) changed slightly over the 387 d. Although the live weight of size class V animals increased and size class IV individuals decreased, these differences were not significant over the course of the experiment, thus permitting a comparison of respiration rates.

Comparison of both individual respiration and metabolic rates for stored material (see Tab. 1) with those for animals measured fresh from the field, by plotting both against live weight, indicated that the stored animal rates fell within the range of variation reported for field animals.

Tab. 2 shows a comparison of the results for day 1 of the storage experiment with data for other field fresh animals obtained during the same summer at Signy Island. The individual live weight and metabolic rate differences for the two groups of animals were just significant ($P < 0.05$); the animals collected earlier in the summer season being heavier, and having a lower rate of metabolism. The individual respiration rate was also lower earlier in the summer period but this was not significant. It may be that the animals used on day 1 (1 March 1972) of the storage experiment were in a different physiological state than those measured earlier in the season. If these later individuals were adapted, physiologically, for the onset of winter and lower environmental temperatures, this may account for their higher metabolic rate at +5°C.

Throughout the experiment the respiration rate of both size class V and IV individuals decreased. Comparison of the correlation coefficient of respiration rate with time confirmed that the decrease was significant from zero: size class V ($P < 0.02$) and IV ($P < 0.05$). For metabolic rate, similar significant decreases with time were recorded, and linear regressions were calculated for $\log_{10}$ metabolic rate (MR: μl O_2 g^{-1} h^{-1}) on $\log_{10}$ time (T: days) for each size class as follows:

V $\log_{10} MR = 2.3043 - 0.1132 \log_{10} T$ (n: 5, r: −0.9711)
IV $\log_{10} MR = 2.3655 - 0.1568 \log_{10} T$ (n: 6, r: −0.7909)

In both cases r was significantly different from zero (V: $P < 0.01$, IV: $P < 0.10$), indicating that the metabolic rate of both size classes declined over the 387 d of the experiment.

As the mean individual live weight varied slightly during the period of storage (Tab. 1), the mean metabolic rate for each occasion was standardised to the mean weight for size classes V (92.19 μg) and IV (60.89

Tab. 2. Comparison of mean live weight, respiration and metabolic rate at +5°C of size class V of *Cryptopygus antarcticus* measured at different times of the austral summer. The mean ±SE and n are shown.

Date	n	Live weight (μg)	Respiration rate (× 10^{-3} μl O_2 ind^{-1} h^{-1})	Metabolic rate (μl O_2 g^{-1} h^{-1})
1 Mar 72 (day 1 storage experiment)	12	87.125 ± 2.532	17.598 ± 2.293	202.319 ± 24.271
13 Dec 71 to 25 Jan 72 (Signy Island fresh animals)	17	89.441 ± 3.505	14.872 ± 1.297	165.574 ± 12.838
Total fresh animals	29	88.413 ± 2.363	16.000 ± 1.218	180.779 ± 12.754
Block and Tilbrook (1975)	mean	92.80	14.01	150.90

Respiration rate			Metabolic rate		
III	IV	V	III	IV	V
–	17.42 ± 6.93 (2)	17.60 ± 2.29 (12)	–	259.90 ± 96.86 (2)	202.32 ± 24.27 (12)
–	–	15.74 ± 1.14 (14)	–	–	175.91 ± 13.50 (14)
–	14.28 ± 1.16 (2)	15.93 ± 1.18 (12)	–	215.11 ± 11.09 (2)	177.34 ± 9.46 (12)
–	6.10 ± 0.0 (1)	14.96 ± 1.21 (13)	–	89.46 ± 0.0 (1)	158.02 ± 16.76 (13)
–	7.79 ± 2.37 (3)	11.12 ± 1.29 (7)	–	136.49 ± 43.82 (3)	117.11 ± 11.98 (7)
3.93 ± 0.50 (3)	7.20 ± 0.85 (6)	–	112.72 ± 12.18 (3)	125.69 ± 13.94 (6)	–
3.62 ± 0.0 (1)	4.38 ± 0.90 (6)	–	109.43 ± 0.00 (1)	81.04 ± 15.86 (6)	–

μg) by reference to data obtained from field fresh animals at Signy Island. It was assumed that the relation of metabolic rate to weight at +5°C was similar for both cultured and field animals, and the rates determined for the cultured specimens were adjusted by reference to the gradient of the fitted regression line for field material. Fig. 1 shows the standardised mean values for metabolic rate of size classes V and IV on each occasion with the exception of size class IV on day 14, which has been ommitted as it contained only one measurement. A regression of $\log_{10}$ metabolic rate on $\log_{10}$ time was computed separately for the two size classes, and also on the combined data. The equations are given in Tab. 3, and regression lines have been fitted to the data in Fig. 1. The slopes of the regression lines representing the decline in metabolic rate of the two size classes with time are just significantly different from each other ($P < 0.05$). When tested individually against the regression line of the combined data, the gradients were found to be similar. It is considered therefore that the equation calculated for the combined size class data:

$$\log_{10} MR = 2.3598 - 0.1447 \log_{10} T$$
(n: 10, r: −0.9191, SE_b: ±0.02193)

adequately represents the decline in metabolism of the larger individuals of *C. antarcticus* during the period of storage at a constant +5°C.

The animals from the experiment consisted of 27♂♂ and 51♀♀. The sex ratio of the whole material was therefore 1♂ : 1.89♀ which is similar to 1:1.86 derived for field animals (Block and Tilbrook 1975). The female grows to a larger size in *C. antarcticus* (Tilbrook 1970), and the sex ratio for size class V over the complete

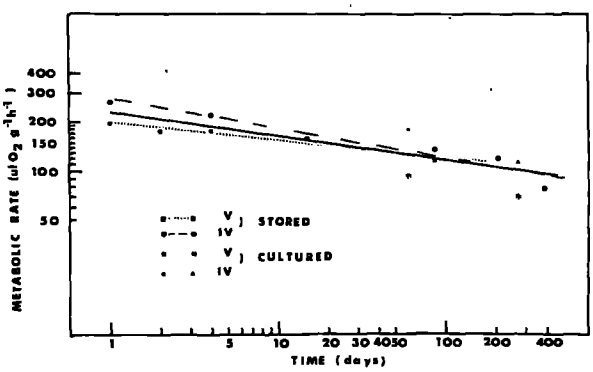

Fig. 1. Decrease in metabolic rate with time for size classes V and IV of *Cryptopygus antarcticus* when stored at +5°C. $\log_{10}$ scales are used and linear regression lines have been fitted to the data for each size class and to the combined data (regression coefficients are given in Tab. 3). Data of metabolic rate at +6°C for U.K. cultured animals are also shown for comparison.

experiment was 1:2.93, whilst that of size class IV was 1:0.89.

Although the female was generally heavier, between sexes there was no significant difference in live weight either for each experimental occasion or for all the animals measured. For respiration rate, on five out of seven occasions, the mean male rate was higher than the female rate, but only on day 1 was this difference significant ($P < 0.01$). In terms of metabolic rate, on six out of seven occasions, the female had a higher rate, but this only achieved significance ($P < 0.05$) again on day 1.

Tab. 3. Regression equations of metabolic rate ($\log_{10}$ μl O_2 g^{-1} h^{-1}) on time ($\log_{10}$ days) for size classes V and IV of *Cryptopygus antarcticus* at +5°C. The number of measurements (n) comprising the mean values used in the regressions together with the correlation coefficient are shown ($P < 0.001$ throughout).

Size class	a	b ± SE	r	n
.....	2.3002	−0.1074 ± 0.0166	−0.9658	58
.....	2.4467	−0.1826 ± 0.0282	−0.9661	19
and IV combined	2.3598	−0.1447 ± 0.0219	−0.9191	7

Overall, there were no detectable differences in respiration or metabolic rates between the sexes.

Comparison of the results of the earlier work on *C. antarcticus* in the U.K. (Tilbrook and Block 1972) with those of this storage experiment were made (Fig. 1). Unfortunately the earlier measurements were made at +6°C, but allowing for this temperature difference some comparison is possible. The mean values for live weight, respiration and metabolic rates for earlier U.K. work (hereafter referred to as cultured animals) were obtained from individuals measured approximately 60 d and 270 d after their collection in the field, transportation and subsequent culture at Leicester University. As far as possible these animals were maintained throughout this time at a temperature of +5 ± 1°C. The comparable values from the present study (hereafter referred to as stored animals) were derived from the linear regressions given above for the original, uncorrected data.

The two sets of data are fairly similar. The mean live weight did not change significantly with 'storage' or 'culture' for either size class. For size V, 'stored' animals had higher respiration and metabolic rates than cultured specimens after 60 d, and 270 d. Size class IV specimens exhibited a slightly different pattern in that after 60 and 270 d, the 'stored' animals had lower respiration and metabolic rates than those which had been kept in 'culture'. Some of these differences may have been due to the differing temperatures, or to small weight differences, but they remain largely unexplained.

Discussion

The experiment has demonstrated that a significant decline in both respiration rate and metabolic rate of *C. antarcticus* occurred during storage at constant temperature (+5°C) over a period of 387 d. The decline in metabolism was evident by day 2 of the experiment. Both size class V and IV individuals were affected similarly.

From a comparison of respiratory data for cultured and field fresh animals, Block and Tilbrook (1975) concluded that the younger stages of *C. antarcticus* were more affected by long-term storage and culture at a constant +5°C. The present results show that differences in respiration and metabolic rates occurred over the small size range covered by size classes V and IV, which were probably all sexually mature individuals. It seems highly likely, therefore, that the differences found for these instars will probably extend to the smaller size classes of *C. antarcticus*, and they may be accentuated. It has been shown that the early instars of several species of micro-arthropods are more active, metabolically, than later instars (Webb 1975, Block 1977).

No comparative information on the metabolic affects of long-term storage at constant temperature exist either for micro-arthropods or Antarctic invertebrates generally. Zeuthen (1947) found that profound adaptations could occur in marine animals if kept at a lower than usual temperature for a long period of time. Such species exhibited firstly a decline in metabolic rate after 20–30 d followed by a period of increased metabolism, indicating that the animal had actively regulated. The reverse was true for changes to higher, constant temperatures. With soil nematodes, no such long-term adaptations were demonstrated. Nielsen (1949) showed that after four months at a variety of constant temperatures (+2°, +9°, +16° and ca. +21°C) individuals of *Mononchus papillatus* Bastian had similar metabolic rates when measured in Cartesian divers at +16°C. He concluded that any temperature adaptation, if it occured in this species, was extremely rapid.

Due to the lack of information on the exact nutritional requirements of *C. antarcticus* there is the possibility that the decline in respiration and metabolism of stored individuals was caused partly by a change in the nutritional conditions at constant temperature. Zinkler (1966) investigated the effect of starvation on the oxygen uptake at +18°C of two Collembola: *Onychiurus fimatus* Gisin and *Tetrodontophora bielanensis* (Waga). During the first four days of food withdrawal live weight and metabolic rate of *O. fimatus* declined by 10% and 32% respectively. Over longer starvation periods (10–14 d), the metabolism of *T. bielanensis* decreased by 42–44%. In both species there was a much greater decrease in metabolism than live weight. In *C. antarcticus* experimental animals were selected on the basis of length (weight) rather than instar so the effect of storage on body weight was not established. That size class V individuals were still present after 86 d, however, with a mean body weight similar to the mean for this class (Tilbrook and Block 1972), suggests that there was no significant change in live weight during storage. After four days of the experiment, respiration rate had decreased by 9.5% and 18.0% in size class V and IV respectively. Similarly, metabolism declined by 12.4% and 17.2% over the same time period. The latter figures are approximately half of that recorded by Zinkler (1966). For both size classes, metabolism at day 15 was 21.9–65.6% of that at day 1 of the experiment, and after 86 d it had declined by 42.1% (V) and 47.5% (IV). This suggests that although decreases of respiration and metabolic rate occurred in *C. antarcticus* during storage at +5°C, which were broadly similar to those found for starving Collembola, they were not directly related to the nutritional conditions of the culture. It appears that the decline recorded during storage was a real effect upon metabolism caused by the constant temperature conditions.

Information on metabolic adaptation in oribatid mites to short-term temperature changes was given in Berthet (1964). In contrast to the present diver technique Berthet measured respiratory rates of individual mites in the same diver successively at +15°, +10°, +5° and

°C in one day. The lowering of temperature in his nicro-respirometer by 5°C took approximately one our, but it required a further 30–60 min equilibration at he new, lower temperature to obtain reproducible neasurements. Thereafter, a constant respiration rate vas recorded, although after 12 h of measurement a owering of oxygen consumption was established in ome cases. This effect has been noticed in *C. antarc-cus* when respiratory measurements were continued or 12–18 h at +15°C. A single mite, *Steganacarus mag-us* (Nicolet), was maintained in a diver at +15°C for 48 by Berthet (1964), and at the end of the experiment it ad an oxygen consumption equal to 87% of its initial equirement. Further studies on individuals of four mite pecies showed that after measurement of oxygen up-ake successively at three or four temperatures, and eturning them to +10° or 15°C overnight, and remeasur-g them after 12 h, the oxygen requirement at the end nged from 59% to 121% of that previously measured +10° or +15°C. In the soil mite *Nothrus silvestris* icolet, Webb (1969) found similar values for metabolic te of field and cultured individuals at +10°C. How-er, the mean rates calculated from Webb's data were 0.27 (field animals) and 95.73 (cultured animals) $\mu l\ O_2$ $^{-1}\ h^{-1}$. Thus there was a depression of metabolic rate of ltured individuals at a constant +10°C in this mite. From these observations it is suggested that oribatids pidly adapt their metabolic rate to small variations in mperature. This is supported for other groups by the ta from the present experiment, and by results from her Collembola (Zinkler 1966) and nematodes Nielsen 1949). The data on short-term metabolic adap-tion in small arthropods are very sparse, however, and e response rate of individuals to environmental temp-ature changes, together with the magnitude of the etabolic adjustment, are areas requiring further study. The implications of the results of the present study on *antarcticus* are important for future experimental ork on cold adapted terrestrial micro-arthropods. As tabolism of *C. antarcticus* has been shown to decline pidly and significantly over a few days and continuing er 387 d at constant +5°C, it is necessary to know the cise thermal history of all live material used in future periments. It is important also to improve culture hniques to enable living material to be transported m the field to the laboratory with minimal distur-nce, and in conditions more closely resembling those he field. For respiratory studies, it is essential that all individuals should be acclimated fully to new temperatures and conditions before measurements are made.

Future research should include an evaluation of the physiological and metabolic effects of constant and fluctuating temperature regimes on similar aged individuals in breeding cultures. The accurate simulation of field temperature conditions in the laboratory for polar species such as *C. antarcticus* is a necessary development. This is particularly relevant where there are difficulties due to isolation, equipment or manpower, which effectively prevent such studies being made near the field site. If the magnitude of such temperature induced changes in respiration and metabolic rates of these arthropods can be assessed, a better understanding of both short and long term adaptation which occur under field conditions will be achieved.

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References

Berthet, P. 1964. L'activité des Oribatides (Acari: Oribatei) d'une Chênaie. – Mém. Inst. r. Sci. nat. Belg. 152: 1–152.
Block, W. 1977. Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus* (Acari: Cryptostigmata). – J. exp. Biol. 68: 69–87.
– and Tilbrook, P. J. 1975. Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. – Oikos 26: 15–25.
Nielsen, C. O. 1949. Studies on the soil microfauna II. The soil inhabiting nematodes. – Natura jutl. 2: 1–131.
Tilbrook, P. J. 1970. The biology of *Cryptopygus antarcticus*. – In: Holdgate, M. W. (ed.). Antarctic ecology. Academic Press, London, vol. 2: 908–918.
– Block, W. 1972. Oxygen uptake in an Antarctic collembole, *Cryptopygus antarcticus*. – Oikos 23: 313–317.
Webb, N. R. 1969. Temperature and respiratory metabolism in a species of soil mite. – In: Evans, G. O. (ed.). Proceedings of 2nd. International Congress of Acarology. Hungarian Academy of Sciences, Budapest, 61–66.
– 1975. Respiratory metabolism of *Steganacarus magnus* (Acari). – Oikos 26: 43–46.
Zeuthen, E. 1947. Body size and metabolic rate in the Animal Kingdom with special regard to the marine micro-fauna. – C. r. Lab. Carlsberg Ser. Chim. 26: 15–165.
Zinkler, D. 1966. Vergleichende untersuchungen zur atmungsphysiologie von Collembolen (Apterygota) und anderen Bodenkleinarthropoden. – Z. vergl. Physiol. 52: 99–144.

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Oxygen uptake by Cryptopygus antarcticus (Collembola) at South Georgia

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Determinations of oxygen uptake of size classes I, II, III and IV of the collembolan *Cryptopygus antarcticus* Willem at +5°, +10° and +20°C were made at South Georgia, sub-Antarctic. The relation of respiration rate to live weight was similar at the three temperatures. Oxygen uptake increased with temperature within the range examined (Q_{10} varying from 1.58 to 2.63). Comparison of South Georgia and Signy Island (Antarctic) data for *C. antarcticus* showed similarities between respiration – weight and respiration – temperature curves especially for the +5° to +10°C temperature range. No significant difference in respiration rate was detected between sexes from both locations, but a difference in body size was observed both between sexes, and between sites. The South Georgian specimens were smaller, lighter in weight and appeared to be sexually mature at a smaller size than those at Signy Island. The similarity of metabolism and the body size difference of *C. antarcticus* in the two populations are discussed.

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Проводились определения потребления кислорода коллемболами *Cryptopygus antarcticus* Willem I, II, III и IV размерных классов при 5, 10 и 20°С в южной Джорджии (Субантарктика). Отношение показателей интенсивности дыхания к живому весу одинакого при всех трех температурах. Потребление кислорода повышается с увеличением температуры в исследуемом диапазоне температур (Q_{10} колеблется в пределах 1,58 - 2,63). Сравнения данных для *C. antarcticus* из южной Джорджии и острова Сайни (Антарктида) показали сходство кривых дыхание-вес и дыхание-температура, особенно в интервале 5-10°С. В обоих местообитаниях не было установлено существенных половых различий по интенсивности дыхания, но наблюдались различия в размерах тела и между особями разного пола и между разными местообитаниями. Коллемболы в южной Джорджии мельче, меньшего веса и достигают кажется,половой зрелости при меньших размерах, чем на острове Сайни. Обсуждается сходство показателей интенсивности метаболизма и различия размеров у *C. antarcticus* из двух популяций.

ccepted 23 August 1977
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1. Introduction

Cryptopygus antarcticus Willem is one of the most abundant and widely distributed terrestrial arthropods in the Maritime Antarctic (Tilbrook 1967a, b). Earlier physiological studies on this species (Tilbrook and Block 1972) were concentrated on the oxygen uptake of cultured, acclimated individuals in the U.K., whilst later respiration data were obtained for freshly collected animals at Signy Island in the Antarctic (Block and Tilbrook 1975). The effects of culture and storage at constant temperature (+5°C) on metabolism were subsequently examined by Block and Tilbrook (1977).

This fourth paper presents data on oxygen uptake of *C. antarcticus* on the sub-Antarctic island of South Georgia, which is situated 950 km north of Signy Island, South Orkney Islands. This study was undertaken to provide data for comparison with that obtained for this species in the Antarctic, and thereby to investigate acclimatisation phenomena. Additionally, the study was a prerequisite for future physiological studies of South Georgian arthropods.

2. Methods

C. antarcticus was abundant under decaying organic debris, including litter of tussock grass *Poa flabellata* (Lam.) Hook. f., along the margins of freshwater pools and seal wallows at King Edward Point, close to the British Antarctic Survey station on South Georgia. Live animals were collected from the field immediately prior to the experiment, and hand sorted from tussock litter. Field temperatures at the time of collection were measured with a Grant thermistor model S. Due to time limitations together with the temperature control of the respirometer thermostat, it was not possible to relate the experimental temperature closely to field collection conditions.

Oxygen uptake was determined by a Cartesian Diver micro-respirometer (Zeuthen 1964) established in an unheated building near the research station. The laboratory temperature varied between +5.3°C and +14.2°C during the period when the experiments were conducted in April 1972. Consequently, the respirometer thermostat temperature was only controlled to ±0.05°C. The instrument had seven chambers. The respirometric technique, experimental methods and calculations were as described by Block and Tilbrook (1975), with stoppered divers of gas volume ranging from 2.43 to 15.60 µl. Three experimental temperatures were used: +5°, +10°, +20°C, and a total of 66 determinations made. Measurements of total body length were converted to live weight using the relationship $W = 6.1894\ L^{3.119} \times 10^{-9}$, where W: live weight (µg) and L: length (µm) (Tilbrook and Block 1972). The sex of adult animals was determined where possible (Block and Tilbrook 1975).

3. Results

The experimental animals were grouped into size classes (Tilbrook and Block 1972); size class V individuals being absent from the collections. Several size class II and III animals in the South Georgia samples possessed genital apertures and may well have been sexually mature, whereas previous work at Signy Island on this species has shown that only rarely are size class III individuals able to breed. From these observations and col-

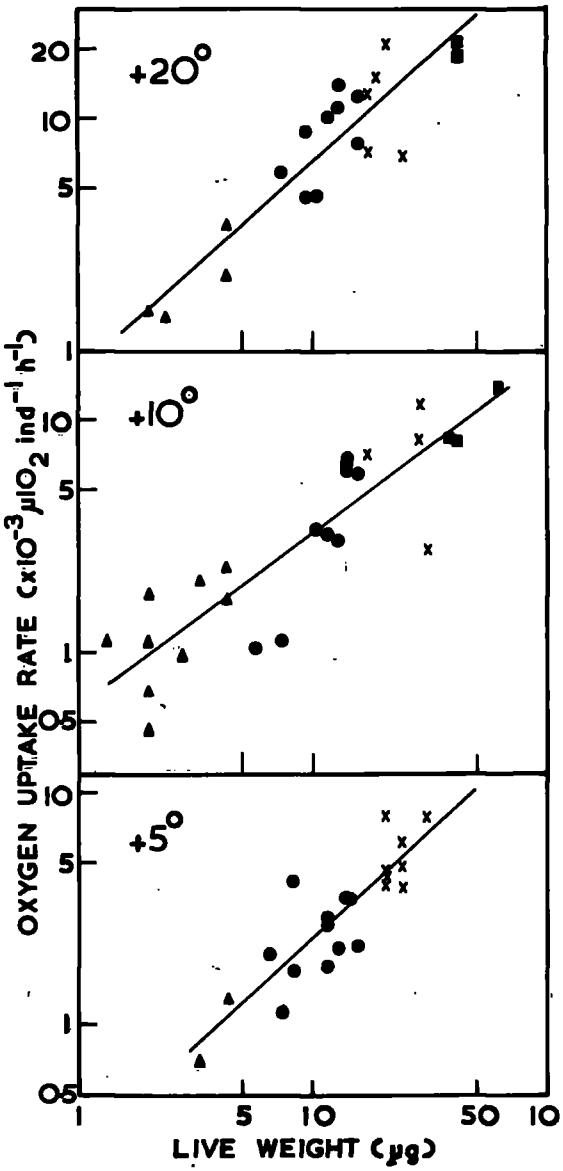

Fig. 1. Oxygen uptake as a function of live weight for *Cryptopygus antarcticus* at +5°, +10° and +20°C at South Georg Data are plotted on a double $\log_{10}$ scale and individual det minations are shown with the fitted linear regression line each temperature. ▲: size class I, ●: size class II, ×: size cl III, ■: size class IV.

Tab. 1. Linear regressions, correlation coefficients and number of determinations for $\log_{10}$ oxygen uptake on $\log_{10}$ live weight for *Cryptopygus antarcticus* at three temperatures. Regressions are given for oxygen uptake rates per individual and per g live weight per hour. Mean live weights and oxygen uptake rates are also given for each temperature.

Temperature (°C)	n	a	b±SE	r (P <0.001)	Mean live weight (µg)	Mean oxygen uptake
x 10^{-3} µl O_2 ind^{-1} h^{-1}						
5	21	0.2824	0.9204 ±0.4391	+0.8723	14.98±1.64	3.535±0.443
10	25	0.5832	0.7543 ±0.0834	+0.8835	14.54±2.99	4.457±0.775
20	20	0.8264	0.9049 ±0.4272	+0.9043	14.87±2.41	9.646±1.389
µl O_2 g^{-1} h^{-1}						
5	21	282.3797	−0.0796 ±0.4391	−0.0232	14.98±1.64	241.93±18.57
10	25	583.1616	−0.2457 ±0.0834	−0.5234	14.54±2.99	387.91±40.12
20	20	775.5384	−0.0726 ±0.4272	−0.1640	14.87±2.41	689.24±51.59

lections of this species from South Georgia and elsewhere, it seems that *C. antarcticus* does not attain the size on South Georgia, South Sandwich Islands and Bouvetøya as found in the Signy Island and Antarctic Peninsula populations.

Oxygen uptake and live weight

Fig. 1 shows the individual determinations of oxygen uptake plotted against live weight on $\log_{10}$ scales for the three experimental temperatures. Tab. 1 provides the linear regression and correlation coefficients for the fitted lines. Oxygen uptake increased with live weight of the animal at the three temperatures. The slopes of the regression lines at +5° and +20°C are very similar; the +10°C line appears to be different probably due to the greater number of size class I determinations at that temperature. A statistical comparison showed that there is no significant change in slope of the respiration-weight line between temperatures. The relationship of oxygen uptake to live weight of *C. antarcticus* is therefore similar at the three temperatures examined at South Georgia. However, overall oxygen uptake of *C. antarcticus* increased with temperature throughout the range studied (Tab. 1).

Examination of the metabolism to live weight relationship (Fig. 2) shows a similar situation with metabolic rate (µl O_2 g^{-1} h^{-1}) decreasing slightly with increasing live weight. As the correlation coefficients (Tab. 1) for all temperatures are low and the regression coefficients are not significantly different from zero, the decrease is not significant.

Comparison of the South Georgian individual respiration data for *C. antarcticus* with those from Signy Island (Block and Tilbrook 1975) at the common temperatures (+5° and +10°C) shows there to be no significant difference between the slopes of the respiration – weight regressions. The metabolism – weight relationship is also similar (Fig. 2). The regression lines from 0°C (Signy Island) and +20°C (South Georgia) have similar slopes to the main data at +5° and +10°C, and their elevations reflect differences in mean oxygen uptake at these temperatures. It is concluded that the relationship between oxygen uptake $individual^{-1}$ and g^{-1} to live weight at +5° and +10°C is similar for the South Georgia and Signy Island populations of *C. antarcticus*.

Oxygen uptake and temperature

The mean (±SE) oxygen uptake rate and live weight for each size class of *C. antarcticus* at the three temperatures examined at South Georgia are given in Tab. 2. The mean live weights of each size class were similar between temperatures. Mean oxygen uptake (×10^{-3} µl O_2 ind^{-1} h^{-1}) of each size class increased with temperature as did mean metabolic rate (µl O_2 g^{-1} h^{-1}). Mean

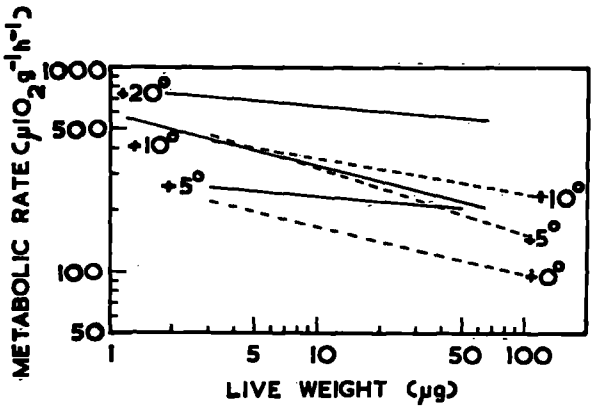

Fig. 2. Metabolic rate as a function of live weight for *Cryptopygus antarcticus* at South Georgia and Signy Island. Data are plotted on a double $\log_{10}$ scale and the linear regression line is shown for each temperature.
———: South Georgia results at +5°, +10° and +20°C
– – – – –: Signy Island results at 0°, +5° and +10°C.

Tab. 2. Mean (±SE) live weights and oxygen uptake rates per individual and per g live weight for four size classes of *Cryptopygus antarcticus* at three temperatures. (n): number of determinations. – : no determination.

Temperature (°C)	Size class	Mean live weight (µg)	Mean oxygen uptake ($\times 10^{-3}$ µl O_2 ind^{-1} h^{-1})	(μl O_2 g^{-1} h^{-1})
5	I	3.83±0.56 (2)	1.024±0.309 (2)	260.83±42.88 (2)
5	II	11.09±0.91 (11)	2.554±0.275 (11)	240.39±31.04 (11)
5	III	23.12±1.26 (8)	5.509±0.589 (8)	239.32±24.78 (8)
5	IV	–	–	–
10	I	2.79±0.35 (10)	1.375±0.214 (9)	539.68±77.16 (9)
10	II	11.78±1.11 (9)	4.145±0.753 (9)	326.76±40.10 (9)
10	III	26.13±3.06 (4)	7.618±1.879 (4)	308.53±77.54 (4)
10	IV	46.58±7.03 (3)	10.421±1.928 (3)	221.90±9.87 (3)
20	I	3.09±0.54 (5)	2.169±0.490 (4)	646.31±85.93 (4)
20	II	11.65±0.94 (9)	8.956±1.42 (9)	768.13±76.08 (9)
20	III	19.51±1.32 (5)	12.639±2.627 (5)	659.98±134.19 (5)
20	IV	40.98±0.0 (2)	20.214±1.115 (2)	493.28±27.10 (2)

respiration rates for both the South Georgia and Signy Island animals are graphed in Fig. 3. This confirms the similarity of the data at +5° and +10°C and suggests that the agreement may be extended over a wider temperature range. This would be more likely for the 0° to +5°C range because this reflects the habitat tempera tures experienced by *C. antarcticus* on the two islands but above +10°C the R-T curves are likely to be diffe rent. In terms of individual respiratory rate size class IV shows the greatest difference at +10°C, but as no result were obtained at +5°C further comparison is precluded For metabolic rates size class I is the most variable fo both populations. Overall there is remarkable similarit in levels of respiration and metabolism of *C. antarcticu* at South Georgia and Signy Island.

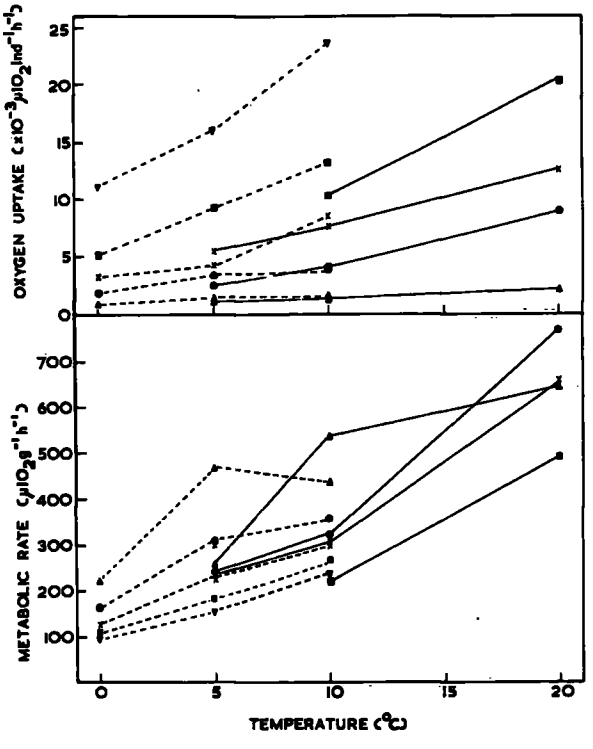

Fig. 3. Mean individual oxygen uptake and mean metabolic rates as a function of temperature for the size classes of *Cryptopygus antarcticus* at South Georgia and Signy Island. ▲: size class I, ●: size class II, ×: size class III, ■: size class IV, and ▼: size class V.
———: South Georgia data.
– – – – –: Signy Island data.

The temperature coefficient (Q_{10}) was calculate from the mean individual respiration rates (Tab. 2) fo each size class over various temperature ranges. Th Q_{10}s are presented and compared to the coefficients fo *C. antarcticus* at Signy Island in Tab. 3. The Q_{10} varie from 1.58 to 2.63 for the South Georgia animals. Siz class II individuals exhibited the highest Q_{10} for all th temperature ranges (2.16 to 2.63). For the componer temperature ranges, size classes I, II and III had lowe Q_{10}s over 10°–20°C than over 5°–10°C. Over the tem perature range 5°–10°C, the South Georgia animals ha slightly higher Q_{10} values than *C. antarcticus* at Sign Island (mean of 2.11 compared to 1.96).

The influence of variable field temperatures at th time of collection on the measured oxygen uptake in th

Tab. 3. Temperature coefficients for various temperature ra ges for four size classes of *Cryptopygus antarcticus* at Sou Georgia compared with Q_{10}s derived for Signy Island anima –: no determination.

Temperature range (°C)	South Georgia			Signy Islan	
	5°–20°	10°–20°	5°–10°	5°–10°	0°–
Size class I	1.65	1.58	1.80	–	4.4
Size class II	2.31	2.16	2.63	1.31	3.6
Size class III	1.74	1.66	1.91	1.74	3.0
Size class IV	–	1.94	–	2.18	2.7
Size class V	–	–	–	2.60	2.4
Mean	2.23	1.83	2.11	1.96	3.2

divers was considered. The field collection temperatures ranged from +1.75° to +4.5°C during the study, and so the respiration rate was always measured at a higher temperature than that of the animal's habitat. On examination of the data, no clear effect of field collection temperature on individual respiration was observed. This may have been due to the small field temperature variation combined with the higher experimental temperature.

Oxygen uptake and sex

As mentioned previously, several size class II individuals were mature, and the overall sex ratio for all the experimental animals was 1♂ : 1.31♀. This is similar to that found at Signy Island (1:1.32). The mean (±SE) live weights (μg) for all the measured animals which could be sexed were: – ♂ : 14.93 ± 2.14, ♀ : 23.34 ± 2.09, but the difference was not significant. These contrast markedly with data from Signy Island: – ♂ : 59.83 ± 4.72, ♀ : 87.79 ± 4.36 (significant at $P < 0.001$), and further emphasizes the distinction between the two populations in terms of body size.

Using pooled data comprising all the size classes at each temperature, both the mean individual respiration and metabolic rates were not significantly different between sexes. There were insufficient data to examine these effects within size classes of *C. antarcticus* at South Georgia. In general, no metabolic differences due to sex have been found for *C. antarcticus* at either site, although the female is significantly heavier than the male in the Signy Island population.

Discussion

Considering the results of the two studies on the metabolism of *C. antarcticus* at South Georgia (present study) and Signy Island (Block and Tilbrook 1975) some preliminary conclusions can be drawn. The relationship of individual oxygen uptake to live weight is essentially similar for the two populations at +5° and +10°C, and there is evidence to suggest that this similarity extends to 0° and +20°C. There are differences in mean respiration rate between temperatures at South Georgia, and similarities of mean respiration rate at the same temperature within size classes in comparing the two populations. Both respiration – temperature and metabolism – temperature curves (Fig. 3) have common features especially in the region of +5° to +10°C. The South Georgia animals had only marginally higher mean Q_{10} values to the Signy Island individuals, and Q_{10} declined with increasing temperature for both. Neither field collection temperature nor sexual maturity appeared to have significant effects on the respiratory rate of individuals from the two sites.

The agreement of the two sets of respiration data suggests that *C. antarcticus* responds similarly to the environmental conditions, especially temperature, during the austral summer at South Georgia and Signy Island. It therefore appears to require larger physical differences between the habitats of this species to produce significant changes in respiration and metabolism.

Mean monthly summer air temperatures at South Georgia (annual mean +1.8°C) typically vary from +1.5°C (October) to +5.3°C (February) (Smith and Walton 1975), whereas at Signy Island (annual mean −3.3°C) the summer range is −2.8°C (October) to +1.3°C (January) (Collins et al. 1975). *C. antarcticus* may therefore experience slightly higher air temperatures at South Georgia compared to Signy Island, but the increase in thermal sum would depend upon the habitat structure and microclimate. Comparable data on the summer temperature regimes within the microhabitats of the two sites are not presently available.

At South Georgia temperatures within vegetation during summer are normally well above ambient (Smith and Walton 1975), being rarely below 0°C near to the surface of moss banks, and approaching +40°C in litter of *Festuca contracta* T. Kirk. The diurnal temperature range in summer within tussocks and litter of *Poa fla-*

ab. 4. Linear regression equations for mean individual respiration (R: x 10^{-3} μl O_2 ind^{-1} h^{-1}) and metabolic (M: μl O_2 g^{-1} h^{-1}) ttes on temperature (T: °C) for each size class of *Cryptopygus antarcticus*. Data for South Georgia and Signy Island are combined r each size class except for V (Signy Island only).

ze class	Equation	P	r
.....	R = 0.7548 + 0.0690 T	<0.01	+0.947
.....	R = 1.0220 + 0.3612 T	<0.001	+0.963
I	R = 3.3342 + 0.4582 T	<0.001	+0.997
/	R = 5.6215 + 0.7116 T	<0.01	+0.967
.....	R = 8.3050 + 1.3726 T	<0.02	+0.989
IV combined	R = 2.3438 + 0.4170 T	<0.01	+0.542
.....	M = 256.1027 + 20.9401 T	<0.01	+0.881
.....	M = 116.2230 + 29.4968 T	<0.001	+0.956
I	M = 96.0512 + 25.9745 T	<0.001	+0.975
/	M = 83.6198 + 19.0797 T	<0.001	+0.974
.....	M = 89.3500 + 14.8100 T	+0.02	+0.989
IV combined	M = 143.9120 + 23.5771 T	<0.001	+0.858

bellata is usually small, eg. +1° to +5°C with a mean of ca. +4°C (Gunn 1976). At Signy Island, extensive data from a *Polytrichum – Chorisodontium* moss turf community (Walton 1977) clearly demonstrate that where *C. antarcticus* is abundant at −1.5 cm in the profile the temperature is between 0° and +5°C for the majority of the time from late October to mid-April in a typical summer. Between 53 and 100% of the hourly temperature records throughout this period are in this range. Only rarely does the temperature exceed +20°C and then for only a short duration (<10% of records). Whilst *C. antarcticus* may experience longer periods of slightly higher temperatures in *Poa flabellata* litter at King Edward Point, South Georgia than in moss banks at Signy Island, the summer microclimate for the two populations may be broadly similar. This would reduce the necessity for metabolic acclimatisation in this species as indicated by the present study.

As the oxygen uptake of *C. antarcticus* is similar for the two areas, the overall relationship of respiration and metabolism to temperature may be examined using the combined data from Fig. 3. Linear regressions were calculated of mean oxygen uptake rates and mean metabolic rates on temperature for each size class and all size classes combined (Tab. 4). These equations form the basis for future computation of the population metabolism of *C. antarcticus*. For size classes I to IV combined, a closer correlation (+0.858) for metabolic rate than for individual respiration rate (+0.542) is obtained. A general equation representing the effect of temperature (T:°C) on metabolism (M: $\mu l\ O_2\ g^{-1}\ h^{-1}$) of size classes I to IV inclusive of *C. antarcticus* was calculated as $\log_{10} M = 2.2355 + 0.0291\ T$ ($n = 23$, $r = +0.850$) for the temperature range 0° to +20°C. This has a lower slope than that derived for ten species of Antarctic terrestrial invertebrates (Block 1977) as $\log_{10} M = 2.2874 + 0.0483\ T$ ($n = 24$, $r = +0.732$) for the range −4° to +22°C.

The temperature coefficient for individual respiration between size classes of *C. antarcticus* ranged from 1.58 to 2.74 (mean 2.16). These are lower Q_{10} values than the mean (3.31) obtained for the Antarctic terrestrial mite *Alaskozetes antarcticus* (Michael) over 0° to +10°C at Signy Island, and for the mean of 3.04 obtained for a range of Antarctic terrestrial invertebrates over −4° to +22°C (Block 1977). The overall response to temperature changes by *C. antarcticus* is not of the same order as most of the other Antarctic terrestrial poikilotherms investigated to date.

There is some geographical variation in the size range of *C. antarcticus* (Tilbrook 1970). In the South Sandwich Islands and Bouvetøya the first instar was similar in size to the Signy Island form, but it did not develop to the same maximum size. The South Georgia material supports these observations in being smaller in terms of total body length.

Because of the difficulty of establishing the number of instars occurring in this species (Tilbrook 1970) all analyses have been carried out using size class categories When comparing data for the two populations of Signy Island and South Georgia, it should therefore be remembered that it is figures for size classes which have been used. The disparity in size range between the two populations and the fact that sexual maturity is apparently reached at a smaller size in the South Georgia animals have already been mentioned. Assuming that *C. antarcticus* has the same number of instars throughout its geographical range and that the full size range was sampled during the Signy Island and South Georgia studies, there is clearly a marked difference between the size of each instar between the two localities. If then the respiration rates of the two populations were compared on a developmental (instar) rather than on a size basis rates for the Signy Island individuals would be progressively higher after the first instar.

The fact that the two sets of data for size classes were so similar, simply emphasises that respiration rate relates to size rather than developmental stage, at least in this non-metamorphosing insect. This being so, and there being some evidence that in Collembola, ecdysis can be induced by factors other than the attainment of a fixed size (Tilbrook 1970), it is clearly important when examining the respiration rate of a field population, to work on a size class basis.

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References

Block, W. 1977. Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus* (Acari : Cryptostigmata). – J. exp. Biol. 68: 69–87.

– and Tilbrook, P. J. 1975. Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. – Oikos 26: 15–25.

– and Tilbrook, P. J. 1977. Effects of long-term storage on the oxygen uptake of *Cryptopygus antarcticus* (Collembola). – Oikos 29: 284–289.

Collins, N. J., Baker, J. H. and Tilbrook, P. J. 1975. Signy Island, Maritime Antarctic. – In: Rosswall, T. and Heal, O. W. (ed.), Structure and function of tundra ecosystems. Ecol. Bull. 20: 345–374. Stockholm, Swedish Natural Science Research Council.

Gunn, T. C. 1976. The autecology of *Poa flabellata* (Lam.) Hook. f. – Ph. D. thesis, University of Manchester.

Smith, R. I. L. and Walton, D. W. H. 1975. South Georgia subantarctic. – In: Rosswall, T. and Heal, O. W. (eds.), Structure and function of tundra ecosystems. Ecol. Bull. 20: 399–423. Stockholm, Swedish Natural Science Research Council.

Tilbrook, P. J. 1967a. The terrestrial invertebrate fauna of the Maritime Antarctic. – Phil. Trans. R. Soc. B. 252: 261–278.

– 1967b. Arthropod ecology in the Maritime Antarctic. – Antarct. Res. Ser. 10: 331–356.

– 1970. The biology of *Cryptopygus antarcticus*. – In: Holdgate M.W. (ed.), Antarctic ecology. Academic Press, London, Vol. 2, pp. 908–918.
– and Block, W. 1972. Oxygen uptake in an Antarctic collembole, *Cryptopygus antarcticus*. – Oikos 23: 313–317.
Walton, D. W. H. 1977. Signy Island Reference Sites: Radiation and soil temperatures 1972–1974. – Br. Antarct. Surv. data. No. 1, Natural Environment Research Council, London.
Zeuthen, E. 1964. Microgasometric methods: Cartesian Divers. – In: Schiebler, T. H., Pearse, A. G. E. and Wolff, H. H. (ed.) 2nd. International Congress of Histo- and Cyto-Chemistry. Wiley, New York, pp. 70–80.

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METABOLIC ADAPTATIONS OF ANTARCTIC TERRESTRIAL MICRO-ARTHROPODS

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Abstract—1. Comparative analyses of standard metabolism, as measured by weight specific oxygen consumption, for Antarctic and temperate terrestrial Acari show that polar forms of the Cryptostigmata and Mesostigmata exhibit an elevation of metabolism of 2–4 times over their normal environmental temperature range.

2. Metabolism–temperature curves of polar and temperate forms are similar for both groups of mites.

3. Q_{10} values for Antarctic mites vary from 1.28 to 3.36, which correspond to the lower portion of the range for temperate species.

4. The elevation of metabolism as a feature of cold adapted poikilotherms is reviewed and discussed.

5. Present evidence suggests that Antarctic terrestrial mites adapt to their low temperature environment by an elevation of standard metabolism.

INTRODUCTION

errestrial Acari or mites are widely distributed roughout the world, and members of this group are mmon inhabitants of the soil and litter community. fact, mites are so cosmopolitan that they are found far north as 80° 87′ N (Slidre Fjiord, Ellesmere land, Canada; Hammer, 1953), and as far south as ° 32′ S (Horlick Mountains, continental Antarctica; ise & Gressitt, 1965). In the absence of higher in-cts, these high latitude tundra communities are minated by Acari together with Collembola, both terms of number of individuals and number of ecies. Both these groups of arthropods provide an portunity for the study of low temperature physi-ogy in general, and of metabolic adaptation and ld tolerance in particular.

Recent studies of oxygen consumption by Antarctic restrial Acari (Block, 1976, 1977; Goddard, 1977*a*, 77*b*) afford an opportunity to compare their tabolism with similar taxa inhabiting more temper-regions. The results demonstrate that Antarctic ecies exhibit an elevation of metabolism at low tem-atures compared to temperate forms, which may termed cold adaptation.

METHODS

he present paper is a synthesis of the available data nite respiration gathered by one method, the Cartesian er micro-respirometer, from a range of species for both ar and temperate habitats.

n order to investigate the way in which the metabolic s of Antarctic terrestrial micro-arthropods, especially Acari, compare to those of temperate species, the data e been analysed as follows. Three orders of free-living s are represented in terrestrial habitats in the maritime arctic as exemplified by Signy Island, South Orkney nds (60° 43′ S, 45° 36′ W). Data from these taxa ther with all the published data for metabolic rates O_2 g^{-1} live weight hr^{-1}) of temperate species have amassed separately for each order, plotted in logarith-mic form against temperature and regression lines fitted by the method of least squares. This allows comparisons to be made between Antarctic and temperate species belonging to the same order. It is considered necessary to treat the three orders of Acari separately on the grounds of differences in size and mode of life.

Members of the Cryptostigmata are well sclerotized mites when adult, of variable size (200–1500 μm in length), and are fungivorous, algivorous or saprophytic. The order is an important component of the soil and surface litter fauna, being widely distributed throughout temperate, tropical and polar areas. It is represented at Signy Island by two species, *Alaskozetes antarcticus* (Michael) and *Halozetes belgicae* (Michael), the former being more abundant. The Mesostigmata are similar in size but may be weakly sclerotized as adults, the body being partly covered by chestnut-brown shields. Its members are either free-living in soil and litter habitats or parasites of both vertebrates and invertebrates. The order is cosmopolitan, and is represented by a single species, *Gamasellus racovitzai* (Trouessart) in the Signy Island fauna. The Prostigmata is the most heterogeneous order of Acari, forms being variable in size and morphology. Its members are mainly phytophagous, but parasitic and predatory forms also occur. The order is cosmopolitan in distribution, and it is the most abundant micro-arthropod group at Signy Island, where seven species occur, the majority of which are minute in size (range 240–750 μm in body length). *Eupodes minutus* (Strandtmann), *Ereynetes macquariensis* (Fain), *Tydeus tilbrooki* (Strandtmann), *Stereotydeus villosus* (Trouessart) and *Nanorchestes antarcticus* (Strandtmann) are the dominant forms. These prostigmatid mites occur in association with mosses and lichens in the maritime Antarctic, but details of their feeding biology are unknown.

RESULTS

The results of the analyses are shown in Figs. 1–4, and the linear regression coefficients are given in Table 1. Figure 1 shows the effect of temperature on $\log_{10}$ metabolic rate of all life stages of cryptostigmatid mites (Oribatei). Regressions have been fitted to the data for the single Antarctic species *Alaskozetes*

Table 1. Linear regression coefficients of $\log_{10}$ metabolic rate ($\mu l\ O_2\ g^{-1}\ hr^{-1}$) on temperature (°C) for Antarctic and temperate species of terrestrial Acari

Taxon	Temperature range (°C)	n	a	$b \pm$ S.E.	r
Cryptostigmata					
(a) All life stages					
Alaskozetes antarcticus	0–10	23	1.9044	0.0471 ± 0.0061	+0.8591
Temperate species (36)	0–15	134	1.4464	0.0656 ± 0.0056	+0.7108
Combined (37)	0–15	157	1.6469	0.0499 ± 0.0049	+0.6360
(b) Adults only					
Alaskozetes antarcticus	0–10	11	1.7831	0.0585 ± 0.0063	+0.9508
Temperate species (36)	0–15	107	1.4630	0.0599 ± 0.0058	+0.7091
Combined (37)	0–15	118	1.5606	0.0523 ± 0.0053	+0.6753
Mesostigmata					
All life stages					
Gamasellus racovitzai	0–10	20	2.4826	0.0330 ± 0.0102	+0.5957
Temperate species (22)	10–25	55	1.7196	0.0687 ± 0.0065	+0.8334
Combined (23)	0–25	75	2.2316	0.0401 ± 0.0041	+0.7512
Prostigmata					
All life stages					
Antarctic species (6)	0–10	29	2.4485	0.0120 ± 0.0165	+0.1392
Temperate species (6)	10–25	15	2.6370	0.0196 ± 0.0059	+0.6739
Combined (12)	0–25	44	2.3948	0.0286 ± 0.0051	+0.6515

The number of observations (n) and the correlation coefficient (r) ($P < 0.001$ throughout) are given.

antarcticus from Block (1977), and for 36 temperate species (Berthet, 1964; Zinkler, 1966; Webb, 1969, 1975; Webb & Elmes, 1972; Wood & Lawton, 1973; Luxton, 1975; Thomas, personal communication). A combined regression line is also shown. The elevation of metabolic rate in the Antarctic species is clearly shown, although there is considerable variability for the different life stages. The data for adult Cryptostigmata only (Fig. 2) provide a better comparison since the variation introduced by the immature and lighter forms is reduced. Again, the increased metabolism of the Antarctic species is evident especially at 0° and 5°C. The slopes of the regression lines for all life stages of the cryptostigmatid mites were tested, and found to be significantly different at $P < 0.02$. However, when adults alone are considered the slopes a similar (Table 1). It is concluded that, in general, t metabolic rate of the Antarctic species is elevat when compared to temperate species at similar te peratures, and that juveniles alter the metabolis temperature relationship, producing a steeper gra ient for the temperate animals compared to the pol species.

Figure 3 displays equivalent data for the ord Mesostigmata. Again, one Antarctic species *Gam sellus antarcticus* (from Goddard, 1977*a*) is compar to 22 temperate species (Webb, 1970; Wood & La ton, 1973; Thurling, 1975). Similar effects are discer ible, with the Antarctic species having elevated me bolic rates, and the slopes of the polar and tempera

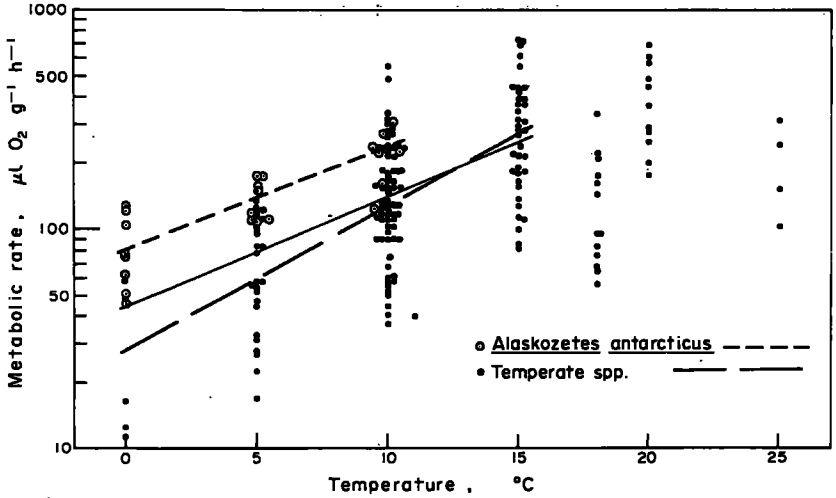

Fig. 1. Relationship of standard metabolism to temperature in terrestrial mites of the order Cryptostigmata. Linear regressions have been fitted to the data for all life stages of *Alaskozetes antarcticus* (----) from Signy Island in the maritime Antarctic, and for 36 species (---) from temperate habitats. A combined regression line (——) is also shown. (Regression equations are given in Table 1.)

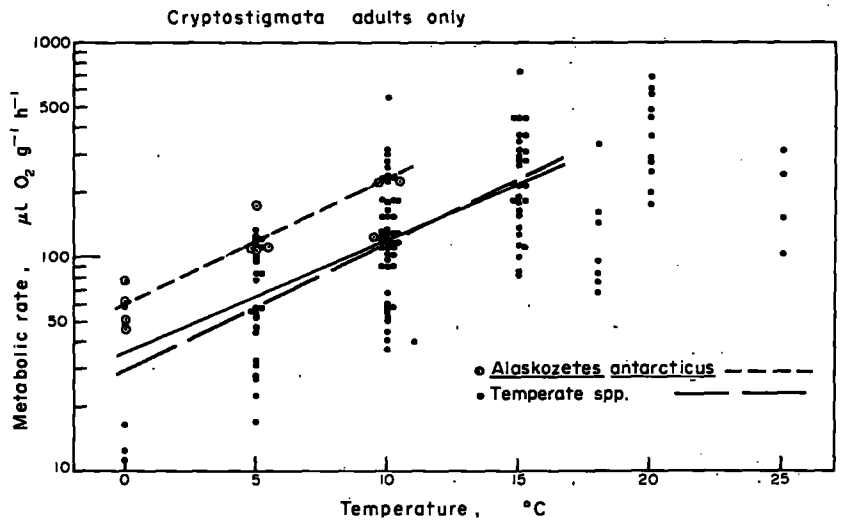

Fig. 2. Relationship of standard metabolism to temperature in adult mites of the order Cryptostigmata. Linear regressions have been fitted as for Fig. 1. (Regression equations are given in Table 1.)

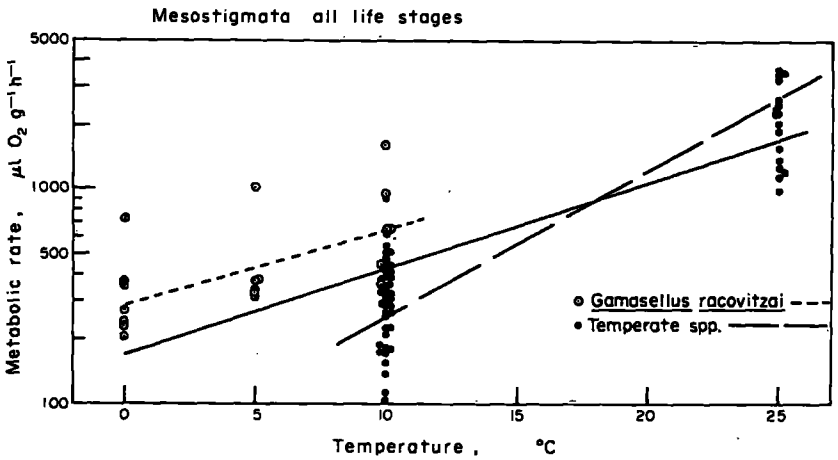

Fig. 3. Relationship of standard metabolism to temperature in terrestrial mites of the order Mesostigmata. Linear regressions have been fitted to the data for all life stages of *Gamasellus racovitzai* (-----) from Signy Island in the maritime Antarctic, and for 22 species (---) from temperate habitats. A combined regression line (——) is also shown. (Regression equations are given in Table 1.)

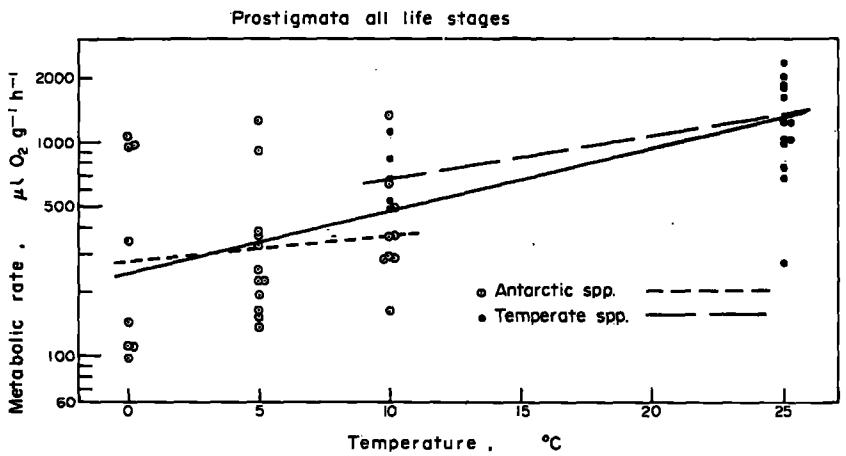

Fig. 4. Relationship of standard metabolism to temperature in terrestrial mites of the order Prostigmata. Linear regressions have been fitted to the data for all life stages of six species (----) from Signy Island in the maritime Antarctic, and for six species (---) from temperate habitats. A combined regression line (——) is also shown. (Regression equations are given in Table 1.)

species regressions differing at $P < 0.01$. There are too few data, however, for final conclusions to be drawn.

The available data for the Prostigmata are shown in Fig. 4. Unfortunately there is insufficient material here for temperate forms—five species measured at 10°C (Wood & Lawton, 1973), and one at 25°C (Thurling, 1975)—although considerable Antarctic data does exist (Block, 1976; Goddard, 1977*b*). Comparison of the slopes of the regressions indicates no significant difference between polar and temperate species, although the Antarctic Prostigmata appear to have lower metabolic rates.

Although only a single Antarctic species has been studied in each of the Cryptostigmata and the Mesostigmata, there is good evidence that despite being relatively heavy animals (only six of the temperate cryptostigmatid species utilized are heavier in live weight terms), which would tend to reduce the metabolic rate, there is distinct elevation of metabolism —by *ca.* two times for the Cryptostigmata and by 3–4 times for the Mesostigmata. This elevation brings their metabolism at Antarctic temperatures to values exhibited by temperate species in their normal temperature range.

As far as temperature coefficients are concerned (Table 2), the Antarctic species of all the orders of Acari are lower than those from temperate habitats over the range 0–10°C. This is most marked in the Mesostigmata. Removal of the juveniles from the Cryptostigmata graph (Fig. 2) shows very similar Q_{10} values (Table 2) for the two groups of mites. The graphical compilation disguises variations between species, so the comparison cannot be taken further, but clearly Antarctic mites have Q_{10} values which fall within the lower portion of the range reported for temperate forms (2–5) over their normal environmental temperature span.

It is worth drawing attention at this stage to the variation between metabolic rates of different Antarctic mites. Working on temperate forms, Wood & Lawton (1973) concluded that besides weight, activity was the most important single factor influencing metabolic rate. They found that, in general, faster moving predatory mites tended to show higher standard metabolic rates than slower moving, non-predatory species of similar size. The available evidence suggests that Antarctic species exhibit the same trend; thus the slow moving, scavenging or herbivorous cryptostigmatid *A. antarcticus* has a lower metabolic rate than the strictly carnivorous, faster movin mesostigmatid, *G. racovitzai*. Since adults of these tw species differ in weight (172.3 and 108.8 μg respect ively) the effects of size have to be eliminated for valid comparison. If a mean (140.5 μg) of the tw adult weights is derived and the metabolism–weigh curves extrapolated to give values that correspond t this mean, then *G. racovitzai* is found to have a leve of metabolism 2–3 times that of the slower movin scavenger.

This of course, poses a problem which is at presen unresolved, namely whether the difference implie that Cartesian Diver microrespirometry is measurin active rather than resting metabolism, or whether means that the resting metabolism of a more activ micro-arthropod is actually higher; in which cas why? Perhaps the more likely explanation is that th maintenance requirement of the more active anima is greater, or alternatively, the metabolic rate diffe ence observed may be simply a reflection of the var ation in degree of sclerotization. In other words, heavily sclerotized mite such as *A. antarcticus*, havin a similar live weight to a lightly sclerotized speci such as *G. racovitzai*, may show a lower standar metabolism merely because it consists of less cellul (respiring) tissue.

Unfortunately, the Prostigmata cannot be fitt into this general picture since their live weights a so much lower than those of the other species co sidered.

Table 2. Temperature coefficients of terrestrial Acari from Antarctic and temperate habitats over 0° to +10°C

Taxon	Q_{10} All life stages	Q_{10} Adults only
Cryptostigmata		
Alaskozetes antarcticus	2.65	3.36
Temperate species (36)	3.89	3.46
Mesostigmata		
Gamasellus racovitzai	1.98	—
Temperate species (22)	4.15	—
Prostigmata		
Antarctic species (6)	1.28	—
Temperate species (6)	1.50	—

DISCUSSION

There are two views concerning the metabolism poikilothermic animals inhabiting cold environmen Present opinion is divided between them since th both appear convincing at first sight. Some worke claim that the standard, or resting metabolism these organisms is elevated at low temperatures co pared to that of temperate species measured at t same temperatures. The implication is that witho this elevation, standard metabolism would fall t low for maintenance purposes. Intuitively this see credible when the ability of polar organisms remain active at temperatures which immobilize th temperate counterparts is considered. Experimen evidence has been forthcoming in support of t hypothesis for several polar animals including f (Scholander *et al.*, 1953; Wohlschlag, 1960, 19 amphipods (Armitage, 1962; Rakusa-Suszczewski Klekowski, 1973), copepods (McWhinnie, 1964) a terrestrial mites (Block, 1977). Proponents of second view, on the other hand, suggest that the st dard metabolism of such poikilotherms is not vated, since this strategy would divert energy fr growth and reproduction and as such would be se tively disadvantageous. Evidence for this has b gathered by Holeton (1973, 1974), Everson (1977) fish, White (1975) for the Antarctic isopod *G tonotus antarcticus* Eights, and Ralph & Max (1977*a* and *b*) for several species of Antarctic ma animals. In addition, Scholander *et al.* (1953) fa to detect elevation of metabolism in the arctic ter trial invertebrates which they studied.

Essentially, this controversy is centred on question of energy utilization, and in particular

partitioning of available resources between growth and reproduction on the one hand, and standard or maintenance metabolism on the other. But the problem disappears if two assumptions are made. The first, which is hardly an assumption in the strict sense because it follows from basic evolutionary principles, is that the standard metabolism of poikilotherms has evolved such that for a given temperature within the normal range experienced by the animal, energy utilization is minimal. This minimum level is sufficient for maintenance of the animal as an organized unit ready for activity, but allows as much as possible of the available energy to be utilized in the production of new tissues and reproductive cells.

Since standard metabolism changes with temperature in many instances (exceptions are quoted in Newell, 1973), it is likely that the maintenance requirement follows a similar trend, that is, it is greater at elevated temperatures and reduced at low temperatures. However, it is debatable whether this relationship holds at temperatures outside the organism's normal range. In the case of a temperate poikilotherm, extrapolation of the metabolism–temperature curve to polar temperatures gives such a low value for metabolism, that it is justifiable to ask whether this is actually sufficient for maintenance. Certainly the abundant evidence for intra-specific acclimation of metabolism and the phenomenon of chill coma suggest otherwise (Bullock, 1955; Prosser, 1958; Prosser & Brown, 1961; Wieser, 1973). In any case, the outcome of the argument depends to some extent on the connotations of the word "maintenance" when used in this context. Thus, if maintenance of an ordered system in the structural sense is meant, then it may well be that a low metabolic rate is sufficient at low temperature. If on the other hand, it is meant to imply the continuation of enzymatic activity, circulation, excretion, muscle tone and digestion in addition to the above, then it is conceivably insufficient. After all, the energy requirement of these processes, which is rate dependent, will only be able to decrease for a limited amount if the animal is to remain potentially active.

The second assumption then is that the level of standard metabolism shown by a temperate organism at polar temperatures is insufficient for active life at those temperatures. In other words, it is suggested that there is a minimum critical threshold of standard metabolism necessary for the maintenance of the organism in a state where it can survive and be active. If this speculative assumption is allowed, then it would be expected that a polar species will exhibit a level of metabolism at a low temperature, which is higher than that of a comparable temperate species measured at the same temperature, but similar to that shown by the latter species at its normal environmental temperature. This is merely an extension of the well documented phenomenon of intra-specific acclimation (Bullock, 1955; Precht *et al.*, 1973; Newell, 1973) to the inter-specific level.

However, it is apparent that the two views outlined above concerning the advantages or otherwise of cold adaptation are reconcilable since the energy involved in maintenance metabolism (using the term in its broad, wider sense) will be similar in both polar and temperate forms when compared at their respective normal habitat temperatures. The question of energy wastage does not therefore arise, provided that in both cases a similar quantity of food energy is ingested, and provided that there is a similarity of metabolism at their respective environmental temperatures.

This conclusion depends entirely on the assumptions made above, so the situation is unresolved, and more evidence is required from a wider range of animal species. It would probably be unwise to suppose that all organisms behave similarly. In the Antarctic, there are vast differences between the environmental conditions experienced by marine and terrestrial poikilotherms, and it is probably justifiable to assume that diverse strategies have evolved in response to differing environmental constraints. Unfortunately the major difficulty in discussions of these matters is that of obtaining reliable and comparable measurements of standard metabolism, partly on account of the variables affecting it (such as size, sex, photoperiod, feeding and cyclic physiological affects), and partly due to the problems involved not only in comparisons between results obtained by different experimental techniques, but also in the techniques themselves.

In conclusion, it appears that the present evidence supports the hypothesis that some terrestrial Antarctic Acari adapt to their low temperature environment by elevation of standard metabolism, in order to achieve (at their normal environmental temperatures) levels comparable to those shown by temperate species at their environmental temperatures. This is probably an adaptation designed to permit active life in hostile surroundings particularly in terms of temperature. Without further evidence, it is difficult to be entirely certain. After all, although zoogeographical evidence (Wallwork, 1973) suggests that the family Podacaridae to which *A. antarcticus* belongs, has experienced a long period of evolution in the Antarctic, the doubt remains that the long life cycle imposed upon this animal by a short growing and reproductive season with a limited heat budget, may give rise to a reduced evolutionary rate and a situation where optimal adaptation cannot be assumed.

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REFERENCES

ARMITAGE K. B. (1962) Temperature and oxygen consumption of *Orchomonella chilensis* (Heller) (Amphipoda: Gammeroidea). *Biol. Bull. mar. biol. Lab., Woods Hole* **109**, 484–503.

BERTHET P. (1964) L'activité des Oribatides (Acari: Oribatei) d'une chênaie. *Mem. Inst. Roy. Sci. Nat. Belg.* **152**, 1–152.

BLOCK W. (1976) Oxygen uptake by *Nanorchestes antarcticus* (Acari). *Oikos* **27**, 320–323.

BLOCK W. (1977) Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus* (Acari: Cryptostigmata). *J. exp. Biol.* **68**, 69–87.

BULLOCK T. H. (1955) Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.* **30**, 311–342.

EVERSON I. (1977) Antarctic marine secondary production and the phenomenon of cold adaptation. *Phil. Trans. R. Soc. B.* **279**, 55–66.

GODDARD D. G. (1977*a*) The Signy Island terrestrial reference sites: VI. Oxygen uptake of *Gamasellus racovitzai* (Trouessart) (Acari: Mesostigmata). *Bull. Br. Antarct. Surv.* **45**, 1–11.

GODDARD D. G. (1977*b*) The Signy Island terrestrial reference sites: VIII. Oxygen uptake of some prostigmatid mites (Acari: Prostigmata). *Bull. Br. Antarct. Surv.* **45**, 101–115.

HAMMER M. (1953) Collemboles and oribatids from the Thule District (North-west Greenland) and Ellesmere Island (Canada). *Meddr Gronland* **135** (5), 16 p.

HOLETON G. F. (1973) Respiration of arctic char (*Salvelinus alpinus*) from a high arctic lake. *J. Fish Res. Bd Can.* **30**, 717–723.

HOLETON G. F. (1974) Metabolic cold adaptation of polar fish: fact or artefact? *Physiol. Zool.* **47**, 137–152.

LUXTON M. (1975) Studies on the oribatid mites of a Danish beechwood soil II. Biomass, calorimetry and respirometry. *Pedobiologia* **15**, 161–200.

MCWHINNIE, M. A. (1964) Temperature responses and tissue respiration in Antarctic crustaceans with particular reference to the krill *Euphausia superba*. *Antarct. Res. Ser. (Am. Geophys. Un.)* **1**, 63–72.

NEWELL R. C. (1973) Environmental factors affecting the acclimatory responses of ectotherms. In *Effects of Temperature on Ectothermic Organisms* (Edited by WIESER W.), pp. 151–164. Springer, Heidelberg.

PRECHT H., CHRISTOPHERSON J., HENSEL H. & LARCHER W. (1973) *Temperature and Life*. Springer, Heidelberg.

PROSSER C. L. (1958) The nature of physiological adaptation. In *Physiological Adaptation* (Edited by PROSSER C. L.), pp. 167–180. American Physiological Society, Washington.

PROSSER C. L. & BROWN F. A. (1961) *Comparative Animal Physiology*. 2nd edn. W. B. Saunders, Philadelphia.

RAKUSA-SUSZCZEWSKI S. & KLEKOWSKI R. Z. (1973) Biology and respiration of the Antarctic amphipod (*Paramoera walkeri* Stebbing) in the summer. *Polskie Archwm Hydrobiol.* **20**, 475–488.

RALPH R. & MAXWELL J. G. H. (1977*a*) The oxygen consumption of the Antarctic limpet *Nacella* (*Patinigera*) *concinna*. *Bull. Br. Antarct. Surv.* **45**, 19–23.

RALPH R. & MAXWELL J. G. H. (1977*b*) The oxygen consumption of the Antarctic lamellibranch *Gaimardia trapesina trapesina* in relation to cold adaptation in polar invertebrates. *Bull Br. Antarct. Surv.* **45**, 41–46.

SCHOLANDER P. F., FLAGG W., WALTERS V. & IRVING L. (1953) Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.* **26**, 67–92.

THURLING D. J. (1975) The energy relations of the mites *Tetranychus cinnabarinus* Boisduval and *Phytoseiulus persimilis* Athias-Henriot. Unpublished Ph.D. Thesis University of Leicester.

WALLWORK J. A. (1973) Zoogeography of some terrestrial micro-Arthropoda in Antarctica. *Biol. Rev.* **48**, 233–259.

WEBB N. R. (1969) The respiratory metabolism of *Nothrus silvestris* Nicolet (Acari). *Oikos* **20**, 294–299.

WEBB N. R. (1970) Oxygen consumption and population metabolism of some mesostigmatid mites (Acari: Mesostigmata). *Pedobiologia* **10**, 447–456.

WEBB N. R. (1975) Respiratory metabolism of *Steganacarus magnus* (Acari). *Oikos* **26**, 43–46.

WEBB N. R. & ELMES G. W. (1972) Energy budget for *Steganacarus magnus* (Acari). *Oikos* **23**, 359–365.

WHITE M. G. (1975) Oxygen consumption and nitrogen excretion by the giant Antarctic isopod *Glyptonotus antarcticus* Eights in relation to cold-adapted metabolism in marine polar poikilotherms. *Proceedings of the 9th European Marine Biology Symposium*, pp. 707–724. Aberdeen University Press, Aberdeen.

WIESER W. (1973) Temperature relations of ectotherms: a speculative review. In *Effects of Temperature on Ectothermic Organisms* (Edited by WIESER W.), pp. 1–23. Springer, Heidelberg.

WISE K. A. J. & GRESSITT J. L. (1965) Far southern animals and plants. *Nature, London.* **207**, 101–102.

WOHLSCHLAG D. E. (1960) Metabolism of an Antarctic fish and the phenomenon of cold adaptation. *Ecology* **41**, 287–292.

WOHLSCHLAG D. E. (1964) Respiratory metabolism and ecological characteristics of some fishes in McMurdo Sound, Antarctica. *Antarct. Res. Ser. (Am. Geophys. Un.)* **1**, 33–62.

WOOD T. G. & LAWTON J. H. (1973) Experimental studies on the respiratory rates of mites (Acari) from beech woodland leaf litter. *Oecologia, Berl.* **12**, 169–191.

ZINKLER D. (1966) Vergleichende untersuchungen zur Atmungsphysiologie von Collembolan (Apterygota) und anderen Bodenkleinarthropoden. *Z. vergl. Physiol.* **53**, 99–144.

STUDIES IN THE ECOLOGY AND PHYSIOLOGY OF FREE-LIVING TERRESTRIAL ARTHROPODS

by

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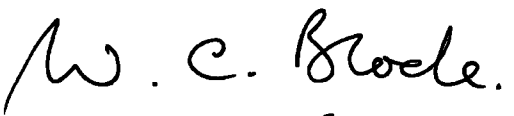
Being a thesis presented in candidature for the degree of Doctor of Science of the University of Durham

1986

CONTENTS

DECLARATION

The material included in this thesis has not been submitted, in whole or in part, for a degree in this or any other University. In the case of the joint publications listed, each author has contributed equally to each.



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ABSTRACT

William Charles Block

Studies in the ecology and physiology of free-living terrestrial arthropods

The underlying theme of the research has been to enlarge the knowledge and understanding of the ecological processes in selected soil ecosystems. The organisms utilised are micro-arthropods - the Acari (mites) and Collembola (springtails). The work began with ecological studies on communities of upland soils in Britain, followed by tropical systems in Uganda and lowland heaths in East Anglia. The investigation later concentrated on the ecophysiology of species inhabiting cold environments (Arctic, Alpine and Antarctic), and this has formed the major part of the work.

A study of the metabolic rate of cold adapted mites and springtails showed that some Antarctic species have greatly elevated rates (2-3 times) compared with similar temperate forms over their normal environmental temperature range. This phenomenon is linked to an ability to avoid body freezing down to temperatures approaching -35°C by the physical process of supercooling. Supercooling is enhanced by antifreeze substances, polyhydric alcohols such as glycerol. These are synthesized in arthropods in response to low temperatures and dehydration at the onset of winter. Experiments on water droplets and mites led to the conclusion that whole body freezing points of intact arthropods are depressed by more than twice their haemo-lymph freezing point depression at any given glycerol concentration. The process of heterogeneous nucleation and the respective roles of gut nucleators, cooling rate and body water were evaluated. Reduced body water content lowers nucleator activity in the Antarctic arthropods studied.

Extrapolating the experimental results to field populations of Antarctic species and the seasonal changes in their cold resistance, an integrated life cycle strategy was demonstrated and its evolutionary implications outlined. A hypothesis has been formulated suggesting that colonisation and occupancy of cold environments by terrestrial arthropods has occurred by the development and extension of pre-existing physiological mechanisms found in related species of warmer habitats.

RESEARCH CONTRIBUTION

My general objective has been to develop the understanding of natural processes occurring within terrestrial ecosystems and of the soil invertebrates in particular. My specialized interest is in the contribution made by free-living arthropods, especially the mites and Collembola, to the integrity and functioning of the soil ecosystem. This has involved a study of their ecological distribution, population dynamics, nutrition and energetics, life cycles and their interrelations with the environment and ecophysiology.

In the 26 years since 1960 when I started my research, the work may be divided into two interconnected phases. Firstly, the ecological studies on micro-arthropods and insects of moorland soils (Durham University), tropical habitats (Makerere University) and Breckland heath communities (Cambridge and Leicester Universities), which form publications numbered 1-7, 19, 41, 44-47. Secondly, the development of my research into studies of the ecological physiology of species inhabiting cold environments (Leicester University and British Antarctic Survey), which resulted in the publications numbered 8-18, 20-40, 42, 43, 48-61. The second phase constitutes my major research contribution and has involved extensive physiological work on respiration and energetics, on cold tolerance and at present, water balance studies. Experiments and fieldwork have been undertaken on a range of arthropod species in Arctic, Alpine and Antarctic environments.

During the first phase of research, I reported the first quantitative information on population density and biomass of one of the most abundant arthropod groups - the Acarina - in moorland soils, and concluded that fluctuations in numbers were directly related to their breeding cycles which were primarily controlled by climate. The influence of cultivation practices and soil organic matter on arthropod and earthworm populations was demonstrated for tropical Ugandan soils. Finally, significant changes in the age structure, cohorts and longevity of two populations of an isopod (Armadillidium vulgare) in Breckland grass heaths were related to grazing affecting habitat structure and heterogeneity.

In the second and more extensive phase of my research, several major contributions were made in the field of low temperature biology as follows:

(a) Obtained the first comprehensive data on the respiratory metabolism of Antarctic species of micro-arthropods and thereby provided evidence for cold adaptation (by elevation of standard metabolic rate by 2-3 times).

(b) Showed that almost 80% of the energy assimilated may be utilized in respiration in cold-adapted species.

(c) Demonstrated the extensive capacity for freezing avoidance by supercooling in Antarctic poikilotherms (to -35°C in some species), and determined the effects of low temperature and desiccation on individual supercooling points and anti-freeze levels.

(d) Discovered with S.R. Young that dehydration of the mite Alaskozetes antarcticus stimulated glycerol synthesis and, experimenting with mites and pure water droplets, determined that the supercooling points of biological systems are depressed by more than twice the melting point depression at any given glycerol concentration.

(e) Obtained the only substantial body of information on field levels of freezing resistance, anti-freeze profiles, chill-coma and survival characteristics for a representative range of maritime Antarctic species. These have been integrated into a composite picture of their life cycle strategies, the evolution of which has been discussed.

(f) Pursued fundamental studies of heterogeneous nucleation in supercooled micro-arthropods with respect to cooling rate, probability of freezing, gut nucleators and body water. With R.J.C. Cannon, I highlighted the importance of water for nucleator activity in winter-hardened and summer forms in the Antarctic.

(g) Advanced the hypothesis that the colonisation and continued occupancy of cold environments by terrestrial arthropods have not necessitated the evolution of specific and novel

physiological and/or biochemical mechanisms. The mechanisms utilized result from the extension and development of pre-existing ones found in a wide range of species inhabiting much less severe climatic zones.

My current research is directed along two lines. Firstly, I am investigating the water economy of physiologically different species of Antarctic arthropods to determine their resistance profiles over the normal environmental temperature range, and the role of body water in their tolerance to freezing temperatures. Secondly, the elucidation of the physical parameter(s) which provide the environmental trigger(s) for seasonal changes in cold resistance of such species. In both lines, the experimental approach is integrated with field studies. It is suggested that the results of my research contribute not only to the general theory of invertebrate cold tolerance, but also help to explain the present day distribution of the south polar land fauna with respect to colonisation and evolution.

PUBLICATIONS

A. MAJOR PUBLICATIONS (REFEREED)

1. Block, W. 1965. The life histories of Platynothrus peltifer (Koch 1839) and Damaeus clavipes (Hermann 1804) (Acarina : Cryptostigmata) in soils of Pennine moorland. Acarologia 7: 735-743.

2. Block, W. 1965. Distribution of soil mites (Acarina) on the Moor House National Nature Reserve, Westmorland, with notes on their numerical abundance. Pedobiologia 5: 244-251.

3. Block, W. 1966. The distribution of soil Acarina on eroding blanket bog. Pedobiologia 6: 27-34.

4. Block, W. 1966. Seasonal fluctuations and distribution of mite populations in moorland soils, with a note on biomass. Journal of Animal Ecology 35: 487-503.

5. Block, W. 1967. Recovery of mites from peat and mineral soils using a new flotation method. Journal of Animal Ecology 36: 323-327.

6. Block, W. & Banage, W.B. 1968. Population density and biomass of earthworms in some Uganda soils. Revue d'écologie et de Biologie du Sol 5: 515-521.

7. Block, W. 1970. Micro-arthropods in some Uganda soils. In Phillipson, J. (ed.), "Methods of study in soil ecology". Proceedings of UNESCO/IBP Symposium: pp.195-202. Unesco, Paris.

8. Tilbrook, P.J. & Block, W. 1972. Oxygen uptake in an Antarctic collembole Cryptopygus antarcticus. Oikos 23: 313-317.

9. Block, W. & Tilbrook, P.J. 1975. Respiration studies on the Antarctic collembolan Cryptopygus antarcticus. Oikos 26: 15-25.

10. Block, W. 1977. Oxygen consumption of the terrestrial mite Alaskozetes antarcticus (Acari: Cryptostigmata). Journal of Experimental Biology 68: 69-87.

11. Block, W. & Tilbrook, P.J. 1977. Effects of long-term storage on the oxygen uptake of Cryptopygus antarcticus (Collembola). Oikos 29: 284-289.

12. Block, W. & Tilbrook, P.J. 1978. Oxygen uptake by Cryptopygus antarcticus (Collembola : Isotomidae) at South Georgia. Oikos 30: 61-67.

13. Block, W. & Young, S.R. 1978. Metabolic adaptations of Antarctic terrestrial micro-arthropods. Comparative Biochemistry & Physiology 61A: 363-368.

14. Block, W. & Young, S.R. 1979. Measurement of supercooling in small arthropods and water droplets. Cryo-Letters 1: 85-91.

15. Young, S.R. & Block, W. 1980. Some factors affecting metabolic rate in an Antarctic mite. Oikos 34: 178-185.

16. Young, S.R. & Block, W. 1980. Experimental studies on the cold tolerance of Alaskozetes antarcticus. Journal of Insect Physiology 26: 189-200.

17. Block, W. 1980. Survival strategies in polar terrestrial arthropods. Biological Journal of the Linnean Society 14: 29-38.

18. Block, W. 1980. Aspects of the ecology of Antarctic soil fauna. In Dindal, D.L. (ed.), "Soil biology as related to land use practices" Proceedings of the VII International Colloquium of Soil Zoology, pp.741-757. Environmental Protection Agency, Washington, D.C.

19. Al-Dabbagh, K.Y. & Block, W. 1981. Population ecology of a terrestrial isopod in two Breckland grass heaths. Journal of Animal Ecology 50: 61-77.

20. Block, W. 1981. Terrestrial arthropods and low temperature. Cryobiology 18: 436-444.

21. Block, W. 1982. Supercooling points of insects and mites on the Antarctic Peninsula. Ecological Entomology 7: 1-8.

22. Block, W. & Sømme, L. 1982. Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. Oikos 38: 157-167.

23. Sømme, L. & Block, W. Cold hardiness of Collembola at Signy Island, maritime Antarctic. Oikos 38: 168-176.

24. Block, W. 1982. The Signy Island terrestrial reference sites: XIV. Population studies on the Collembola. British Antarctic Survey Bulletin No.55: 33-49.

25. Block, W. 1982. Respiration studies on some South Georgian Coleoptera.
Comité national français des recherches antarctiques No.51: 183-192.

26. Block, W. 1982. Cold hardiness in invertebrate poikilotherms.
Comparative Biochemistry & Physiology 73A: 581-593.

27. Block, W. 1983. Heterogeneous ice nucleation in supercooled micro-arthropods.
Cryo-Letters 4: 155-162.

28. Block, W. & Sømme, L. 1983. Low temperature adaptations in beetles from the sub-Antarctic island of South Georgia.
Polar Biology 2: 109-114.

29. Sømme, L. & Block, W. 1984. Ecophysiology of two inter-tidal mites at South Georgia.
Oikos 42: 276-282.

30. Block, W. 1984. A comparative study of invertebrate supercooling at Signy Island, maritime Antarctic.
British Antarctic Survey Bulletin No.64: 67-76.

31. Block, W., Burn, A.J. & Richard, K.J. 1984. An insect introduction to the maritime Antarctic.
Biological Journal of the Linnean Society 23: 33-39.

32. Block, W. 1985. Arthropod interactions in an Antarctic terrestrial community.
In Siegfried, W.R., Condy, P. & Laws, R.M. (eds.), "Nutrient cycling and food webs in the Antarctic", pp.614-619.
Springer-Verlag, Berlin.

33. Cannon, R.J.C., Block, W. & Collett, G.D. 1985. Loss of supercooling ability in Cryptopygus antarcticus (Collembola: Isotomidae) associated with water uptake.
Cryo-Letters 6: 73-80.

34. Worland, M.R. & Block, W. 1986. Survival and water loss in some Antarctic arthropods.
Journal of Insect Physiology 32: 579-584.

35. Schenker, R. & Block, W. 1986. Micro-arthropod activity in three contrasting terrestrial habitats on Signy Island, maritime Antarctic.
British Antarctic Survey Bulletin No.71: 31-43.

36. Block, W., Turnock, W.J. & Jones, T.H. Cold resistance and overwintering survival of the cabbage root fly Delia radicum (Anthomyiidae), and its parasitoid Trybliographa rapae (Cynipidae) in England.
Oecologia (Berlin) (in press).

37. Heal, O.W. & Block, W. Soil biological processes in the north and south polar regions.
Ecological Bulletins (Stockholm) (in press).

38. Block, W. Adaptations of polar arthropods to cold.
Biological Reviews (submitted).

39. Block, W., Cannon, R.J.C., Worland, M.R., Richard, K.J., Collett, G.D. & Hemmings, A.D. Long-term fluctuations in cold hardiness of terrestrial arthropods at Signy Island, Antarctica.
Comparative Biochemistry & Physiology (in preparation).

40. Cannon, R.J.C. & Block, W. Arthropod cold hardiness: the evidence from Antarctica.
Cryobiology (in preparation).

C. MINOR PUBLICATIONS

44. Block, W. 1966. Some Arctic Oribatei.
Acarologia 8: 161-162.

45. Block, W. 1966. Some characteristics of the Macfadyen high gradient extractor for soil micro-arthropods.
Oikos 17: 1-9.

46. Block, W. 1968. Some lamellicorn beetles (Col., Scarabaeoidea) from East Africa.
Entomologist's Monthly Magazine 103: 284-285.

47. Block, W. 1968. Ticks from waterbuck and warthog in the Queen Elizabeth National Park, Uganda.
East African Wildlife Journal 6: 140-141.

48. Block, W. 1976. Oxygen uptake by Nanorchestes antarcticus (Acari).
Oikos 27: 320-323.

49. Block, W., Young, S.R., Conradi-Larsen, E.-M. & Sømme, L. 1978. Cold tolerance of two Antarctic terrestrial arthropods.
Experientia 34: 1166-1167.

50. Block, W. 1979. Cold tolerance of micro-arthropods from Alaskan taiga.
Ecological Entomology 4: 103-110.

51. Block, W. 1979. Oxygen consumption of the Antarctic springtail Parisotoma octooculata (Willem) (Isotomidae).
Revue d'écologie et Biologie du Sol 16: 227-233.

52. Block, W. 1979. Terrestrial invertebrates.
In Furse, C., "Elephant Island - Antarctic Expedition".
Appendix E: 226-229.
Anthony Nelson, Shrewsbury.

53. Block, W. 1979. Nanorchestes antarcticus Strandtmann (Prostigmata) from Antarctic ice.
Acarologia 21: 173-176.

54. Block, W. & Zettel, J. 1980. Cold hardiness of some Alpine Collembola.
Ecological Entomology 5: 1-9.

55. Block, W. 1981. Low temperature effects on micro-arthropods.
Journal of Thermal Biology 6: 215-218.

56. Block, W. 1983. Low temperature tolerance of soil arthropods - some recent advances.
In Lebrun, P. et al. (eds.), "New Trends in Soil Biology", pp.427-431.
Dieu-Brichart, Louvain-la-Neuve.

57. Fain, A., Sømme, L. & Block, W. 1983. Hyadesia maxima sp. n. (Acari, Hyadesiidae) from South Georgia.
Bulletin Annuale de la Société royale de belge Entomologique 119: 171-176.

58. Block, W. 1985. Antarctic: Survival on land. Biologist 32 (3): 133-138.

59. Block, W. 1985. Ecological and physiological studies of terrestrial arthropods in the Ross Dependency, Antarctica. British Antarctic Survey Bulletin No. 68: 115-122.

60. Block, W. & Christensen, B. 1985. Terrestrial Enchytraeidae from South Georgia and the maritime Antarctic. British Antarctic Survey Bulletin No. 69: 65-70.

61. Block, W. 1986. Seasonal changes in cold resistance of soil arthropods. IX International Colloquium of Soil Zoology, Moscow 1985 (in press).

PUBLISHED PAPERS

Cryo-Letters 1, 85 - 91(1979).

MEASUREMENT OF SUPERCOOLING IN SMALL ARTHROPODS AND WATER DROPLETS

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SUMMARY

Methods employed for the determination of supercooling points of the Antarctic mite *Alaskozetes antarcticus* and of water droplets are described and the results are compared. In both systems, a given quantity of glycerol depresses the supercooling point more than it does the melting point, but this effect is more marked in the mites.

KEY WORDS

Supercooling, Glycerol, Heterogeneous nucleation, Antarctic mite.

INTRODUCTION

The survival of low temperatures by certain arthropod species depends on the ability to supercool, ie. to avoid tissue freezing at temperatures below the melting point of their body fluids. It has often been demonstrated that glycerol depresses temperatures of spontaneous body freezing, or supercooling points, of insects and other arthropods[1,2], particularly of those that do not tolerate freezing. It has also been reported[3] that glycerol and other solutes lower the homogeneous nucleating temperature of water. In animals, however, nucleation is more frequently heterogeneous, ie. foreign particulate matter acts as a centre for ice crystal formation[4]. This is apparent since freezing occurs at temperatures above the homogeneous nucleating temperature of water. In this paper, the effect of glycerol on the heterogeneous nucleating temperatures of individuals of the Antarctic terrestrial mite *Alaskozetes antarcticus* (Michael) and of small water droplets is described, together with an account of the techniques employed.

MATERIALS AND METHODS

The cooling equipment used in these experiments (Fig. 1) consisted of a glass walled methanol bath (c. 1.5 ℓ volume), the temperature of which was controlled by an immersion cooler (Neslab Cryocool CC-100) and a 0.5 kW immersion heater. The latter was switched by a controller (Neslab Exatrol) linked to a temperature programmer (Neslab ETP 3) that could be used for constant temperature operation or for linear cooling rates up to a maximum of $1.5^{\circ}C\ min^{-1}$. Information was relayed to the temperature controller from a platinum resistance sensor immersed in the bath, while mixing was accomplished by means of a motor driven stirrer. Polystyrene insulation surrounded the bath and the apparatus was situated in a perspex box.

Animal supercooling points were measured by attaching the mites (with small spots of grease) to 36 swg copper-constantan thermocouples (1-5 mites $thermocouple^{-1}$) contained in air-filled glass tubes (Fig. 2), and suspended vertically in the bath from a polystyrene float. A six-channel potentiometric chart recorder (Mitsui DBE 6) displayed body temperature traces from the thermocouples, and supercooling points were identified by the release of latent heat of fusion which caused a temporary, but distinct, rise in body temperature. A cooling rate of $1^{\circ}C\ min^{-1}$ was used; since supercooling points vary with rate of cooling, Salt[4] has recommended that this rate be used for comparative purposes.

Supercooling points were measured in individual mites after several different acclimation regimes. These experiments are reported fully elsewhere [5].

The following technique was employed for the measurement of supercooling points of distilled water droplets. The exterior surface of a glass capillary (3 mm o.d.) was coated with a thin layer of paraffin wax and water droplets of c. 1 mm diameter (similar in size to the mites) were applied to this coating using a micropipette. It was found that surface tension forces were sufficient to prevent spreading or running of droplets in the appropriate size range. The capillary was inserted vertically into an air-filled glass tube and held away from the sides and base of the tube by means of a cork. This assembly was suspended in the cooling bath from a polystyrene float.

A light beam was passed through the bath from rear to front via holes cut into the insulation, and crossed polarizing filters were inserted into the light path (one on each side of the sample holder). The droplets were observed during cooling ($1^{\circ}C\ min^{-1}$) by means of a horizontal microscope and spontaneous freezing detected by the effect of the ice crystals on the plane of polarization. Temperatures were read on an alcohol in glass thermometer in the bath, and were in close agreement with values obtained simultaneously by means of thermocouples inside air filled tubes in the bath.

The supercooling points of 12 to 14 droplets were measured at each of four glycerol concentrations.

RESULTS AND DISCUSSION

Supercooling points of individual mites were in the range $-2^{\circ}C$ to $-35^{\circ}C$ depending on their acclimation conditions and feeding state, while glycerol concentrations varied from 0 to c. 50 $\mu g\ mg^{-1}$ body water (approximately 0.5 molal). Glycerol concentrations were linearly related to mean supercooling points of non-feeding animals, which varied from -26.5° to $-30^{\circ}C$. Assuming that glycerol was the only solute varying in concentration in the experiments and therefore the only solute responsible for the observed lowering of the supercooling point, this relationship can be expressed in the form of a ratio of supercooling point depression to melting point depression induced by glycerol. Such an analysis shows that supercooling points of *A. antarcticus* are depressed by $3.26^{\circ}C$ by the amount of glycerol that would, theoretically, be expected to lower the haemolymph melting point by $1^{\circ}C$[6]. Because other solutes are present, although there is no evidence that they vary in concentration, this is only an approximation.

Measurement of melting points of body fluid from individuals with different glycerol concentrations was attempted in order to check this

relationship, but since *A. antarcticus* possesses a viscous haemolymph containing many lipid droplets, ice crystals were only observed with difficulty. However, five samples were measured (with a Clifton Technical Physics Nanolitre Osmometer) at a single glycerol concentration. The mean (± S.E.M.) haemolymph melting point was -1.46 ± 0.044°C. The lowering of the melting point due to a glycerol concentration of the magnitude involved was found (from tables) to be -0.21°C; the haemolymph melting point depression due to other solutes was therefore -1.25°C to a first approximation. This value is lower than that reported[7] for most insects (-0.5° to -0.9°C), but is comparable to other arachnids and cold hardy insects[6].

The results of the water droplet experiments are shown in Fig. 3. It is clear that heterogeneous nucleation occurred, since individual values ranged from -15° to -30°C. There is much variation (presumably due to differences in contaminant nucleating efficiency) but a linear regression of supercooling points on glycerol concentrations yielded a regression coefficient that differed significantly from zero ($P < 0.001$). Consequently it was concluded that glycerol depresses temperatures of heterogeneous nucleation in water. Expressing the results in a form compatible to those obtained for *A. antarcticus* showed that supercooling point depression was equal to 2.17°C per degree of calculated melting point depression.

In a study of homogeneous nucleation, MacKenzie[3] showed that supercooling points were lowered by about twice the melting point depression by a variety of solutes (sucrose, glucose, ethylene glycol, sodium chloride, urea, ammonium fluoride and glycerol in single solute systems). This relationship was linear over a wide range of solute concentrations (0° to -20°C melting point depression). However, there were exceptions to this uniform behaviour; these were two polyethylene glycols which lowered supercooling points by 5°C per degree of melting point depression.

These results, together with those of the present study raise two issues that demand further study. The first is that glycerol appears to exert a similar effect on both heterogeneous and homogeneous nucleating temperatures in water. This resemblance could be coincidental, in that it might have arisen out of the particular conditions used in the present experiments. Further studies are required to rule out this possibility. Additionally, it is difficult to imagine a mechanism whereby glycerol and other solutes could exert a predictable and regular influence on supercooling both in the presence and absence of foreign nucleating agents. However, Lusena[8] found supercooling points of water to be affected only

to the same extent as melting points by solutes, in the presence of a highly efficient nucleating agent.

The second issue concerns the apparent dissimilarity between the animal and physical systems that emerges from the present experiments. These relationships are shown in Fig. 4 (lines 1 and 3) together with MacKenzie's data[3] (line 2) and two approximate relationships drawn from the literature on insect supercooling. Line 4 based on the work of Salt[1] has a gradient of c. 1.3, but that from a study by Sømme[9] possesses a slope of 3.71. The latter case is significant because it is derived from the average of the gradients of six supercooling points - solute concentration regression lines (which did not differ significantly) divided by the average of the gradients of three melting point - solute concentration regression lines, based on melting point determinations, rather than on theoretical values.

The latter relationship, together with the present results, suggests that, despite the behaviour of aqueous solutions, the supercooling points of biological systems may be depressed by more than twice the melting point depression at any given glycerol concentration. This may be of considerable adaptive significance in cold tolerant arthropods. However, research is required to obtain further evidence and to elucidate the mechanisms involved.

ACKNOWLEDGEMENTS

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REFERENCES

1. R.W. Salt, Canadian Journal of Zoology 37, 59-69 (1959).
2. L. Sømme, Canadian Journal of Zoology 42, 87-101 (1964).
3. A.P. MacKenzie, Philosophical Transactions of the Royal Society of London Series B 278, 167-189 (1977).
4. R.W. Salt, Annual Review of Entomology 6, 55-74 (1961).
5. S.R. Young and W. Block, Journal of Insect Physiology (in press).
6. S.R. Young, Unpublished Ph.D. Thesis, University of Leicester (1979).
7. D.W. Sutcliffe, Comparative Biochemistry and Physiology 9, 121-135 (1963).
8. C.V. Lusena, Archives of Biochemistry and Biophysics 57, 277-284 (1955).
9. L. Sømme, Journal of Insect Physiology 13, 805-814 (1967).

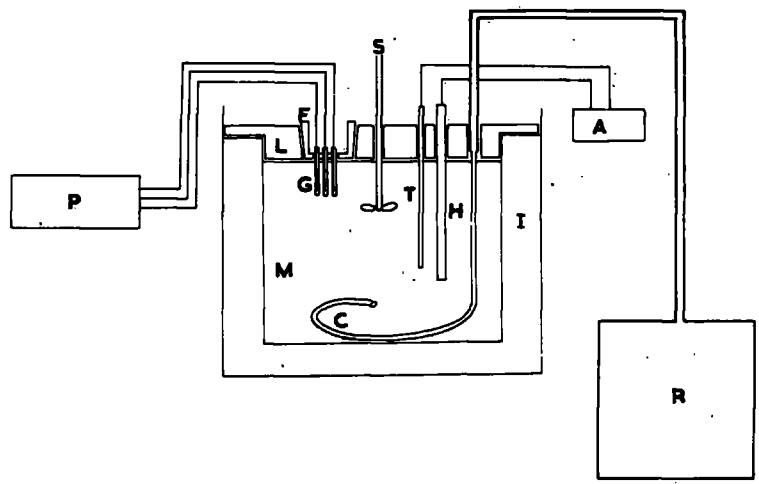

Fig. 1. Apparatus for measurement of supercooling points. M: methanol bath, C: cooling coil, R: compressor unit, H: heater, T: temperature sensor, A: thermostat and temperature programmer, S: stirrer, I: polystyrene insulation, L: insulated lid, F: polystyrene float, G: thermocouple assembly, P: potentiometric recorder.

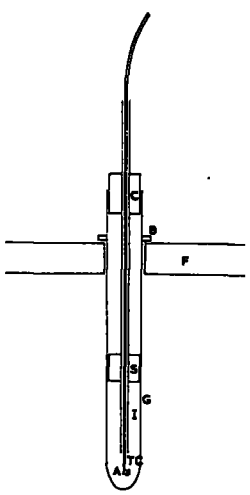

Fig. 2. Thermocouple assembly. F: polystyrene float, G: outer glass tube, I: inner glass tube, TC: thermocouple tip, S: spacer, C: cork, B: rubber band.

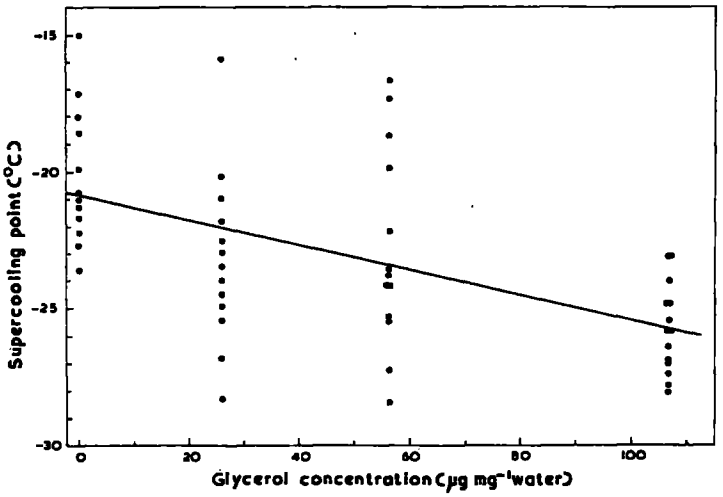

Fig. 3. Effect of various concentrations of glycerol on the supercooling points of individual droplets of distilled water. The linear regression line is described by the equation Y = -20.85 - 0.046X, where Y: supercooling point, X: glycerol concentration (S.E. of regression coefficient: ± 0.010, t: 4.575, P<0.001, d.f.: 50).

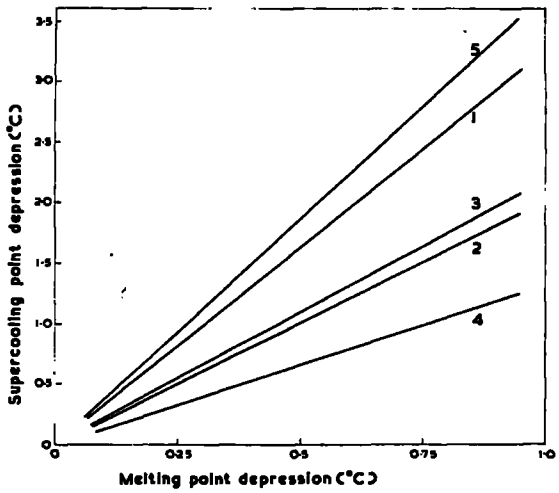

Fig. 4. Relation between melting point depression and supercooling point depression. 1: *Alaskozetes antarcticus* 2: mean line redrawn from Mackenzie[3], 3: experimentally obtained relationship for water droplets plus glycerol, 4: derived from results of Salt[1] for *Bracon cephi*, 5: line derived from Sømme[9] (see text).

OIKOS 34: 178–185. Copenhagen 1980

Some factors affecting metabolic rate in an Antarctic mite

S. R. Young and William Block

Young, S. R. and Block, W. 1980. Some factors affecting metabolic rate in an A
tarctic mite. – Oikos 34: 178–185.

1. Determinations of live weight-specific oxygen consumption (metabolic rate)
adults of the Antarctic terrestrial mite *Alaskozetes antarcticus* (Michael) showed th
starvation resulted in metabolic suppression.
2. Food materials were shown to influence metabolic rates and depletion of oxyg
concentration in Cartesian Divers resulted in decreased oxygen uptake.
3. The effects of sex and reproductive condition on metabolic rates were explicab
on the basis of weight differences between males, gravid females and non-grav
females.
4. Long periods of laboratory culture tended to result in lower weights and metabo
rates, but short term temporal variation in weight-specific oxygen consumpti
within individuals was also demonstrated.
5. Oxygen consumption rates of adult *A. antarcticus* were measured at –4°C a
found to be slightly lower than values previously measured at 0°C.

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Определения связи живого веса и потребления кислорода (скорость мета-
болизма) у взрослых антарктических почвенных клещей *Alaskozetes antar-
cticus* (Michael) показали, что голодание приводит к подавлению метабо-
лизма.
Показано, что пищевой материал влияет на интенсивность метаболизма, и
истощение запаса кислорода в респирометре приводит к снижению потреб-
ления кислорода.
Влияние половых различий и полового созревания на скорость метаболизм
рассматривается на основе различий веса у самцов, беременных и небере-
менных самок.
Длительные периоды лабораторного культивирования приводят к снижению
веса и интенсивности метаболизма, но кратковременные опыты по определ
нию зависимости веса и потребления кислорода у отдельных особей также
проводились.
Потребление кислорода у взрослых *A. antarcticus*, определенные при -4°
несколько ниже, чем результаты более ранних измерений при 0°C.

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. Introduction

Metabolic rates are often highly variable between individuals of a species and it is of considerable importance that the causes of this variation be identified. Among the arthropods for example, various groups have received this sort of attention such as crustaceans (Newell 1973, Newell et al. 1974), centipedes (Riddle 1976) and insects (reviewed by Keister and Buck 1964).

Although extensive studies have been carried out on the respiratory metabolism of mites (Acari) on account of their importance in soil and litter communities (Berthet 1964, Webb 1969, 1975, Wood and Lawton 1973, Luxton 1975), little attention has been paid to the effects of variables other than size and temperature on metabolic rates. This is doubly unfortunate because not only does it imply that calculations of population metabolism may be more subject to errors than is normally assumed (Humphreys 1978), but also that mite ecological physiology in general is relatively underdeveloped compared to that of some other arthropod groups.

The experiments reported here on the Antarctic mite *Alaskozetes antarcticus* (Michael) together with a further analysis of data from earlier studies on this animal (Young 1979 a, b) were not designed to fill this gap, but the results suggest some aspects of metabolic variation that would repay further study. They were undertaken as a subsidiary part of a major study of environmental physiology in *A. antarcticus* and were performed with a view to gaining comprehension of the large degree of metabolic variation that became apparent in that programme. In addition, adult oxygen consumption rates at –4°C, measured by means of a simple modification of the Cartesian Diver technique, are reported.

Materials and methods

. General

antarcticus is a terrestrial cryptostigmatid mite, which is endemic to the maritime Antarctic and Sub-antarctic regions and is of circumpolar occurrence. It feeds on algae, lichens and organic detritus in the field, and is especially numerous in areas stabilized by vertebrates, such as seals and penguins. Further descriptions are given in Strong (1967) and Block (1977).

Individuals of *A. antarcticus* were collected in the austral summers of 1975–6 and 1976–7 at Signy Island, South Orkney Islands (a typical Maritime Antarctic locality) and transported by ship, in refrigerated containers, to the U.K. where they were maintained in culture at 2–4°C. Plastic containers with gauze lids and a plaster of paris substrate were used and the animals were subjected to a LD 12:12 photoperiod regime. Food was supplied in the form of the foliose lichen *Xanthoria candelaria* (L.) and the green alga *Prasiola crispa* (Lightf.) Menegh., both of which occur at Signy Island. All experiments were carried out on adult mites, and within each experiment mites were used which had been cultured for similar periods of time before respirometry.

Measurements of individual oxygen consumption rates were made by means of a Cartesian Diver micro-respirometer (Holter 1943, Linderstrøm-Lang 1943) operated in a controlled (± 2°C) temperature room. The temperature of the respirometer bath was thermostatically controlled to ± 0.01°C. Individual animals (seven in each experiment) were used in stoppered divers (Zeuthen 1964) and each experimental run was continued for 3–4 h. At the end of this period, oxygen consumption was calculated on both an individual and a unit live weight basis (metabolic rate). Weighings were performed on a Cahn electrobalance.

2.2. Experimental details:

Effect of starvation

Two experiments were undertaken in order to determine whether starvation exerts an influence on metabolic rate in *A. antarcticus*. The first of these was carried out at 10°C and the second at 5°C on animals previously cultured at their respective experimental temperatures. In both cases, the oxygen consumption of animals starved for two weeks (10°C) or four weeks (5°C) were compared to those of control groups fed on *P. crispa* at the appropriate temperature. Animals from the 10°C experiment were cleared in lactic acid in an attempt to observe their gut contents directly, but clearing of the cuticle caused the food material to disappear. In the 5°C experiment, feeding state was confirmed by dissection.

Effect of different food materials

This experiment was designed to show whether different food materials affected metabolic rate in *A. antarcticus*. Three groups of animals were cultured at 10°C, each with a different food, namely *X. candelaria*, *P. crispa* and guano from chinstrap penguins *Pygoscelis antarctica* (Forster). After two weeks, the oxygen consumption of seven animals from each group was measured at 10°C.

Effect of variability within individuals (1)

Although it is apparent from metabolic studies that a certain degree of variation exists between metabolic rates of different individuals, it is not clear whether large changes may occur in the standard metabolic rate of one individual at different times. This, and the following experiment were designed to examine this possibility.

In the first experiment, adult *A. antarcticus* from a culture that had been maintained at 10°C for ca. one month, were cultured individually in small glass containers with *X. candelaria* as food at 10°C. Oxygen consumption rates of seven specimens were then measured at 10°C and the animals returned to their containers after respirometry. The respiration rates of the same individuals were then measured on two subsequent occasions, although there was some mortality, which was attributed to the diver unloading procedure.

Effect of variability within individuals (2)

In order to look further at the possibility of intra-individual variation, a group of seven adult *A. antarcticus* (previously cultured at 10°C) were loaded into divers at 10°C and their oxygen consumption rates measured over a three day period, with hourly measurements for the first 36 h and for two further 10 h periods. The divers were refurnished with air after the first 36 h, in order to allow continued measurement.

Effects of sex, reproductive condition and length of culture time

Earlier data (Young 1979 a, b) were analysed further to yield information on the effects of sex, female reproductive condition, and length of culture period on live weights and metabolic rates.

Respiration below 0°C

Measurements of oxygen uptake were made on adult *A. antarcticus* at –4°C. This proved to be the lowest temperature that the Cartesian Diver system could maintain. In this experiment, a more concentrated diver flotation medium (1.6N NaOH) was

substituted for the standard solution (0.1N NaOH) to avoid its freezing in the respirometer. Measurements were made on five animals only, since the diver technique does not lend itself to the use of strongly caustic solutions at such low temperatures. A correction was developed for use in the calculation of oxygen consumption, as previously measured diver gas volumes were not applicable to flotation in a denser medium. The following equation was derived for this purpose:

$$V_1 - V_2 = W\,(1/\varrho_1 - 1/\varrho_2),$$

where V_1 is the volume of air in a diver of weight W, floating in a medium of density ϱ_1 and V_2 is the volume of air in the same diver floating in a medium of density ϱ_2.

3. Results and discussion

3.1. Effect of starvation

The results of the starvation experiments are shown in Tab. 1, which presents mean (± S.E.) live weights, respiration rates (nl O_2 $ind^{-1}h^{-1}$) and metabolic rates (µl O_2 $g^{-1}h^{-1}$). Metabolic rates are of critical importance in these results, since weight affects these less than it does respiration rates.

In the first experiment, starvation for two weeks at 10°C did not result in significantly different metabolic rates to those of controls fed on *P. crispa*, although starved animals did show some metabolic suppression. Live weights were not significantly different, although respiration rates were ($P < 0.05$), those of the starved group being substantially lower than those of the fed group.

Results were more conclusive in the second test. Live weights of starved animals were not significantly different from those of fed controls (in fact, they were slightly higher), but respiration rates and metabolic rates were significantly different ($P < 0.002$, $P < 0.005$ respectively), being lower in the starved group. Feeding status was investigated by dissection and was found to correspond to the treatment received; thus 'starved' animals possessed empty colourless guts, while 'fed' individuals showed a green colouration in the paired lateral caeca and green faecal pellets in the rectum.

There is no information in the literature on th metabolic effects of starvation in mites, although thes effects are widely documented in other groups. In mos cases metabolic rate suppression has been demonstrate (examples among the arthropods include spiders (An derson 1974), crabs (Marsden et al. 1973), isopod (Newell et al. 1976), centipedes (Riddle 1976) and mil lipedes (Gromysz-Kalkowska 1970)), although ther are exceptions (Stickle and Duerr 1970). In addition changes in the effect of temperature on metabolic rate have also been reported to accompany starvation i some cases (Marsden et al. 1973; Riddle 1976). Al though it was not possible to examine this latter possi bility in *A. antarcticus*, the results of this study agre with the majority of those reported elsewhere.

Metabolic rate suppression is thought to be an adap tive response to a lowered food supply (since minimises the depletion of metabolic reserves), bu whether it is an active process or merely a consequenc of lack of substrates is not clear.

3.2. Effect of different food materials

The results of this experiment are given in Tab. 2 whic shows mean (± S.E.) live weights, respiration rates an metabolic rates for animals on the three food materia tested. One way analysis of variance showed a signifi ant lack of homogeneity in the respiration an metabolic rate values, but not in the live weights. Student-Newman-Keuls least significant range te (Sokal and Rohlf 1969) was used to investigate diffe ences between pairs of mean values. In the case of r spiration rates, it was found that although animals fe on *X. candelaria* showed a significantly different valu to those fed on penguin guano ($P < 0.05$), there was n significant difference between the former group an those supplied with *P. crispa*, which in turn were n significantly different from guano fed individuals. Mea values however, showed a trend from the lowest rate guano fed individuals to the highest in those fed lichen.

Tab. 1. Mean (± S.E.) live weights, respiration rates and metabolic rates of *Alaskozetes antarcticus* adults fed on *Prasiola cris* and starved at 10° and 5°C. Number of replications (n) is shown together with results of t-tests between fed and starved me values. NS: not significant.

Treatment	n	Live weight (µg)	Respiration rate (nl O_2 $ind^{-1}h^{-1}$)	Metabolic rate (µl O_2 $g^{-1}h^{-1}$)
10°C				
Fed	7	229.99±14.56	54.53±3.55	239.92±15.48
		NS	$P < 0.05$	NS
Starved 2 wk	7	212.79± 9.97	38.30±4.05	181.98±21.83
5°C				
Fed	5	219.36± 7.15	46.53±3.25	213.61±18.16
		NS	$P < 0.002$	$P < 0.005$
Starved 4wk	7	223.07±10.70	29.15±2.49	132.85±13.11

Tab. 2. Mean (± S.E.) live weights, respiration rates and metabolic rates of adult *Alaskozetes antarcticus* given different food materials at 10°C. Number of replications (n) is shown.

Food material	n	Live weight (µg)	Respiration rate (nl O_2 $ind^{-1}h^{-1}$)	Metabolic rate (µl O_2 $g^{-1}h^{-1}$)
Chinstrap penguin guano	7	198.91± 6.31	33.33±2.45	167.14±10.24
Prasiola crispa	7	234.14±13.48	40.31±3.02	174.75±14.10
Xanthoria candelaria	6	211.70±12.68	49.09±3.96	233.32±16.13

A similar trend emerged from the metabolic rate values. Guano gave the lowest rates and differed significantly from the lichen ($P < 0.05$), which yielded the highest metabolic rates. Additionally, animals fed on the latter showed metabolic rates that differed significantly ($P < 0.05$) from those of individuals given *P. crispa* as food, although guano and the alga did not yield significantly different rates.

It is concluded therefore, that food materials may affect metabolic rates in adult *A. antarcticus,* but how this occurs is not clear. It is possible that the differences observed in the results are attributable to feeding behaviour, in the sense that *A. antarcticus* may prefer one food to another and consume larger quantities of it. On the other hand, the three food materials may be assimilated at different efficiencies and this may be reflected in the results. Whatever the mechanism involved, it is of importance that this factor be taken into account in feeding-metabolism experiments and calculations of population metabolism.

3. Effect of variability within individuals (1)

When measured on two successive days, the respiration rates of the animals under test underwent changes. Four of these exhibited a decrease on day 2 as compared to day 1, one remained almost constant and the other two showed an increase. Percentage changes

$$\frac{(\text{Day 2 rate} - \text{Day 1 rate} \times 100)}{\text{Day 1 rate}}$$

were: −8.6%, +5.1%, −16.0%, −26.5%, −6.7%, −0.5% and +17.6%, where negative signs denote a decrease on day 2. Despite their magnitude, these changes resulted in respiration rates that fell within the normal range of variation for *A. antarcticus* at 10°C. On the third occasion of measurement (6 d later) all animals measured showed a decrease relative to day 1, while two had increased. It seems therefore, that repeated diver loading and unloading may impose constraints on this type of experiment, by affecting the viability of the animals under test.

Nevertheless, the changes between days 1 and 2 illustrate the existence of short term temporal variation within individuals. This is probably not due to activity changes, since these animals under Cartesian Diver conditions rarely move. If they do, the animal invariably finds its way into the sodium hydroxide in the diver neck and is discounted in the analysis.

The question as to the mechanism behind these changes can only be answered speculatively, since our knowledge of metabolic processes in mites is poor by any standards. But since all exogenous factors are constant in this case, as are certain endogenous ones, such as activity, weight and developmental stage, it must be assumed that these variations are due to changes in the maintenance requirement with time, which in turn depends on the rate at which various physiological (and energy requiring processes, such as digestion, chemical synthesis and excretory metabolism, are proceeding. Whether this can fully explain the fluctuations observed is open to question, but clearly, further studies are required to investigate this issue.

3.4. Effect of variability within individuals (2)

In this experiment, which was designed to circumvent the problems encountered in experiment 3.3 the oxygen consumption of seven animals was monitored for a three day period without removing them from the divers. Respiration was found to decline in each case, initially in an almost linear fashion and then at a declining rate (Fig. 1). Rates of decline varied from one animal to another. It proved impossible to follow two of the specimens for the full 36 h of the experiment, since in one case the animal entered the sodium hydroxide in the diver neck, and in the other a sudden decline in respiration to ca. 20% of the original level occurred suggesting that the individual was becoming moribund.

It is important however, to explain the observed decline in oxygen consumption. The idea that depletion of oxygen in the air bubble of the diver (caused by the animal's respiration) is responsible, has much to recommend it (Wightman 1977), since respiratory decline occurred at different rates in different divers. Since the divers contained different volumes of air, the effects of a respiring adult *A. antarcticus* would be most pronounced in those of smallest volume. Then, if oxygen

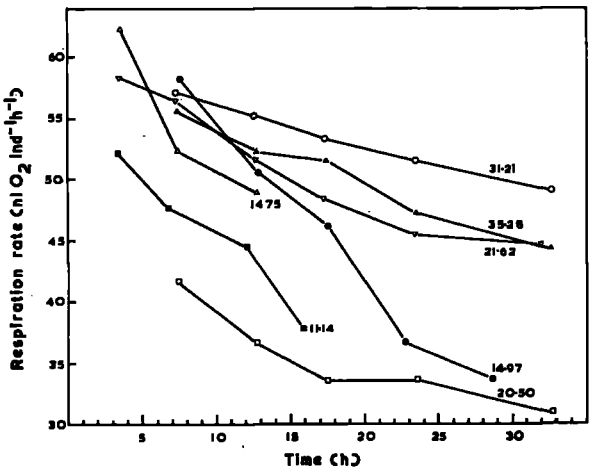


Fig. 1. The effect of time on respiration rate of adult *Alaskozetes antarcticus* in experiment 3.4. Each line represents an individual animal with its corresponding diver volume (µl).

depletion is responsible for the respiratory decline observed in the experiment, rates of decline would be expected to be greatest in the smallest divers.

To test this, a linear regression (respiration rate on time) was fitted to the data for each animal up to 36 h (or to the last measurement, if earlier than 36 h) and the oxygen consumed up to an arbitrary time from the beginning of the experiment (1000 min ≡ 16.7 h) was derived by integration. This was used to give the percentage of oxygen remaining in the air bubble at 16.7 h (taken as 21% at Oh). Corresponding respiration rates

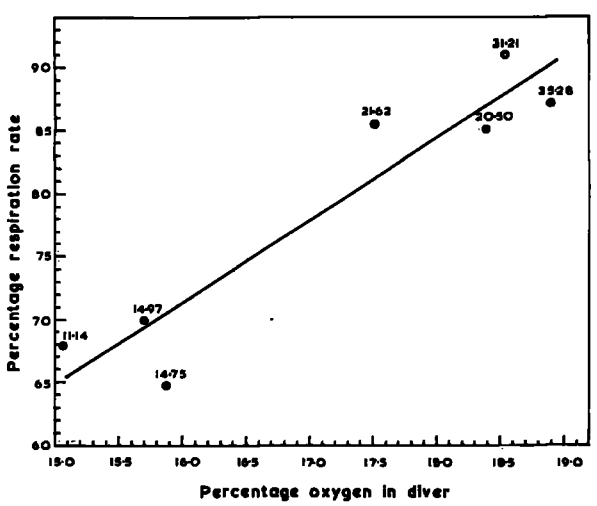


Fig. 2. The effect of oxygen concentration (percentage in diver air bubble at 16.7 h) on respiration rate (percentage of original rate at 16.7 h) in adult *Alaskozetes artarcticus*. A linear regression line is shown, which is described by the equation: R = 6.45V − 31.85, where R is the percentage of original respiration rate and V is the percentage of oxygen in the air bubble at 16.7 h. Diver volumes (µl) are also given.

at 16.7 h were also calculated for each animal and then divided by original rates (Oh) to give percentages. These values were plotted against percentage of oxygen in the divers at 16.7 h (Fig. 2) and a regression line calculated (r: + 0.94, d.f.: 5, $P < 0.01$). It is clear from this analysis that respiration rate declined further in the smaller divers, which as expected show more oxygen depleted atmospheres.

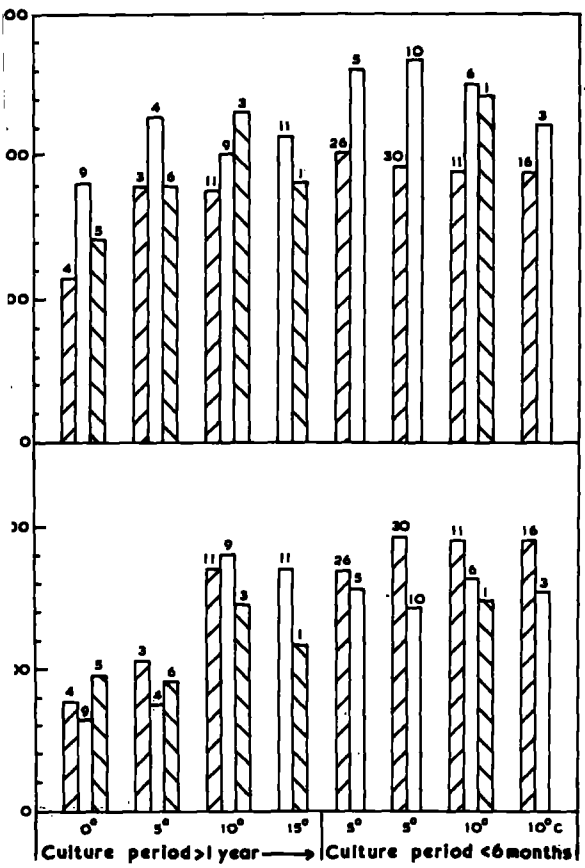
These results show that respiration rate decline is strongly correlated with oxygen depletion. Adding air to the divers failed to restore respiration to former levels, but since only one fifth of the additional air was oxygen, such a response would not necessarily occur.

Dependence of oxygen uptake on oxygen concentration has been previously reported in all life stages of terrestrial insects (reviewed by Keister and Buck 1964) and is widespread amongst land invertebrates. In the field, this process may be more important than appears at first sight. *A. antarcticus* for example, frequently becomes encased in ice in its habitat at Signy Island during winter. At high subzero temperatures, metabolism may be considerable (see below) and despite diffusion of oxygen through ice (Scholander et al. 1953), the oxygen content of the thin layer of air surrounding the animal may become reduced. Under these conditions metabolism will be suppressed, although the possibility of anaerobiosis cannot be ruled out (Sømme and Conradi-Larsen 1977). This response is possibly adaptive in that as respiration is suppressed, the available oxygen will be depleted more slowly than would have been the case had respiration continued at previous levels.

3.5. Effect of sex, reproductive condition and length of culture time

Fig. 3 shows the results of a further analysis of live weight and metabolic rate data previously reported for *A. antarcticus* (Young 1979 a, b), from which the following trends emerge. Gravid females are heavier than males and in most cases display a lower metabolic rate at the same temperature. These effects go together since metabolic rate is negatively correlated with live weight in this species (Young 1979 a). The difference between males and non-gravid females are less consistent, although smaller numbers of replicates were involved. Non-gravid females are lighter than gravid females in all but one instance and metabolic rates reflect this difference, except where there was little replication for the former.

Fig. 3 also shows that animals cultured for short periods are generally heavier ($P < 0.01$, males; $P < 0.001$, gravid females) and display, although not in all cases, higher metabolic rates (e.g. males and gravid females at 5°C, males at 10°C). This finding conflicts with the assertion that metabolic rate is negatively correlated with live weight. The solution to this difficulty probably lies in the effects of continuous culture



g. 3. Mean live weights and metabolic rates of male ▨, avid female □, and non-gravid female ▧ *Alaskozetes antcticus* cultured for different time periods. Number of replitions is given. Data from separate experiments at 5° and °C are presented as individual histograms.

etabolic parameters – effects which at present are orly understood.

Despite this observation, Fig. 3 allows general consions to be drawn in relation to sex and reproductive ndition. These are (a), that metabolic rate differences tween males and gravid females are explicable on the sis of weight differences and (b), that allowing for all numbers, differences between gravid and n-gravid females can probably be explained on the ne basis.

These conclusions contrast with those of some other dies of mite metabolism, in which the effects of sex ve been examined. Block (1977), working on ld-fresh *A. antarcticus*, reported that whereas weight ferences between gravid and non-gravid females ıld explain metabolic rate differences, males and vid females possessed similar metabolic rates despite ferences in live weights (the females were heavier). is implies a relative elevation of gravid female rates, sumably linked to egg development. In support of ı, Goddard (1977) found higher metabolic rates in females of *Gamasellus racovitzai* (Trouessart), an Antarctic mesostigmated mite, despite their being heavier than males. Additionally, Webb (1969) reported that gravid female *Nothrus silvestris* Nicolet showed a 25% increase in metabolic rate compared to non-gravid adults (males and females). On the other hand, Wood and Lawton (1973) showed no consistent sex based patterns in their oribatid and mesostigmatid respiration data. Since other major studies (Berthet 1964, Luxton 1975) combined male and female rates in their results, the question is at present unresolved. Elevation of gravid female metabolic rates is likely to be caused either by the metabolic requirements of egg synthesis and food store deposition or by the metabolism of the developing embryos themselves. Both of these factors vary in importance with time and this may explain the apparent discrepancies in the data.

As far as the effects of culture periods are concerned, the analysis presented here show how complex those effects can be both on live weights and metabolic rates. The only relevant quantitative study of this problem is that of Block and Tilbrook (1977) on the Antarctic collembolan *Cryptopygus antarcticus* Willem. They were able to monitor a decline in metabolic rate at intervals over a period of 387 d in mature springtails at a constant temperature of 5°C, although live weights underwent no significant changes. Other data for this species suggest that juveniles may not undergo the same process (Tilbrook and Block 1972, Block and Tilbrook 1975). In *A. antarcticus*, comparison of field-fresh (Block 1977) and cultured animals produces a similar trend to that found in the collembolan (Young 1979 a).

These points are of considerable importance for all studies that depend on the use of cultured invertebrates and further research is needed to elucidate the magnitude and causes of the effects outlined above.

3.6. Respiration below 0°C

Results of oxygen uptake measurements made at –4°C were as follows (mean ± S.E, n = 5): respiration rate: 9.09 ± 0.49 nl O_2 $ind^{-1}h^{-1}$, metabolic rate: 43.08 ± 4.46 µl O_2 $g^{-1}h^{-1}$. For comparison, rates measured at 0°C range from 9.08 to 12.40 nl O_2 $ind^{-1}h^{-1}$ and from 50.87 to 78.31 µl O_2 $g^{-1}h^{-1}$ (Block 1977, Young 1979 a), but these data were collected on lighter animals. Thus it appears that metabolic rates at –4°C are close to those measured at 0°C. Further research is required to establish whether oxygen uptake continues at lower subzero temperatures.

Scholander et al. (1953) measured subzero metabolic rates in Arctic chironomid larvae, although some body water is apparently frozen, even at high subzero temperatures, in these animals. At –5°C metabolic rate was ca. 6 µl O_2 $g^{-1}h^{-1}$. This is far lower than the values for *A. antarcticus* at –4°C, although weight differences play a

part here (chironomid larvae may weigh 100 times more than adult *A. antarcticus*). Scholander and his co-workers were able to measure metabolic rates down to –15°C, but since they were dealing with a largely frozen animal, the results are not strictly comparable to *A. antarcticus* which supercools to –25° or –30°C and dies if frozen (Block et al. 1978).

Oxygen uptake has been measured in several other species of frozen and supercooled insects at temperatures as low as –16°C (Lozina-Lozinskii 1974). According to Kanwisher (1966), oxygen is consumed by frozen *Littorina littorea* (L.) at –10°C.

Lozina-Lozinskii (1974) distinguished two types of oxygen uptake response to subzero temperatures. In one category, Q_{10} values increased markedly below 0°C (respiration declines more rapidly below 0°C than above), whereas in the other group, there may be a decrease in the magnitude of Q_{10} values. The chironomid studied by Scholander et al. (1953) clearly fits the former category in that a sharp rise in Q_{10} occurred below 0°C. The category into which *A. antarcticus* fits is not clear at present; the derivation of a Q_{10} for the range 0° to –4°C is not appropriate because of differences in live weights and length of culture periods between the 0° and –4°C groups.

It has been thought that the two types of response reflect the occurrence or absence of freezing (Scholander et al. 1953), but Lozina-Lozinskii (1974) reported a similarity of oxygen uptake rates in frozen and supercooled specimens of the same insect at –4.6°C.

Metabolic variation poses something of a problem to invertebrate physiologists, and the complexities that emerge from the effects of the many factors involved are only now being unravelled. In *A. antarcticus,* weight and exposure temperature have been examined in previous studies (Block 1977, Young 1979 a), as has acclimation temperature (Young 1979 b). Food and starvation effects have been investigated briefly in the present study, but activity remains the most problematic variable for this and other micro-arthropod metabolism work, since its effects are likely to be considerable and yet it is difficult to quantify.

Other factors cannot be ignored however, such as culture periods and intra-individual effects, as the present data show. Research is needed in these areas, especially as regards their influence on population metabolism estimates and more fundamental physiological studies.

Acknowledgements – The research facilities provided by the British Antarctic Survey were appreciated. This work was financed by a Natural Environment Research Council research grant (GR.3/2797) to W. Block, which is gratefully acknowledged.

References

Anderson, J. F. 1974. Responses to starvation in the spider *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). – Ecology 55: 576–585.

Berthet, P. 1964. L'activité des Oribatides (Acari: Oribatidae) d'une Chênaie. – Mem. Inst. r. Sci. nat. Belg. 152: 1–152.

Block, W. 1977. Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus* (Acari: Cryptostigmata). – J. exp. Biol. 68: 69–87.

– and Tilbrook, P. J. 1975. Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus.* – Oikos 26: 15–25.

– and Tilbrook, P. J. 1977. Effects of long term storage on the oxygen uptake of *Cryptopygus antarcticus* (Collembola). – Oikos 29: 284–289.

– , Young, S. R., Conradi-Larsen, E.-M. and Sømme, L. 1978. Cold tolerance of two Antarctic terrestrial arthropods. – Experientia 34: 1166–1167.

Goddard, D. G. 1977. The Signy Island terrestrial reference sites: VI. Oxygen uptake of *Gamasellus racovitza* (Trouessart) (Acari: Mesostigmata). – Bull. Br. Antarct. Surv. 45: 1–11.

Gromysz-Kalkowska, K. 1970. The influence of body weight, external temperature, seasons of the year and fasting on respiratory metabolism in *Polydesmus complanatus* L. (Diploda). – Fol. Biol. 18: 311–326.

Holter, H. 1943. Technique of the Cartesian Diver. – C. r. Trav. Lab. Carlsberg Ser. Chim. 24: 399–478.

Humphreys, W. F. 1978. Ecological energetics of *Geolycosa godeffroyi* (Araneae: Lycosidae) with an appraisal of production efficiency in ectothermic animals. – J. Anim. Ecol. 47: 627–652.

Kanwisher, J. W. 1966. Freezing in intertidal animals. – In Meryman, H. T. (ed.), Cryobiology, Academic Press, London, pp. 487–494.

Keister, M. and Buck, J. 1964. Respiration: some exogenous and endogenous effects on rate of respiration. In: Rockstein, M. (ed.), The physiology of Insecta, Vol. II. Academic Press, London, pp. 617–658.

Linderstrøm-Lang, K. U. 1943. On the theory of the Cartesian Diver micro-respirometer. – C. r. Trav. Lab. Carlsberg Ser. Chim. 24: 333–398.

Lozina-Lozinskii, L. K. 1974. Studies in cryobiology. – Wiley, New York.

Luxton, M. 1975. Studies on the oribatid mites of a Danish beech wood soil II. Biomass, calorimetry, and respirometry. – Pedobiologia 15: 161–200.

Marsden, I. D., Newell, R. C. and Ahsanullah, M. 1973. The effect of starvation on the metabolism of the shore crab *Carcinus maenas.* – Comp. Biochem. Physiol. 45A: 195–213.

Newell, R. C. 1973. Factors affecting the respiration of intertidal invertebrates. – Am. Zool. 13: 513–528.

– Wieser, W. and Pye, V. I. 1974. Factors affecting oxygen consumption in the woodlouse *Porcellio scaber* Latr. – Oecologia (Berl.) 16: 31–51.

– , Roy, A. and Armitage, K. 1976. An analysis of factors affecting the oxygen consumption of the isopod *Ligia oceanica.* – Physiol. Zool. 49: 109–137.

Riddle, W. A. 1976. Respiratory metabolism of the centipede *Nadabius coloradensis* (Cockerell): influence of temperature, season and starvation. – Comp. Biochem. Physiol. 55A: 147–151.

Scholander, P. F., Flagg, W., Hock, R. J. and Irving, L. 1953. Studies of the physiology of frozen plants and animals in the Arctic. – J. cell. comp. Physiol. 42: Suppl. 1, 1–56.

Sokal, R. R. and Rohlf, F. J. 1969. Biometry. – Freeman, San Francisco.

Sømme, L. and Conradi-Larsen, E.-M. 1977. Anaerobiosis in overwintering collembolans and oribatid mites from windswept mountain ridges. – Oikos 29: 127–132.

Stickle, W. B. and Duerr, F. G. 1970. The effects of starvation on the respiration and major nutrient stores of *Thais lamellosa*. – Comp. Biochem. Physiol. 33: 689–695.
Strong, J. 1967. Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. – Antarct. Res. Series. (Am. Geophys. Un.) 10: 357–371.
Tilbrook, P. J. and Block, W. 1972. Oxygen uptake in an Antarctic collembole *Cryptopygus antarcticus*. – Oikos 23: 313–317.
Webb, N. R. 1969. The respiratory metabolism of *Nothrus silvestris* Nicolet (Acari). – Oikos 20: 294–299.
– 1975. Respiratory metabolism of *Steganacarus magnus* (Acari). – Oikos 26: 43–46.
Wightman, J. A. 1977. Respirometry techniques for terrestrial invertebrates and their application to energetics studies. – N.Z.J. Zool. 4: 453–469.
Wood, T. G. and Lawton, J. H. 1973. Experimental studies on the respiratory rates of mites (Acari) from beech-woodland leaf litter. – Oecologia (Berl.) 12: 169–191.
Young, S. R. 1979 a. Respiratory metabolism of *Alaskozetes antarcticus*. – J. Insect. Physiol. 25: 361–369.
– 1979 b. Effect of temperature change on the metabolic rate of an Antarctic mite. – J. Comp. Physiol. 131: 341–346.
Zeuthen, E. 1964. Microgasometric methods: Cartesian Divers. – In: Schiebler, T. H., Pearse, A. G. E. and Wolff, H. H. (ed.), 2nd Int. Congr. Histo- & Cyto-chemistry, Wiley, New York, pp. 70–80.

. Insect Physiol., Vol. 26, pp. 189 to 200.
) Pergamon Press Ltd. 1980. Printed in Great Britain.

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EXPERIMENTAL STUDIES ON THE COLD TOLERANCE OF *ALASKOZETES ANTARCTICUS*

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Abstract—The cold tolerance mechanism of the Antarctic terrestrial mite *Alaskozetes antarcticus* (Michael) was investigated in cultured animals. Freezing is fatal in this species and winter survival occurs by means of supercooling, which is enhanced by the presence of glycerol in the body. There is an inverse, linear relationship between the concentration of glycerol and the supercooling point, which may be as low as −30°C. Feeding detracts from supercooling ability by providing ice nucleators in the gut which initiate freezing at relatively high sub-zero temperatures. Experiments on the effects of various environmental factors showed that low temperature acclimation gave rise to increased glycerol concentrations and suppressed feeding, while desiccation also stimulated glycerol production. Photoperiod had no effect on cold tolerance in this species. The juvenile instars of *A. antarcticus* were found to possess a greater degree of low temperature tolerance than adults.

Key Word Index—Cold tolerance, Antarctic mite, glycerol, supercooling points, ice nucleators

INTRODUCTION

OLD hardiness in arthropods consists either of the bility to tolerate freezing of the body or of the apacity to resist it by supercooling. In the latter case, eezing is often fatal; such animals are referred to as eezing susceptible, whilst the former type are termed eezing tolerant.

Previous studies of both freezing tolerant and eezing susceptible types have suggested that the bility to survive low temperatures varies seasonally. nvironmental cues, such as low temperature (BAUST nd MILLER, 1970, 1972; SØMME and CONRADI-ARSEN, 1977) increase cold tolerance in the autumn. hotoperiod or temperature (or a combination of both ictors) are involved in those species exhibiting a iapause stage (CHINO, 1957; SØMME, 1964, 1965b). xposure to low relative humidity may result in ncreased solute concentration and thereby enhance upercooling (SALT, 1961). Compounds such as sugars nd sugar alcohols have frequently been detected in old-hardy arthropods. In freezing susceptible forms ey facilitate supercooling (SØMME, 1964), while in eezing tolerant species they may aid in the survival of eezing (ASAHINA, 1969). Glycerol is the most widely curring of these substances (ASAHINA, 1969).

The research reported here was designed to give an count of the cold tolerance of the Antarctic rrestrial mite *Alaskozetes antarcticus* (Michael). Few vestigations have been undertaken on the cold tolerance of Antarctic terrestrial arthropods. Early studies were concerned with lethal temperatures and cold stupor and did not examine the mechanism of survival (DALENIUS and WILSON, 1958; PRYOR, 1962; JANETSCHEK, 1967; FITZSIMONS, 1971; ROUNSEVELL, 1977). Recently, research has been directed at the mechanisms themselves. Thus, BLOCK *et al.* (1978) and SØMME (1978a) have shown that the springtail *Cryptopygus antarcticus* (Willem) from the maritime Antarctic survives temperatures as low as −30°C by means of supercooling, while SØMME (1978b) has demonstrated that certain prostigmatid mites from continental Antarctica tolerate similar temperatures but are also susceptible to freezing. On the other hand, BAUST and EDWARDS (1979) have found that larvae of the wingless midge *Belgica antarctica* (Jacobs) tolerate freezing and contain several polyhydroxy compounds that may be important in this respect.

A preliminary study of *A. antarcticus* showed that freezing was fatal in this species (BLOCK *et al.*, 1978). Fed animals displayed a bimodal distribution of individual supercooling points (temperatures of spontaneous tissue freezing), with one group occurring between −5° and −15°C and the other between −25° and −30°C. It was found that starvation improved cold tolerance by increasing the proportion of animals supercooling to low temperatures. BLOCK *et al.* (1978) concluded that the bimodality was due to feeding differences between individuals. Those animals supercooling to relatively high sub-zero temperatures (high group animals) were thought to possess gut contents containing efficient ice nucleating agents, and those supercooling to relatively low temperatures (low group animals) to lack such material. These authors also showed that a substance with an R_f value equal to that of glycerol, on paper

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chromatograms, was present in mites acclimated at 0°C.

In the present study, emphasis was placed on the identification of the substance thought to be glycerol and its relation to supercooling, and on the effect of starvation, temperature, photoperiod and relative humidity on the cold tolerance of adult animals. It was hoped that the seasonal cues responsible for increased cold tolerance would be identified. In addition, information on the cold hardiness of juvenile stages would be obtained.

MATERIALS AND METHODS

Alaskozetes antarcticus is a terrestrial cryptostigmatid mite of the family Podacaridae. It has a circumpolar distribution in the Sub-antarctic zone and is widely distributed in the maritime Antarctic. *Alaskozetes* is dark brown–black in appearance, *ca.* 1 mm long and 0.75 mm wide and weighs 200–300 μg when adult. It is both a detritivore and algivore, being common in areas fertilized by birds and seals and in association with the green foliose alga *Prasiola crispa* (Lightf.) Menegh. upon which it feeds. The life cycle is not seasonal and all life stages overwinter in the field (STRONG, 1967; TILBROOK, 1973), sometimes in dense aggregations of thousands of individuals, which may disperse in summer (STRONG, 1967).

The animals used in the present series of experiments were collected by the British Antarctic Survey in 1977 and 1978 at Signy Island (60° 43′S 45° 36′W) in the South Orkney Islands (where ground surface temperatures in winter may be below −25°C; WALTON, 1977). The animals were returned to the U.K. in refrigerated containers and cultured in plastic vessels until required for experimentation. Water and food (the alga *P. crispa*) were supplied as required.

In the experiments described below, the following methods were employed. Supercooling points were measured by monitoring body temperature with fine (36 swg) copper–constantan thermocouples, whose output was continuously displayed on a potentiometric chart recorder (SALT, 1961, 1966). Animals were attached to thermocouples by means of a small spot of grease on the dorsal surface and cooled at a constant rate of 1°C/min^{-1} in a small air-filled tube in a methanol bath, by means of an immersion cooler balanced against a heater, which was controlled by a temperature programming device. Supercooling points were measured as the point of origin of the small, but significant, temperature rise that accompanied emission of latent heat during freezing.

Extracts for chromatographic analysis of polyhydroxy compounds were prepared by macerating *ca.* 20 adult animals (weighed collectively) in 70% ethanol, centrifuging (3000 rev/min for 10 min), washing the precipitate, recentrifuging as before and combining the supernatants before evaporating (using a compressed air stream) and dissolving the residue in 25 μl distilled water. Samples were stored deep frozen prior to chromatography.

Glycerol concentrations were determined after one dimensional separation on paper chromatograms (Whatman No. 1, 20 × 20 cm), using an ascending solvent of butan-1-ol:acetic acid: water (12 : 3 : 5) by estimation of the areas of the spots produced (SØMMI 1964). In this method, a relationship between th weight of glycerol applied and the area of the spot produces after development is linear over a wide rang (SØMME, 1964; BAUST and MILLER, 1970, 1972). In th present study the relationship was found to be linea from 2.5 to 50 μg applied glycerol. Areas of spots wer estimated by tracing onto tracing paper and weighin Three determinations were made on each sample and mean glycerol content in μg mg^{-1} fresh weigh derived. Percentage water content values were the used to calculate glycerol concentration in μg mg^{-} body water and μg mg^{-1} dry body weight minu weight of glycerol.

1. *Identification of glycerol*

For the identification of the substance detected i *Alaskozetes* by BLOCK *et al.* (1978) and thought to b glycerol, extracts of adult animals were examinec together with a glycerol standard, in five on dimensional chromatographic systems for com parison of R_f values. These systems were butan-1-o1 acetic acid:water (12:3:5), the top layer of butan-1 o1: acetic acid: water (4 : 1 : 5; KOWKABANY, 1961) ethyl acetate: pyridine: water (12 : 5 : 4; SØMME, 1964 and propan-2-o1: water (4 : 1; SØMME, 1964) on pape (ascending) and butan-1-o1: acetic acid: diethyl ethe water (9 : 6 : 3 : 1; MANSINGH and SMALLMAN, 1972) o 250 μm silica gel thin layer plates. Other sugars an alcohols were chromatographed in two of thes systems (the second and fifth) for comparativ purposes.

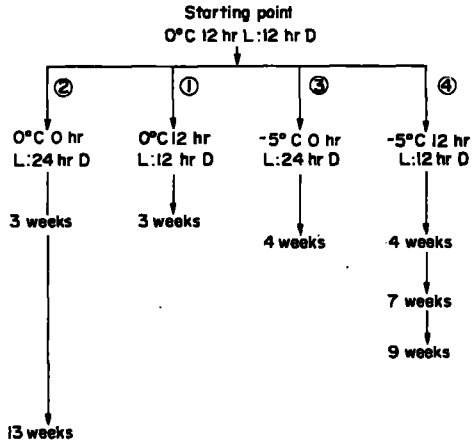
2. *Effect of starvation on cold tolerance*

Several hundred adult *Alaskozetes* were remove from a stock culture (0°C, LD 12:12, 90–100% r.h. and placed in glass, gauze-lidded jars without food o plaster of Paris (the latter was omitted to avoid th possibility of it being ingested by the animals). Thes jars were then placed at +5°C at LD 12:12 an 90–100% r.h. (maintained by situating the jars in larg plastic boxes with moist plaster of Paris substrates) Animals were sampled from this population after 0, 1 3 and 5 weeks for supercooling point and glycero determinations, but as fungal growth occurred in th cultures after 4 weeks, the experiment wa discontinued. Each sample consisted of 42 animals fo supercooling point determinations and 60 individua for glycerol measurements (3 subsamples of 2 animals each).

3. *Effect of temperature, photoperiod and humidity o cold tolerance*

3(a). *Effect of temperature and photoperiod.* Adu *Alaskozetes*, from a culture that had been maintaine at 0°C for several months at LD 12:12 and high r.h were sorted into four groups and one group place under each of the conditions shown in Fig. Humidity was maintained at 95–100% and food (th alga *P. crispa*) was provided, so that if any fact resulted in the cessation of feeding, it would b discernible in the results (see below).

Supercooling point determinations on *ca.* 4 animals and glycerol concentration measuremen (three samples of 20 individuals sample^{-1}) were ma



ig. 1. Acclimation schedule for experiment 3(a). Effect of emperature and photoperiod on cold tolerance in *laskozetes antarcticus*. Samples were analysed after the time eriods shown under each set of acclimation conditions temperature, photoperiod). Relative humidity was 95–100% throughout.

n animals from the original stock culture at the time f establishment of the experiment and from the arious treatments at the times shown in Fig. 1. Water ontent of animals was not measured.

3(b). *Effect of humidity and photoperiod.* Adult *laskozetes*, from a culture maintained at 0°C under D 12:12 and a high r.h. were removed and ubcultured under four different sets of conditions Fig. 2). One hundred per cent r.h. was obtained by the rovision of open containers of distilled water in the ulture chambers. Under these conditions free water roplets collected around the walls and lids of the ulture vessels. Sixty per cent r.h. was achieved with lica gel in the culture exposed to the shorter day ngth, but conditions in the long-day temperature abinet prevented its realization and resulted in a value f *ca.* 95%. Treatment (2) was, therefore, a duplicate of ie first treatment.

Each group was sampled for supercooling point and lycerol determinations as shown in Fig. 2. In ddition, the original stock culture was sampled at the

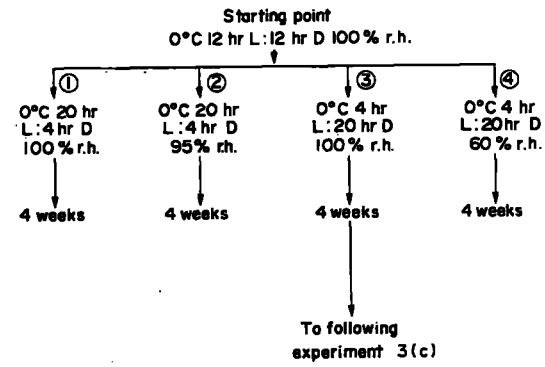


Fig. 2. Acclimation schedule for experiment 3(b). Effect of photoperiod and humidity on cold tolerance in *Alaskozetes antarcticus*. Samples were analysed after the time periods shown under each set of conditions (temperature, photoperiod, humidity).

time of subculture. Water content of the animals under the four experimental treatments was obtained by removing three groups of 15 individuals from each and measuring the live and dry weights of each group.

3(c). *Effect of temperature and humidity.* A stock culture that had been maintained at 0°C under LD 12:12, high r.h. and an abundant food supply for several months, was transferred to LD 4:20, 100% r.h. regime, but was otherwise unchanged. After 5 weeks, supercooling point and glycerol determinations were made. This provided the starting point for the experiment that followed. Firstly, two subcultures were established (Fig. 3), one of these being exposed to 40% r.h. and the other to −5°C. After 4 weeks animals subjected to these treatments were sampled together with the original culture, which had now been subjected to LD 4:20 at 0°C for 9 weeks. The −5°C treatment was subsequently sampled after a further 7 weeks.

After a further week the 0°C LD 4:20 stock culture became the starting point for another test, in which two more subcultures were established (Fig. 3). One of these was desiccated for 2 weeks at 0°C (sampling at the end of this period) and then placed at −5°C (50% r.h.), while the second was exposed to −5°C for

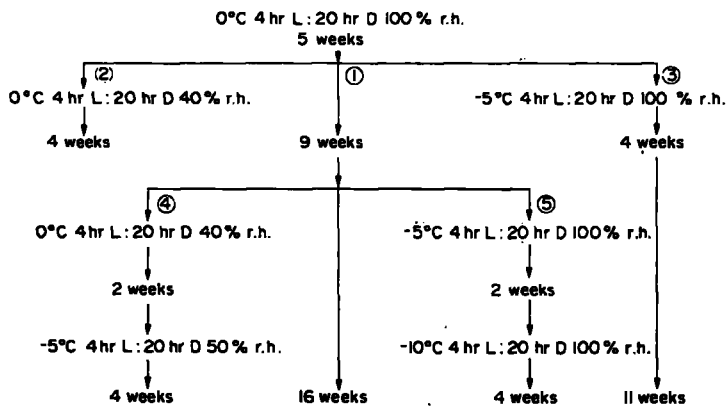


Fig. 3. Acclimation schedule for experiment 3(c). Effect of temperature and humidity on cold tolerance in *Alaskozetes antarcticus*. Samples were analysed after the time periods shown under each set of conditions (temperature, photoperiod, humidity). Treatment (5) was not sampled after exposure to −5°C for 2 weeks.

2 weeks before moving to a −10°C environment. These two subcultures were sampled after 4 weeks in their final conditions (i.e. 6 weeks after initial subculture), together with the stock culture, which had now been subjected to the short day photoperiod at 0°C for 16 weeks. Water content was determined as before by measuring the live and dry weights of three groups of 10–15 animals from each treatment.

The results of these experiments were expressed as low group mean supercooling points, glycerol concentrations and frequency patterns of the distribution of individuals in high and low supercooling point groups for each experimental treatment. Low and high supercooling point groups were defined by reference to the results of the starvation experiment (see below), using a dividing temperature of −24°C to distinguish between animals lacking nucleating gut contents and those possessing them, respectively. The low group mean supercooling point was derived by calculating the mean freezing temperature of the animals that froze at temperatures equal to, or below −24°C. Glycerol concentrations were expressed per unit of dry weight (to reveal changes in concentration irrespective of changes in body water content) and per unit of body water (for use in the investigation of the relationship between glycerol and supercooling). Where water content was not measured under a particular treatment, a mean value from several similar treatments was obtained.

Comparisons between treatments in terms of the numbers of animals in high (> −24°C) and low (≤ −24°C) supercooling point groups were difficult in instances where different acclimation temperatures were used. This was because some animals maintained in subzero temperature cultures died as a result of freezing during the acclimation period, whereas this did not occur at 0°C. Therefore, the frequency distributions of supercooling points from −5°C cultures, for example, were deficient in animals freezing at temperatures between 0°C and −5°C and comparisons between them and those from 0°C treatments were affected. The solution adopted was to consider that the high supercooling point group from 0°C cultures consisted only of animals that supercooled to temperatures between −5° and −24°C. This correction procedure was justified because −5°C cultures lacked animals supercooling to temperatures between 0° and −5°C, but contained individuals with supercooling points only slightly below −5°C, which implies that only the former were killed by the treatment.

Therefore the following rules were used in the comparison of numbers of animals in high and low supercooling point groups between treatments:

1. In comparison of any two treatments by χ^2 tests (see below) no correction was applied in cases where the two treatments involved exposure to the same temperature. A suitable correction was applied in all 0° to −5°, 0° to −10° and −5° to −10°C instances.

2. For the initial comparison of several treatments (in all but the second experiment where the temperature was constant at 0°C) each treatment was subject to the correction explained above. The distribution of animals in the two supercooling point groups was expressed as a corrected L/L+H ratio as: L/L+H = Number of animals in low supercooling point group (≤ −24°C)/Number in lo group+Number in high group (−5° > supercoolir point > −24°C). The −10°C treatment was omitte from this analysis. In the second experiment (3(b where 0°C treatments only were involved, a uncorrected L/L+H ratio was derived by dividing th number of animals in the low supercooling poi group by the total examined.

Significance of differences between mea supercooling points and between mean glycer concentrations was investigated by *t*-tests, while th significance of differences between treatments in term of the numbers of animals in high and lo supercooling point groups was determined by mear of χ^2 tests. In each comparison, the significance of th difference between the treatment and its control wa examined and a significant result was considered to b established when the probability of it arising by chanc was less than 0.05. *T*-tests were carried out using 'mea square within groups' values derived from analysis c variance procedures, as overall estimates of varianc except in one instance where variance heterogeneit was detected in the data.

4. *Cold tolerance of juvenile stages of* Alaskozetes

Supercooling points and glycerol concentrations c mixed juvenile stages of *Alaskozetes* were measure after 4–5 weeks acclimation at 0° and −5°C (LD 4:2(100% r.h. and food available). For comparison wit adults from identical culture backgrounds, these tw sets of measurements were taken at times when adu samples were being analysed in the course c experiment 3(c).

RESULTS

1. *Identification of glycerol*

The five chromatographic systems gave th following results with adult samples. There was onl one major periodate oxidizable compound in th extracts (others were present in trace amounts only This substance gave R_f values similar or identical t those of glycerol in each system. Since none of th other compounds tested had R_f values similar t glycerol in the two systems used, these values are goo evidence for the identity of the compound *Alaskozetes.*

2. *Effect of starvation on cold tolerance*

The results are shown in Table 1 as low group mea supercooling points and numbers of animals in hig and low supercooling point groups. Glycerol leve were also measured, but with the exception of the fir sample (mean ± S.E.M.: 2.58 ± 0.43 μg glycerol mg fresh weight, $n = 3$) trace amounts only were preser This suggests that glycerol was present in the initi stock culture at 0°C, but was lost when the anima were exposed to +5°C. Low group mean supercooli points varied only slightly throughout the course the experiment.

Table 1 shows that the proportion of animals in t low supercooling point group increased during weeks starvation at +5°C, but that this trend was n continued. The explanation of this lies in t experimental procedure and the consequent growth

Table 1. Low group mean (±S.E.M.) supercooling points and numbers in high and low supercooling point groups (see text) after starvation of adult *Alaskozetes antarcticus* for various periods at +5°C.

Acclimation temperature and starvation period (weeks)	Low group mean (±S.E.M.) supercooling point (≤ −24.0°C) (°C)	Number in low group (≤ −24.0°C)	Number in high group (> −24°C)
+5°C 0	−27.84±0.29	22	20
1	−27.67±0.17	28	14
3	−27.53±0.19	33	9
5	−27.11±0.24	25	17

fungi in the culture chambers. Although efforts were made to select animals from the chambers least affected by such growths, the sample from five weeks was from a potentially fed culture.

Frequency distribution histograms depicting the supercooling points obtained in the first three samples are shown in Fig. 4. These illustrate the selection of −24°C as dividing temperature between the high and low supercooling point groups. Frequency changes during the course of the experiment were analysed by χ^2 tests, which showed that although starvation for one week did not result in significant changes in the number of animals in high and low supercooling point groups, a further two week period did exert a significant effect compared to the initial sample ($P<0.025$).

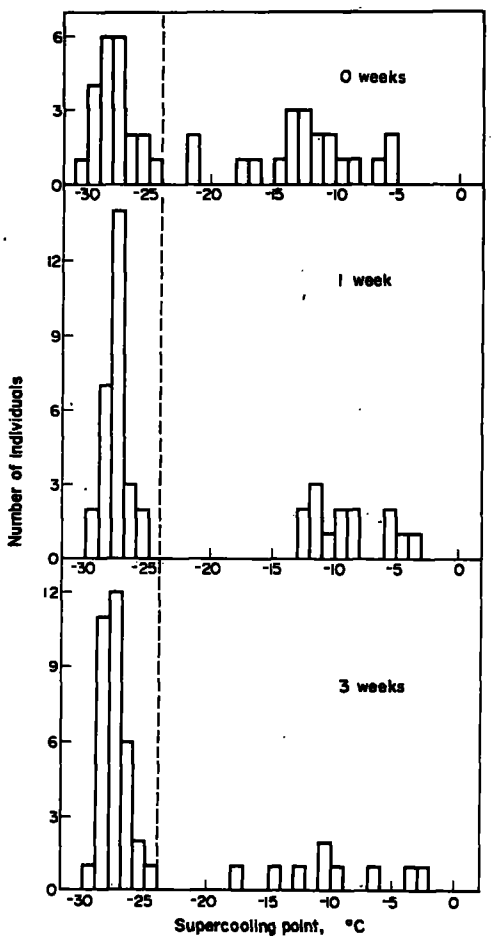


Fig. 4. Frequency distribution histograms showing the effect of starvation for 1 and 3 weeks on individual supercooling points in adult *Alaskozetes antarcticus*.

3(a). *Effect of temperature and photoperiod on cold tolerance.* These results are given in Table 2. Analysis of variance for low group supercooling points and glycerol levels (dry weight basis) indicated that F was significant in each case ($P<0.001$). Bartlett–Box tests for homogeneity of variances showed that there was no significant degree of variance heterogeneity in the data.

Table 3 shows the results of statistical tests carried out on the data. It is apparent that low temperature (−5°C) exerted a significant effect on cold tolerance under both photoperiods, while photoperiod was ineffective at both temperatures. Glycerol was lost by the animals under LD 0:24 conditions at 0°C, but no explanation of this can be offered at present. Cold tolerance increased during 4–9 weeks exposure at −5°C (LD 12:12). Glycerol concentration was higher in the later sample ($P<0.01$), more animals supercooled to relatively low temperatures ($P<0.01$), but although the low group mean supercooling point was depressed, this difference was not significant. These changes appeared to be complete after seven weeks. Long term exposure to 0°C, LD 0:24 did not depress the low group mean supercooling point or bring about resynthesis of glycerol, but did result in a greater proportion ($P<0.005$) of animals supercooling to low temperatures.

3(b). *Effect of photoperiod and relative humidity on cold tolerance.* Analysis of variance was carried out on the results of this experiment, together with the results of 3(c) and the data obtained on nymphal stages (see 4 below). This was undertaken because these experiments were performed on animals from the same Antarctic collections, whereas the preceding ones had utilized animals cultured for longer periods prior to experimentation. Such a combined analysis also simplifies the examination of certain long term effects.

Analysis of variance for low group supercooling points and dry weight glycerol concentrations showed that F was significant ($P<0.001$) in both cases, but a significant departure from variance homogeneity was disclosed in the glycerol data. This necessitated the use of t-tests operated according to the following rules:

(1) Standard t-tests for small numbers were used where the variance of samples in a specific comparison were not significantly different.

Table 2. Effect of temperature and photoperiod on the cold tolerance of adult *Alaskozetes antarcticus*.

Treatment	Low group mean (±S.E.M.) supercooling point (°C)	L	H	Corrected L/L+H ratio	Mean (±S.E.M.) glycerol concentration ($n=3$) ($\mu g\ mg^{-1}$ dry weight −glycerol)	($\mu g\ mg^{-1}$ water)
Initial stock (0°C LD 12:12)	−27.65±0.82	8	33	0.29	26.78±3.53	11.28±1.45
0°C LD 12:12 3 weeks ①	−26.55±0.42	8	33	0.29	21.38±1.61	9.06±0.67
0°C LD 0:24 3 weeks ②	−27.15±0.27	16	28	0.57	0.0	0.0
0°C LD 0:24 13 weeks ②	−26.99±0.24	30	12	0.73	0.0	0.0
−5°C LD 0:24 4 weeks ③	−28.46±0.30	26	19	0.58	38.74±0.37	16.15±0.15
−5°C LD 12:12 4 weeks ④	−28.27±0.30	27	16	0.63	40.21±2.72	16.74±1.09
−5°C LD 12:12 7 weeks ④	−28.73±0.29	37	7	0.84	51.61±2.50	21.25±0.98
−5°C LD 12:12 9 weeks ④	−28.96±0.31	43	5	0.90	50.79±1.17	20.93±0.46

Low group mean (±S.E.M.) supercooling points, numbers of animals in low (L) and high (H) supercooling point groups corrected L/L+H ratios and mean (±S.E.M.) glycerol concentrations are shown (n: number of determinations)

Table 3. Results of statistical tests showing the effect of temperature and photoperiod on the cold tolerance of adult *Alaskozetes antarcticus*

Treatment	Control	SCP	L:H	Glycerol
−5°C LD 12:12 4 weeks ④	0°C LD 12:12 3 weeks ①	$P<0.02$	$P<0.025$	$P<0.001$
−5°C LD 0:24 4 weeks ③	0°C LD 0:24 3 weeks ②	$P<0.02$	NS	$P<0.001$*
0°C LD 0:24 3 weeks ②	0°C LD 12:12 3 weeks ①	NS	NS	$P<0.01$*
−5°C LD 0:24 4 weeks ③	−5°C LD 12:12 4 weeks ④	NS	NS	NS

SCP: low group mean supercooling point; L:H: numbers of animals in low and high supercooling point groups; Glycerol: glycerol concentration expressed per unit dry body weight; *: Glycerol present in trace amounts only under 0°C, LD 0:24 conditions. Relative humidity was 95–100% throughout.

Table 4. Effect of photoperiod and relative humidity on the cold tolerance of adult *Alaskozetes antarcticus*.

Treatment	Mean (±S.E.M.) water content (% fresh weight, $n=3$)	Low group mean (±S.E.M.) supercooling point (°C)	L	H	Uncorrected L/L+H ratio	Mean (±S.E.M.) glycerol concentration ($n=3$) ($\mu g\ mg^{-1}$ dry weight−glycerol)	($\mu g\ mg^{-1}$ water)
Initial stock (0°C LD 12:12 100% r.h.)	n.d.	−26.24±0.37	5	37	0.12	3.96±0.22	1.71±0.09
0°C LD 20:4 100% r.h. 4 weeks ①	68.62±0.11	−26.25±0.34	12	30	0.29	8.65±3.24	3.91±1.46
0°C LD 20:4 95% r.h. 4 weeks ②	70.35±0.61	−26.43±0.51	7	35	0.17	9.37±2.76	3.91±1.14
0°C LD 4:20 100% r.h. 4 weeks ③	67.82±0.53	−27.62±0.26	17	25	0.40	14.92±3.22	6.97±1.48
0°C LD 4:20 60% r.h. 4 weeks ④	61.00±0.58	−27.41±0.38	7	35	0.17	42.10±4.83	25.81±2.83

Mean (±S.E.M.) water contents, low group mean (±S.E.M.) supercooling points, numbers in low (L) and high (H supercooling point groups, uncorrected L/L+H ratios, and mean (±S.E.M.) glycerol concentrations are shown (n: number determinations). n.d. not determined.

Table 5. Results of statistical tests showing the effect of photoperiod and relative humidity on the cold tolerance of adult *Alaskozetes antarcticus*

Treatment	Control	SCP	L:H	Glycerol
0°C LD 4:20 100% r.h. ③	0°C LD 20:4 100% r.h. ①	$P<0.05$	NS	NS
0°C LD 4:20 60% r.h. ④	0°C LD 4:20 100% r.h. ③	NS	$P<0.05$*	$P<0.01$

Abbreviations as in Table 3. *Higher numbers were present in the low supercooling point group of the control. All tests were carried out after 4 weeks aclimation.

(2) An approximate method (BAILEY, 1959) was sed where significant differences were detected etween variances.

For purposes of clarity the results will be described ı turn, beginning with the effect of photoperiod and umidity. These data are given in Table 4 with the :sults of statistical tests for comparison of treatments ı Table 5.

Photoperiod had no effect on glycerol concen- ations but supercooling point depression did occur. ı contrast, 60% r.h. was associated with significant :cumulation of glycerol expressed on a dry weight asis to rule out concentration effects. However, fewer ıimals supercooled to relatively low temperatures ter low humidity treatment, and supercooling points ere not depressed.

3(c). *Effect of temperature and relative humidity on ld tolerance*. The results of these experiments are ven in Table 6. Statistical tests (Table 7) confirmed e findings of experiment 3(a) in that low temperature -5°C) was associated with a significant accumulation of glycerol. Supercooling points were not depressed by the treatment, but this may reflect sampling variation (see below). The proportion of animals in the low supercooling point group was not increased at −5°C. This also contradicts part of the findings of experiment 3(a). Perhaps the long exposure period in the present experiment resulted in an enhanced ability to remain active at low temperatures. This did not occur in experiment 3(a), however, indicating that differential culture periods in the laboratory may affect supercooling.

Supercooling points were depressed from 4 to 11 weeks at −5°C and glycerol levels were slightly increased, but these effects were not significant.

Low relative humidity (40%) was found to depress the mean supercooling point of low group animals and to result in glycerol synthesis, but, as occurred in experiment 3(b), fewer animals supercooled to relatively low temperatures, although this was not significant.

3(d). *Effect of dry pretreatment (2 weeks at* O°C 40%

Table 6. Effect of temperature and relative humidity on the cold tolerance of adult *Alaskozetes antarcticus*

eatment	Mean (±S.E.M.) water content (% fresh weight, $n=3$)	Low group mean (±S.E.M.) supercooling point (°C)	L	H	Corrected L/L+H ratio	Mean (±S.E.M.) glycerol concentration ($n=3$) ($\mu g\ mg^{-1}$ dry weight−glycerol	($\mu g\ mg^{-1}$ water)
itial stock							
C LD 4:20 0% r.h. 5 weeks	n.d.	−27.29±0.62	7	41	0.19	13.74±0.85	5.87±0.36
C LD 4:20 0% r.h. 9 weeks	70.61±0.18	−27.49±0.40	15	27	0.44	28.54±2.06	11.54±0.81
C LD 4:20 % r.h. 4 weeks	59.73±0.88	−28.80±0.38	13	29	0.33	56.17±2.64	35.86±1.60
5°C LD 4:20 0% r.h. 4 weeks	71.54±0.87	−28.12±0.46	16	25	0.39	62.05±0.48	23.24±0.17
5°C LD 4:20 0% r.h. 11 weeks	68.66±0.36	−28.62±0.27	12	30	0.29	93.99±8.75	39.16±3.35
C LD 4:20 0% r.h. 16 weeks	72.07±0.24	−28.84±0.29	24	18	0.59	53.69±3.40	19.74±1.19
C LD 4:20 % r.h. 2 weeks	62.99±1.56	−28.85±0.46	16	26	0.38	52.08*	29.07*
5°C LD 4:20 % r.h. 4 weeks	65.19±2.10	±30.51±0.33	31	11	0.74	87.58±2.84	43.00±1.28
5°C LD 4.20 0% r.h. 2 weeks							
0°C LD 4:20 0% r.h. 4 weeks	67.61±0.37	−29.66±0.31	39	3	n.d.	103.20±8.76	44.76±3.42

Mean (±S.E.M.) water contents, low group mean (±S.E.M.) supercooling points, numbers in low (L) and high (H) ercooling point groups, corrected L/L+H ratios and mean (±S.E.M.) glycerol concentrations are shown (n: number of erminations). *$n=2$; n.d. not determined.

Table 7. Results of statistical tests showing the effect of temperature and relative humidity on the cold tolerance of adult *Alaskozetes antarcticus*

Treatment	Control	SCP	L:H	Glycerol
−5°C LD 4:20 100% r.h. 4 weeks ③	0°C LD 4:20 100% r.h. 9 weeks ①	NS	NS*	$P<0.001$
−5°C LD 4:20 100% r.h. 11 weeks ③	0°C LD 4:20 100% r.h. 16 weeks ①	NS	$P<0.025$*	$P<0.02$
0°C LD 4:20 40% r.h. 4 weeks ②	0°C LD 4:20 100% r.h. 9 weeks ①	$P<0.05$	NS*	$P<0.002$

Abbreviations as in Table 3. * Higher numbers were present in the low supercooling point group of the controls. Controls and treatments were sampled simultaneously.

r.h.) followed by 50% r.h. at 5°C (4 weeks). Compared to the 0°C 100% r.h. control, this treatment gave significant supercooling point depression ($P<0.001$), increased glycerol concentration ($P<0.002$) and caused an increase in the L/L + H ratio (although a decrease attended desiccation at 0°C) (Table 6). However, the latter difference was not significant.

Compared to animals cultured at −5°C (100% r.h.) for 11 weeks (simultaneous measurements), there was a significant difference between the mean supercooling points of the two samples ($P<0.001$), the dry pretreatment animals exhibiting a lower value. Glycerol levels were approximately equal, but the L/L + H ratio was higher in the sample from the lower relative humidity treatment ($P<0.001$).

3(e). *Effect of −10°C (following exposure for 2 weeks at −5°C).* Compared to the 0°C control, exposure to −10°C depressed the low group mean supercooling point (NS), enhanced glycerol accumulation ($P<0.01$) and resulted in a higher proportion of animals in the low supercooling point group (NS) (Table 6). Compared to treatment at −5°C for 11 weeks, supercooling points were slightly depressed at −10°C, while glycerol concentrations were elevated. However, these differences were not significant. The proportion of animals in the low supercooling point group was greater at the lower temperature ($P<0.001$). It therefore appears that −10°C was only slightly more effective at stimulating glycerol accumulation than was −5°C.

3(f). *Effect of long term exposure to* 0°C, LD4:20. The results of experiments 3(b) and 3(c) allowed the examination of long term changes under short day length conditions at 0°C. Comparison of the effects of 0 and 16 weeks and of 9 and 16 weeks gave the following results.

Exposure to LD 4:20 at 0°C resulted in the depression of the mean supercooling point (0 compared to 16 weeks: $P<0.002$; 9–16 weeks: $P<0.02$), while the proportion of animals in the low supercooling point group increased (0–16 weeks: $P<0.001$; 9–16 weeks: NS). Glycerol concentrations also increased significantly during the experiment (0–16 weeks: $P<0.01$; 9–16 weeks: $P<0.005$).

These results may be ascribed to an effect of photoperiod, although this is unlikely (see below). Alternatively, they may be due to exposure to 0°C although such a trend was not discerned in experiment 3(a). Again, this may reflect differences in the length of time for which these animals had been cultured.

3(g). *Relationship between glycerol concentration and supercooling.* A relationship between glycerol and supercooling is expected from physical considerations (SALT, 1961; MACKENZIE, 1977). To investigate this in *Alaskozetes* all the data collected in experiment 3 were combined. Glycerol concentrations were expressed as $\mu g\ mg^{-1}$ water and gram molecules kg^{-1} water.

The relationship between the two variables (Fig. 1) can be expressed by the linear regression equation $Y = -26.71 - 0.07X$, where Y is mean supercooling point (°C) and X the mean glycerol concentration ($\mu g\ mg^{-1}$ water). The correlation coefficient is −0.8 ($n = 22$, $P<0.001$), whereas the regression coefficient is significantly different from zero (S.E. of regression coefficient = ±0.0093; $t = 7.492$; $P<0.001$). If the data from desiccated animals are excluded from the regression, the resulting regression coefficient does not differ significantly from that given above. It also has a value of −0.07 and is significantly different from zero at the 0.1% level. Paradoxically, the absolute value of the correlation coefficient is slightly lower (−0.84) but this also differs from zero at the 0.1% level.

The existence of the relationship shown in Fig. 1 suggests that glycerol concentrations provide a more reliable guide to the effects of various treatments on cold tolerance than measured supercooling points. This distinction rests on two factors. Firstly, glycerol concentrations were based on three samples of five animals in each case (with one exception), whereas the group mean supercooling points were based on as few as five animals (in samples where feeding behaviour was such that most of the 40 animals tested were hidden group members), or as many as 40 in other instances. Secondly, the relationship between these two parameters is not as regular as that between glycerol concentration and the melting point. Large numbers are required to obtain a statistically satisfactory mean supercooling point for each concentration of glycerol. These two factors operate together to cause divergence between glycerol and supercooling points in particular experiments.

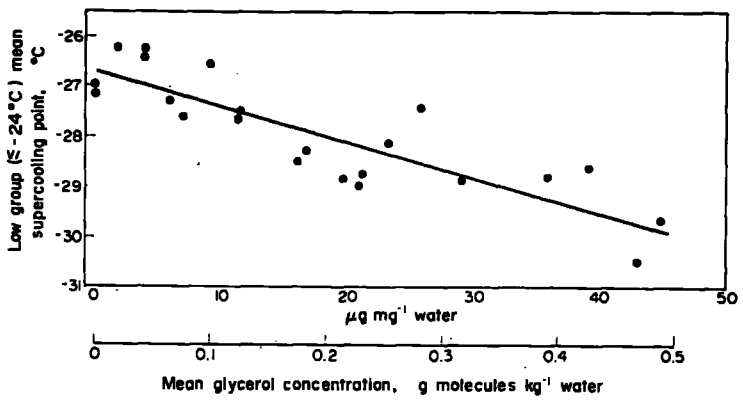


Fig. 5. Effect of glycerol concentration (expressed as $\mu g\ mg^{-1}$ body water and gram molecules kg^{-1} water) on low group mean supercooling points in adult *Alaskozetes antarcticus*. The fitted linear regression line for the data is described by the equation $Y = -26.71-0.07X$, where Y is mean supercooling point and X is mean glycerol concentration.

. *Cold tolerance of juvenile stages of* Alaskozetes

Table 8 shows the results of supercooling point and lycerol measurements on mixed juvenile life stages of *llaskozetes*. Adult values, measured after culture nder conditions identical to those experienced by ıeir nymphal counterparts, are shown for ɔmparison. No attempt was made to characterize the ɔld tolerance of individual instars since numbers in ıe experiment were weighted towards tritonymphs, as ery few protonymphs or deutonymphs were vailable.

Compared to adults, juvenile *Alaskozetes* showed ıwer supercooling points (0°C: $P<0.02$; −5°C: <0.05), slightly higher glycerol levels (NS at both ımperatures) and a greater proportion of animals ıpercooling to, or below, −24°C (0°C: $P<0.001$; 5°C: $P<0.005$).

Experiment 3 showed that adult mites increased ıeir cold tolerance on exposure to low acclimation mperatures. Tests comparing nymphs at the two :climation temperatures showed that although mean ıpercooling points of low group animals did not ffer significantly, glycerol concentrations were gher in the −5°C sample ($P<0.02$). The proportion animals in the low supercooling point group was creased by the low temperature treatment, but not gnificantly. However, there was an overall tendency r cold tolerance to be greater at −5°C.

Preliminary GLC analysis of polyols in juvenile *Alaskozetes* have suggested that ribitol, arabitol, xylitol, mannitol, inositol, rhamnitol and fucitol may be present in addition to glycerol. The functional significance of these substances is being investigated and they are likely to exert an influence similar to that of glycerol on supercooling ability in these animals.

DISCUSSION

1. *Glycerol and supercooling*

In *Alaskozetes*, glycerol was shown to increase supercooling ability. This has frequently been observed in other species. SALT (1959) described supercooling point depression to −47°C in the freezing tolerant parasitic wasp *Bracon cephi* (Gahan), which was correlated with glycerol concentrations of up to five molal. SØMME (1964, 1965b) observed a similar relationship in several overwintering insects, in addition to parallel cases based on other solutes. BAUST and MILLER (1970, 1972) also showed a linear relationship between glycerol and supercooling in the freezing tolerant carabid *Pterostichus brevicornis* (Kirby), as did SULLIVAN (1965) in his study of the overwintering of eggs of three species of the sawfly *Neodiprion*.

Similar considerations apply to mites. This is

Table 8. Cold tolerance of simultaneously sampled adult and juvenile *Alaskozetes antarcticus*.

Stage and treatment		Low group mean (±S.E.M.) supercooling point (°C)	L	H	Mean (±S.E.M.) glycerol concentration ($\mu g\ mg^{-1}$ dry weight−glycerol)
Nymphs	0°C	−29.00±0.29	26	22	20.09±3.78
Adults	0°C	−27.29±0.62	7	41	13.74±0.85
Nymphs	−5°C	−29.22±0.31	37	14	93.28±15.58
Adults	−5°C	−28.12±0.46	16	25	62.05±0.48

Low group mean (±S.E.M.) supercooling points, mean (±S.E.M.) glycerol concentrations and numbers in low (L) and high (H) supercooling point groups at 0°C and −5°C are shown.

demonstrated by the work of SOMME (1965a) on mite eggs containing sorbitol and that of SOMME and CONRADI-LARSEN (1977) on the adult mites *Calyptozetes sarekensis* (Tragardh) and *Carabodes labyrinthicus* (Michael) which exhibited lower supercooling points after glycerol accumulation.

There are some exceptions. In some freezing tolerant insects, ice nucleation (mediated by haemolymph components produced by the animal) may occur at temperatures close to 0°C, even in the presence of large quantities of glycerol (ZACHARIASSEN, 1977). In such cases glycerol appears to function exclusively as a means of protection against the effects of freezing.

2. *Effect of starvation on cold tolerance*

There is considerable support for the supposition that a bimodal distribution of animal supercooling points reflects the presence or absence of gut contents containing ice nucleating agents. Where freezing occurs at a relatively high temperature, it is considered that animals have retained food materials in the gut (see SALT, 1961 for a review). Many authors have found evidence that food-borne nucleating agents are responsible for decreased supercooling ability in otherwise cold hardy arthropods. For example, SØMME and CONRADI-LARSEN (1977) showed, by microscopical examination of the collembolan *Tetracanthella wahlgreni*, that the majority of animals supercooling to relatively high temperatures possessed gut contents, whereas those supercooling to lower temperatures contained no visible food materials in the digestive tract. The results of the present study are in agreement with these findings, the significance of which is the necessity for freezing susceptible species to overwinter with empty guts in order to realise their full potential for cold tolerance.

3. *Environmental stimuli and cold tolerance*

Glycerol concentrations are increased in adult *Alaskozetes* upon exposure to low acclimation temperatures. Conditions of low relative humidity also lead to raised glycerol levels, expressed per unit dry weight of animal, indicating that glycerol formation occurs under these circumstances. Low temperature results in an increase in the proportion of animals supercooling to relatively low temperatures. This is interpreted as a consequence of feeding suppression. Low relative humidities do not exert a similar influence on high and low supercooling point group numbers. On the contrary, there is a suggestion that slight increases in the proportion of high supercooling point group animals accompany such treatments. Photoperiod affects cold tolerance minimally, and the results suggest an influence on the proportion of animals in high and low supercooling point groups rather than on glycerol levels.

Differences were apparent in the cold tolerance of *Alaskozetes* collected in different years. These are probably the result of the differential culture periods experienced by the animals prior to experimentation, rather than the outcome of intrinsic differences between individuals. In this connection, the results obtained on control animals over the course of experiments 3(b) and (c) showed considerable variation. This was possibly an effect of short da length, but the lack of decisive effects in othe experiments on this factor argue against this, as doe the fact that animals exposed to 20 hr L:4 hr D i experiment 3(b) also increased their glycer concentrations over a four week period. Therefore, seems probable that glycerol accumulation due t exposure at 0°C occurred, and that the differer behaviour of animals collected in the previous seaso (where no accumulation was recorded at 0°C) was consequence of a longer period of laboratory cultur This is consistent with the findings of SØMME an CONRADI-LARSEN (1979) on an alpine beet (*Melasoma collaris* L.) which accumulated an subsequently lost some glycerol during long ter exposure to 0°C.

The results show that *Alaskozetes* is capable c supercooling to −26.5°C (Fig. 5) without measurab glycerol in the body, provided that nucleating gu contents are absent. This degree of cold tolerance ma aid *Alaskozetes* to survive Antarctic summer subzer temperatures, but would be insufficient in winte conditions. In certain years, such as 1972 (WALTON 1977), this would result in a high degree of mortalit Therefore, the protection afforded by glycerol is c considerable importance and the fact that lo acclimation temperatures are partially responsible fc initiating its production and also suppress feeding is c survival value in the field.

Immediately prior to the onset of winter, mean dail moss surface temperatures at Signy Island are close t 0°C for *ca.* 1 month and fluctuations are minim (WALTON, 1977). This phase is followed by a perio when mean daily temperatures appear to lie betwee 0° and −10°C, although daily minima may be lowe The results of the present experiments suggest th much of the additional cold hardiness of *Alaskozetes* built up during these two phases. At this point feedir suppression is more important than supercoolir point depression, but, as subzero conditions contin and temperature minima are lowered, glycer production becomes critical for survival.

Mean monthly atmospheric relative humidities screen height at Signy Island fluctuate only slight throughout the year (84–88% with the highest valu in winter and autumn) (COLLINS *et al.*, 197 However, humidities near the surface of stones more exposed areas would be much lower, especially wind speeds were high. At Hallett Station, continent Antarctica, surface humidities are lower than tho recorded above the surface and may be as low as 40 (PRYOR, 1962). Therefore, low humidities may occur the habitat of *Alaskozetes* before the appearance snow cover, in which case the glycerol production th accompanies desiccation will play a role in t overwintering mechanism of this species.

Under desiccating conditions, mites may feed replace water (WHARTON and ARLIAN, 1972). T may explain the relative increases in numbers animals in the high supercooling point group th occurred under dry conditions.

There is no clear evidence from the pres experiments that photoperiod plays an important r in the development of supercooling ability *Alaskozetes*. This may seem surprising si photoperiod is the most reliable guide to seaso

changes in the habitat. However, in maritime Antarctic localities, such as Signy Island, where subzero temperatures may occur in any season, it is clear that a direct response to temperature is of greater survival value than one to photoperiod alone.

The environmental cues that initiate the production of glycerol and similar compounds have been widely studied in insects, and there is some information on mites. Temperature has been implicated in some of the studies on this latter group. SØMME and CONRADI-LARSEN (1977) found that exposure to low temperature led to increased glycerol concentration in two oribatid mites from mountain sites in South Norway.

In insects, such as Collembola, temperature also affects polyol levels and supercooling points. *Tetracanthella wahlgreni* accumulated glycerol during 5°C and −10°C acclimation, but, unlike *Alaskozetes*, the rate of increase and the final concentration were lower at the lower temperature (SØMME and CONRADI-LARSEN, 1977).

In other insects, low temperature may stimulate glycerol production, but the situation is complicated by the occurrence of diapause. Three basic types are apparent: (1) Non-diapausing species with polyol formation being temperature dependent, for example the bark beetle studied by RING (1977); (2) Diapausing species that produce polyols in a temperature dependent fashion, such as the silkworm egg (CHINO, 1957) and several overwintering insects studied by SØMME (1964, 1965b); (3) Diapausing species that either (a) only produce polyols on exposure to low temperatures, such as the butterfly *Limenitis archippus* (Cramer) (FRANKOS and PLATT, 1976) or (b) produce greater quantities of polyols at elevated rates on low temperature exposure, for example the *Cecropia* silk moth pupa (ZIEGLER and PLATT, 1975). The adaptiveness of these mechanisms is difficult to assess, but it is clear that a complex interaction of photoperiod and temperature effects is involved in their initiation.

No previous animal cold tolerance study has shown the occurrence of glycerol formation on desiccation. SALT (1961) maintained that the effect of dehydration on supercooling is merely one of solute concentration and that near-lethal desiccation is required to induce effects of this type. SØMME (1964) increased the glycerol concentration (per unit of body water plus glycerol) of a gallfly pupa from 5.1 to 8% by dehydration, but glycerol synthesis did not occur.

Cold tolerance of juvenile stages of Alaskozetes

Nymphal stages of *Alaskozetes* possess a greater degree of low temperature tolerance, as measured by supercooling points, than adult animals. This is consistent with the presence in the body of other polyols besides glycerol. An additional effect may be exerted on supercooling points by the size of the animals concerned (SALT, 1966). The results also showed that a lower proportion of nymphs were feeding at both temperatures examined, when compared to adults. This may either reflect an enhanced low temperature response by juveniles as it heralds cessation of feeding in preparation for winter, or be a consequence of moulting cycles, which involve a non-feeding period in *Alaskozetes*.

Most other studies of cold tolerant arthropods have been concerned with species in which only one life stage overwinters, rather than with forms in which all instars are involved, such as *Alaskozetes* (STRONG, 1967; TILBROOK, 1973). STENSETH (1965) showed that eggs and larvae supercooled to lower temperatures than adult females in the mite *Tetranychus urticae* Koch, while juveniles of the spider *Clubiona similis* Koch from Sweden possessed lower lethal temperatures than adult females (ALMQUIST, 1970). Additionally, BLOCK and ZETTEL (1980) report that juvenile Collembola of several alpine species show greater cold tolerance than adults.

These findings imply that juveniles of many species utilize a cold tolerance mechanism that allows a greater 'safety margin', in the sense that field temperatures would only result in nymphal mortality if they reached lower levels than those lethal to adult animals. Why this should occur in *Alaskozetes*, where all life stages overwinter under similar temperature conditions, is difficult to comprehend.

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REFERENCES

ALMQUIST S. (1970) Thermal tolerances and preferences of some dune living spiders. *Oikos* **21**, 230–236.

ASAHINA E. (1969) Frost resistance in insects. *Adv. Insect Physiol.* **6**, 1–49.

BAILEY N. T. J. (1959) *Statistical Methods in Biology*. English Universities Press, London.

BAUST J. G. and EDWARDS, J. S. (1979) Mechanisms of freezing tolerance in an Antarctic midge, *Belgica antarctica*. *Physiol. Entomol.* **4**, 1–5.

BAUST J. G. and MILLER L. K. (1970) Variations in glycerol content and its influence on cold hardiness of the Alaskan carabid beetle *Pterostichus brevicornis*. *J. Insect. Physiol.* **16**, 979–990.

BAUST J. G. and MILLER L. K. (1972) Influence of low temperature acclimation on cold hardiness in the beetle *Pterostichus brevicornis*. *J. Insect Physiol.* **18**, 1935–1947.

BLOCK, W. and ZETTEL J. (1980) Cold hardiness of some Alpine Collembola. *Ecol. Entomol.* (in press).

BLOCK, W. YOUNG S. R. CONRADI-LARSEN E.-M. and SØMME L. (1978) Cold tolerance of two Antarctic terrestrial arthropods. *Experientia* **34**, 1166–1167.

CHINO H. (1957) Conversion of glycogen to sorbitol and glycerol in the diapause egg of the *Bombyx* silkworm. *Nature, Lond.* **180**, 606–607.

COLLINS N. J., BAKER J. H. and TILBROOK P. J. (1975) Signy Island, maritime Antarctic. In Structure and function of tundra ecosystems (Ed. by ROSSWALL T. and HEAL O. W.). *Ecol. Bull. (Stockholm)* **20**, 345–374.

DALENIUS P. and WILSON O. (1958) On the soil fauna of the Antarctic and of the Sub-antarctic Islands. The Oribatidae (Acari). *Ark. Zool.* **11**, 393–425.

FITZSIMONS J. M. (1971) Temperature and three species of Antarctic arthropods. *Pac. Insects Monogr.* **25**, 127–135.

FRANKOS V. H. and PLATT A. P. (1976) Glycerol accumulation and water content in larvae of *Limenitis archippus*; their importance to winter survival. *J. Insect Physiol.* **22**, 623–628.

JANETSCHEK H. (1967) Arthropod ecology of South Victoria Land. *Antarct. Res. Ser. (Am. Geophys. U.)* **10**, 205–293.

KOWKABANY G. N. (1961) Chromatography of carbohydrates and related compounds. In *Chromatography* (Ed. by HEFTMANN E.), pp. 502–533. Reinhold, New York.

MACKENZIE A. P. (1977) Non-equilibrium freezing behaviour of aqueous systems. *Phil. Trans. R. Soc. Ser. B* **278**, 167–189.

MANSINGH A. and SMALLMAN B. N. (1972) Variation in polyhydric alcohol in relation to diapause and cold hardiness in the larvae of *Isia isabella*. *J. Insect Physiol.* **18**, 1565–1571.

PRYOR M. E. (1962) Some environmental features of Hallett Station, Antarctica, with special reference to soil arthropods. *Pacif. Insects* **4**, 681–728.

RING R. A. (1977) Cold hardiness of the bark beetle, *Scolytus ratzeburgi* Jans. (Col., Scolytidae). *Norw. J. Entomol.* **24**, 125–136.

ROUNSEVELL D. E. (1977) The ecology of the pan-Antarctic mite *Nanorchestes antarcticus* (Strandtmann). In *Adaptations within Antarctic Ecosystems* (Ed. by LLANO G. A.), pp. 1023–1033. Smithsonian Institution, Washington.

SALT R. W. (1959) Role of glycerol in the cold hardening of *Bracon cephi* (Gahan). *Can. J. Zool.* **37**, 59–69.

SALT R. W. (1961) Principles of insect cold-hardiness. *A. Rev. Ent.* **6**, 55–74.

SALT R. W. (1966) Factors influencing nucleation in supercooled insects. *Can. J. Zool.* **44**, 117–133.

SØMME L. (1964) Effects of glycerol on cold-hardiness in insects. *Can. J. Zool.* **42**, 87–101.

SØMME L. (1965a) Changes in sorbitol content and supercooling points in overwintering eggs of the European red mite (*Panonychus ulmi* (Koch)). *Can. J. Zool.* **43**, 881–884.

SØMME L. (1965b) Further observations on glycerol and cold-hardiness in insects. *Can. J. Zool.* **43**, 765–770.

SØMME L. (1978a) Cold hardiness of *Cryptopygus antarcticus* (Collembola) from Bouvetøya. *Oikos* **31**, 94–97.

SØMME L. (1978b) Notes on the cold-hardiness of prostigmat mites from Vestfjella, Dronning Maud Land. *Norw. J Entomol.* **25**, 51–55.

SØMME L. and CONRADI-LARSEN E.-M. (1977) Cold-hardines of collembolans and oribatid mites from windswep mountain ridges. *Oikos* **29**, 118–126.

SØMME L. and CONRADI-LARSEN E.-M. (1979) Fros resistance in alpine, adult *Melasoma collaris* (Coleoptera *Oikos* **33**, 80–84.

STENSETH C. (1965) Cold hardiness in the two-spotted spide mite (*Tetranychus urticae* Koch). *Entomologia exp. appl.* 33–38.

STRONG J. (1967) Ecology of terrestrial arthropods at Palme Station, Antarctic Peninsula. *Antarct. Res. Ser. (An Geophys. U.)* **10**, 357–371.

SULLIVAN C. R. (1965) Laboratory and field investigations o the ability of eggs of the European Pine sawfly, *Neodipric sertifer* (Geoffrey) to withstand low winter temperature *Can Ent.* **97**, 978–993.

TILBROOK P. J. (1973) Terrestrial arthropod ecology at Sign Island, South Orkney Islands. Unpublished Ph.D. thesi University of London.

WALTON D. W. H. (1977) Radiation and soil temperatur 1972–74: Signy Island terrestrial reference sites. *B Antarct. Surv. Data* 1.

WHARTON G. W. & ARLIAN L. G. (1972) Utilization of wat by terrestrial mites and insects. In *Insect and Mite Nutriti* (Ed. by RODRIGUEZ J. G.), pp. 153–165. North Hollan Amsterdam.

ZACHARIASSEN K. E. (1977) Effects of glycerol in freez tolerant *Pytho depressus* L. (Col., Pythidae). *Norw. Entomol.* **24**, 25–29.

ZIEGLER R. and WYATT G. R. (1975) Phosphorylase a glycerol production activated by cold in diapausi silkmoth pupae. *Nature, Lond.* **254**, 622–623.

Survival strategies in polar terrestrial arthropods

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Survival strategies in polar terrestrial arthropods

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Three components of the survival strategy of a terrestrial Antarctic mite, *Alaskozetes antarcticus* (Acari: Cryptostigmata) are considered: overwintering survival, energetics and life history. Supercooling is an important feature of its cold tolerance, whilst elevation of standard metabolism allows activity at low temperatures, both of which contribute to a long development and maximum survival of individuals in the population. These are facets of the overall survival strategy evolved by such a species in response to the Antarctic terrestrial environment, but which may be widespread in polar invertebrates.

KEY WORDS:—strategies–arthropods–supercooling–energetics–cold adaptation–life cycles.

CONTENTS

INTRODUCTION

Survival is often regarded as the keynote to the existence of invertebrate poikilotherms in terrestrial habitats of polar regions. But, as Williams (1966) pointed out, "the central biological problem is not survival as such, but the design for survival". It is these designs or strategies which are the concern of this paper. The term strategy may be defined as a set of co-adapted traits, designed by natural selection, to solve particular ecological problems.

Adaptations of animals, both invertebrate and vertebrate, may be viewed as solutions to problems posed by environments. The solutions have evolved by natural selection. By the study of such solutions or adaptations in poikilotherms,

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it is possible to deduce certain aspects of the underlying strategy of the species or animal group in relation to its environment.

An analogy of this type extends naturally to terrestrial invertebrates living in extreme environments such as those characterized by low temperatures. As such, low environmental temperatures present two major problems to poikilotherms by (a) producing a general deceleration of metabolism resulting in reduced activity, feeding and growth, and (b) exposure to extreme low temperatures resulting in freezing of the tissues. In the former case, lower metabolic rates are more general and the seasonal time available for activity is much reduced, whilst in the latter, the proximity of snow and ice accentuates the freezing effect by seeding of ice crystals through the body surface.

Invertebrate animals living in polar and other low temperature habitats have evolved both physiological and ecological adaptations which are solutions to these two problems. The aims of this paper are to examine three components of the overall survival strategy of polar arthropods: overwintering survival, energetics and life history pattern, to highlight some of the more important solutions adopted and thereby contribute to a knowledge of their environmental biology. This paper will concentrate on terrestrial arthropods in general (see Block, in press, for a review) and on the Antarctic mite, *Alaskozetes antarcticus* (Michael) (Acari: Cryptostigmata) in particular, about which there is a considerable amount of information. The picture is far from complete, but hopefully such a treatment will aid future research in this field.

Alaskozetes is a large (200–300 μg adult live weight) cryptostigmatid mite belonging to the Family Podacaridae. When adult it is *c.* 1 mm in length and dark brown in colour. There are four post-embryonic life stages besides the adult: a six-legged larva and three eight-legged nymphal stages (proto-, deuto- and tritonymph). All stages are slow moving. *Alaskozetes* is both a herbivore and a detritivore feeding on lichens, foliose algae and organic debris mainly of vertebrate origin. In the field, the mite is found in a variety of habitats ranging from moss and organic material to the undersides of stones and rocks. Occasionally it occurs in dense local aggregations of several thousands of individuals representing all life stages. This species has been extensively studied at Signy Island, South Orkney Islands in the maritime Antarctic zone.

OVERWINTERING SURVIVAL

The major environmental stresses for land arthropods in polar habitats are temperature, both minimum and maximum levels, and at times, desiccation due to freezing of free water and exposure to high winds. A recent study (Young & Block, 1980a) allows the definition of the cold tolerance strategy adopted by *Alaskozetes* (Table 1). The main feature is that this species, in common with the majority of polar arthropods examined, is freezing susceptible, i.e. freezing is lethal for all individuals in all life stages. Individuals avoid freezing by supercooling, which is enhanced by glycerol in the body fluids. In addition, juveniles of this species are slightly more cold tolerant than adults, which has implications for the life cycle (see below). Furthermore, the utilization of a low temperature cue (overall decline from 0° to −10°C) to bring the mechanism into operation and the direct effect of desiccation to promote glycerol production, are both of considerable adaptive significance in this animal.

Table 1. Summary of the cold tolerance strategy of *Alaskozetes antarcticus* (after Young & Block, 1980a)

a.	Freezing susceptible
b.	Survive sub-zero temperatures by supercooling
c.	Gut contents detract from supercooling ability
d.	Individuals supercool to −26°C
e.	Supercooling enhanced to −31°C with glycerol
f.	Supercooling point and glycerol concentration directly correlated
g.	Significant increases in glycerol concentration caused by low temperature and desiccation
h.	Photoperiod has no effect on glycerol levels
i.	Juveniles are more cold tolerant than adults

This mechanism of low temperature survival by extensive supercooling has been widely reported in micro-arthropods (Acari and Collembola), spiders, scorpions, beetles and several other insects (Sømme, 1964) together with terrestrial pulmonates, marine invertebrates, Antarctic fish and reptiles. The alternative strategy of freezing tolerance, in which individuals survive tissue freezing, appears to be less widespread in poikilotherms (see Miller, 1978 for a review).

Consideration of the thermal regime in the habitats of *Alaskozetes* at Signy Island, shows that the species is uniquely adapted to its maritime Antarctic environment. Figure 1 shows 10-day mean temperatures together with extreme minimum and maximum temperatures recorded on the surface of a moss turf in a typical year (Walton, 1977). Mean temperatures ranged from + 9.6° to − 18.1°C, whilst the extreme minimum recorded was − 26.5°C and the maximum exceeded 30°C in that year. In an average year it appears that *Alaskozetes* is well able to survive winter temperatures by supercooling alone without the additional protection afforded by polyols such as glycerol. Conversely, during the five months of the short austral summer, the mites are subjected to much higher temperatures above freezing, albeit for short periods of time, possibly only a few hours.

Prior to the onset of winter at Signy Island, mean daily temperatures at the ground surface (Walton, 1977) are close to 0°C for *c.* 4–6 weeks with minimal fluctuations. This is also the period when an increasing proportion of the hourly temperature records occur in the 0° to −5°C range (Fig. 2). In March–April 1972, 60–80% of the hourly data were in this zone, as compared to 40–60% in the 0° to + 5°C range. An abrupt transition was observed in May, which coincided with winter freeze-up. Chambers (1966) monitored eight to nine separate freeze-thaw cycles at 1 cm depth in a fine rock debris site during an autumn period, and totals of 19 to 23 such cycles per year in a study at Signy Island. The results of experimental work on *Alaskozetes* (Young & Block, 1980a) suggest that much of its additional cold hardiness is built up during the pre-winter period, when successive waves of freeze-thaw temperature oscillations occur.

Melt-off with its concomitant temperature rise occurs rapidly at Signy Island, normally in October or early November. Ten-day mean temperatures rise above 0°C (Fig. 1), and there is a rapid reversal of temperatures from just below 0°C to just above zero (Fig. 2). For between 5–6 months each year the land fauna at Signy Island is subject to continuous freezing temperatures, but it should be

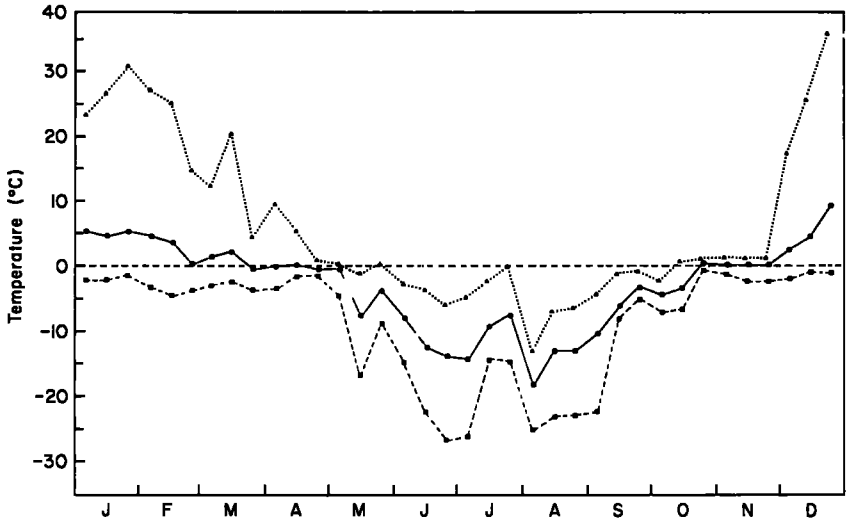

Figure 1. Annual temperature cycle for the surface of a moss turf community at Signy Island in a typical year (1972), which is representative of the thermal regime experienced by *Alaskozetes antarcticus*. ●—● 10 day mean temperature; ■ - - ■, minimum temperature; ▲ . . . ▲, maximum temperature.

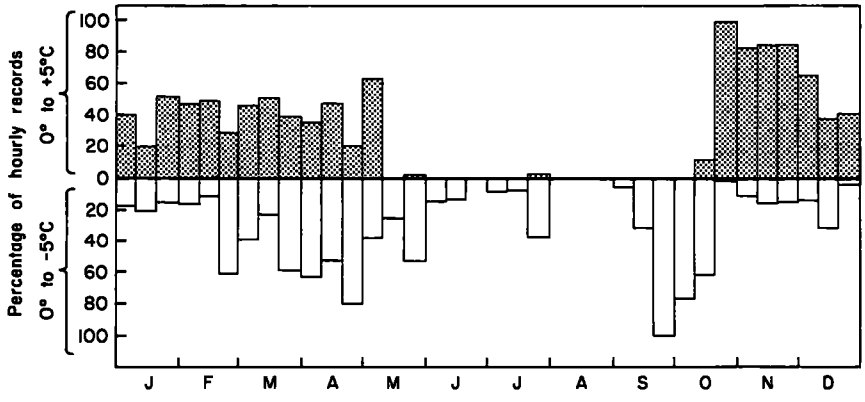

Figure 2. Proportions of hourly temperatures in the 0° to −5°C and 0° to +5°C zones per 10-days which were recorded at the surface of a moss turf at Signy Island in 1972.

pointed out that freezing tolerant arthropods have not been found there. Th effects of such an annual temperature cycle on the life history of *Alaskozetes* ar discussed below.

ENERGETICS

The partitioning of the energy ingested and assimilated to the pathways o respiration and production by poikilotherms living in polar habitats is a critic feature of their survival strategies. Although oribatid (cryptostigmatid) mit have generally lower metabolic rates than other comparable sized invertebrates, has been demonstrated that *Alaskozetes* has an elevated rate of standard metaboli compared to temperate orbatids (Block & Young, 1978). It is able therefore t partly avoid the depressant effect of low temperatures on activity, feeding, growt and reproduction. It is adapted to maintaining its biological functions in th

temperature range −4° to + 15°C (Block, 1977; Young, 1979a; Young & Block, 1980b), which are generally prevalent during daytime in summer at Signy Island. Young (1979a) has postulated that lowering of the activation energy for certain reactions may constitute part of the mechanism behind the metabolic cold adaptation of this mite.

In terms of diurnal and seasonal temperature fluctuations, *Alaskozetes* does not compensate metabolically for such changes (Young, 1979b). Such a mechanism enables it to exploit the relatively warm conditions of the austral summer, and to conserve its energy resources in low temperature conditions. In other words, metabolic conformity may be of greater strategic value than metabolic regulation to these animals in polar enviroments. However, Prosser (1975) has suggested that highly variable thermal environments are associated with the ability to undergo metabolic compensation, and clearly, *Alaskozetes* is an exception to this. It may be that limitations of the Antarctic terrestrial environment are responsible rather than the control of metabolism by important biochemical substances (Precht, Christopherson, Hensel & Larcher, 1973).

The relationship of the metabolic response to temperature has been used to assess an invertebrate's overall performance. The model proposed by MacLean (1975) illustrated some of the limitations imposed by temperature on poikilotherm energy budgets. In type I of the MacLean model, *A* (assimilation rate) is greater than *R* (respiration rate) at all temperatures normally encountered by the animal, thus allowing a favourable energy balance (with positive *P*–production). In type II, *A* increases more rapidly with rising temperature than *R*, and thus the amount of energy available for growth increases with temperature. Such an animal may be unable to complete its life cycle at low temperatures because of an unfavourable energy balance. Type III (*R* increases more rapidly with temperature than *A*) is the pattern of an obligate polar species, which is able to maintain a positive energy balance only at low temperatures. Polar terrestrial invertebrates may be grouped under type I or III, and evidence is accumulating which shows that Antarctic oribatids such as *Alaskozetes,* have several features of the obligate polar form. Feeding and energy studies of this and other related Antarctic species are currently in progress.

LIFE HISTORY

Within the life cycle of oribatid mites there are several critical periods when survival of the individual is at greater risk than at other times. These include the time of egg hatch for the larva, and successively the four moults to complete the development: larva→proto-→deuto-→trito-nymph→adult. During moulting the mites are especially vulnerable to desiccation and extremes of temperature. These two environmental stresses are accentuated in the maritime Antarctic environment, where sub-zero temperatures occur frequently in summer, and free water may be at a premium due to rapid freeze-thaw cycles (Chambers, 1966). It is pertinent to review briefly our knowledge of the biology of a typical polar marine in order to develop a hypothesis concerning its overall life history strategy (Table 2). Oviposition by *Alaskozetes* occurs in spring and throughout the Antarctic summer (Strong, 1967; Tilbrook, 1973), with females carrying up to 12 eggs (usually 4–6 eggs per female). Prelarvae are found within the eggs inside the female, but do not hatch immediately after deposition. Development times for the larva and the three nymphal stages at field temperatures are probably long

Table 2. Life history strategies of oribatid mites in temperate and polar environments

Parameter	Temperate	Polar
Population density	High in summer and autumn	High in summer
Oviposition	Spring to mid-summer	Spring and throughout summer
Development (egg-adult)	Variable: 23–275 days	At least 1 year
Longevity	1–3 years	2+ years
Mortality	Temperature extremes, desiccation	Freezing
Metabolic rate	Low	Low with elevation
Cold tolerance (freezing susceptible)	Supercooling	Supercooling

(Block, unpublished data). Individual longevity estimated from field experiments shows considerable variation, but adults may live for longer than one year, whilst nymphal longevity estimates range between 4–9 months dependent on instar and environmental conditions. Examination of field populations and dense aggregations of *Alaskozetes* in spring, shows considerable overwintering mortality probably from freezing. Life cycle length (egg to adult) is long compared to temperate species (see Mitchell, 1977 for review), being at least one year. As all postembryonic stages overwinter, a mixed population of all the nymphal instars and mature individuals is found in all seasons, which is comparable to some prostigmatid mites (Goddard, 1979). Growth and development is limited to the period mid-October to April, and Fig. 3 shows a postulated life cycle for *Alaskozetes*. As both juveniles and adults overwinter, it is advantageous that the juveniles are at least as cold hardy as the adults to ensure survival of the species. This is particularly important in a severe Antarctic winter.

Evidence from culture studies shows that females of *Alaskozetes* oviposit on several occasions after reaching maturity, and that an individual may breed in at least two successive summers. The advantages of iteroparity (repeated breeding) for a polar terrestrial invertebrate are many (Fig. 4). Once the female has reached breeding condition after a long, slow and energetically costly development, egg production occurs when environmental conditions allow, and iteroparity combined with extended individual longevity of both sexes will enhance the survival potential of the species. Semelparity or 'big bang reproduction' would appear to have no place in such a life history strategy.

Life cycles lasting longer than one year occur in many (but not all) Arctic invertebrates (MacLean, 1975, & in press). Species with annual life cycles may have been eliminated from such tundra faunas by a succession of severe summers. Temperature and length of the Antarctic growing season (Fig. 1) determine the long life cycle of *Alaskozetes,* which in turn exposes the animal to increas

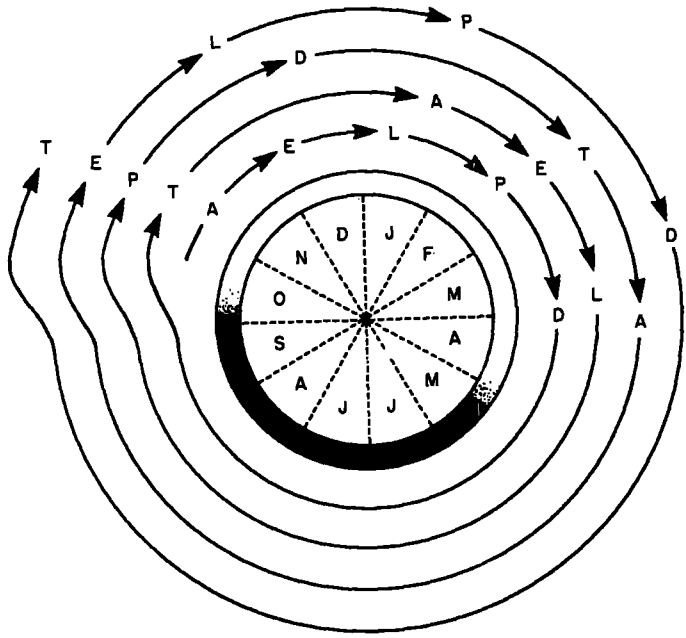

Figure 3. Postulated life cycle of *Alaskozetes antarcticus* under maritime Antarctic conditions. E: egg, L: larva, P: proto-nymph, D: deuto-nymph, T: trito-nymph, A: adult. Inner sections indicate possible snow cover and months: J, January; F, February; etc.

nortality. Thus the population must be able to sustain the additional mortality ncurred during prolonged development in order for it to survive there. *Alaskozetes* appears to have evolved the strategy of increasing the probablity of urvival by cold tolerance mechanisms and maximizing reproduction by oviposition over a long time period and repeated breeding. Adult body size, growth rate and environmental severity have interacted to produce such a pattern.

It is a fashionable proposition to place an Antarctic species such as *Alaskozetes* nto the r- and K- selection continuum (Dobzhansky, 1950; Pianka, 1970). In this pecies selection has favoured slow development with delayed reproduction, ecreased mortality, longevity > 1 year, and with only a small proportion of the otal energy intake devoted to breeding. But *Alaskozetes* also has a small body size, ew breeding periods per year and lives in a lax competitive situation, all features f an r-strategist. It is difficult, on present evidence, to suggest that *Alaskozetes* is iore of an r- or K-strategist, and due to the highly seasonal nature of its nvironment a polymorph between opportunism and stability may result. This ontrasts with the oribatid mites of some hot desert systems, which are r-rategists (Wallwork, in press). The effects of stable and fluctuating nvironments on the development of r- and K-strategies in relation to juvenile id adult mortalities have been discussed by Stearns (1976), Southwood (1977) id others. Terrestrial mites occupy relatively stable environments in the aritime Antarctic with well defined, predictable changes in season and resource ailability. Also, on the available evidence for field survival and longevity mbined with increased juvenile cold tolerance, it is thought that adult ortality may be more variable than that of the immatures. Thus the criticism of

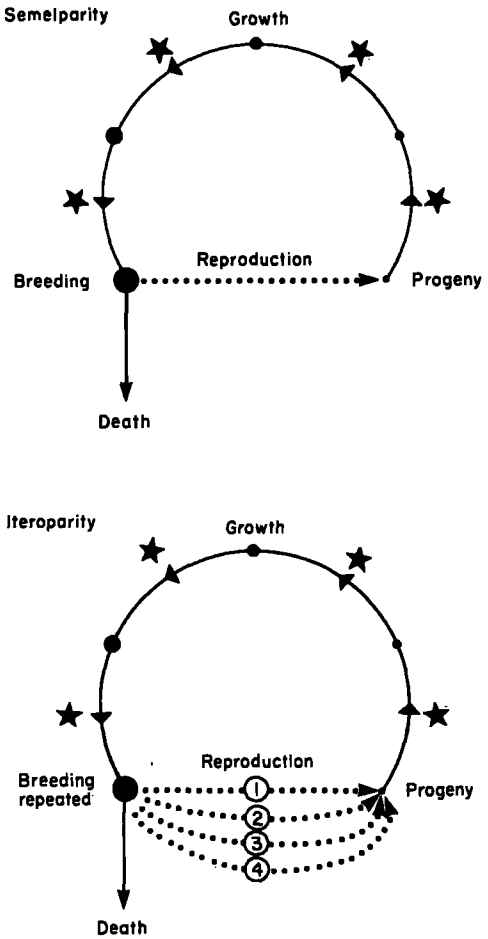

Figure 4. Generalized breeding patterns applied to oribatid life cycles. The five post-embryonic life stages are depicted commencing with progency (=larva). ★, timing of moults at which mortality is greatest.

the usefulness of the 'r–K approach' (Stearns, 1977) is upheld by the present dat for *Alaskozetes*. It is interesting to note the suggestion of Clarke (1979) that th Antarctic marine benthic environment appears in some cases to favour th evolution of K-strategies in the fauna. It may be that the effects of lo temperature, acting in different ways in the terrestrial and marine environmen of polar regions, are fundamental to the widespread evolution of such life cycles

CONCLUSIONS

Several adaptations are exhibited by polar arthropods such as the mi *Alaskozetes,* which overcome the ecological and physiological problems posed b the severe Antarctic environment. Low temperature effects of metabolism a overcome by elevation of standard metabolic rate, or cold adaptation, whi enable individuals to function at temperatures which immobilize their tempera counterparts. Freezing of the tissues at extreme low temperatures is avoided by complex supercooling mechanism initiated primarily by low temperature cu

heightened by the desiccating atmosphere at freeze-up. These physiological adaptations have enabled the evolution of a life history pattern which incorporates several features which are similar to those described for a K-strategist. Thus, *Alaskozetes* appears to be closely adapted to its polar environment, which supports Wallwork's (1973) contention that representatives of the Family Podacaridae have undergone a long period of evolution in the southern polar region.

The preliminary analysis presented here illustrates some of the more prominent features of the underlying adaptational strategy of the Antarctic mite, *Alaskozetes antarcticus*. It is well able to endure the winter severities of its environment, as well as being able to capitalize on the shorter, favourable summer periods to grow, develop and reproduce. Such features are part of an overall strategy which is probably typical of polar arthropods and may well be representative of many other terrestrial invertebrates living in low temperature habitats.

SUMMARY

The Antarctic terrestrial mite *Alaskozetes antarcticus* (Cryptostigmata) displays many adaptational features in respect of its low temperature environment which are demonstrated in its overwintering survival, energetics and life history. Such adaptations may be typical of the strategies adopted by a wide range of terrestrial invertebrates living in similar environments.

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REFERENCES

BOCK, W., 1977. Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus* (Acari: Cryptostigmata). *Journal of Experimental Biology, 68:* 69–87.

BOCK, W., In press. Aspects of the ecology and physiology of Antarctic soil fauna. In D. L. Dindal (Ed.), *Soil Biology as Related to Land Use Practices.* New York: State University of New York. (Soil Zoology Colloquium VII, Syracuse, New York, 1979).

BOCK, W. & YOUNG, S. R., 1978. Metabolic adaptations of Antarctic terrestrial arthropods. *Comparative Biochemistry and Physiology, 61A:* 363–368.

CHAMBERS, M. J. G., 1966. Investigations of patterned ground at Signy Island, South Orkney Islands: II. Temperature regimes in the active layer. *British Antarctic Survey Bulletin.* No. *10:* 71–83.

CLARKE, A., 1979. On living in cold-water: K-strategies in Antarctic benthos. *Marine Biology, 55:* 111–119.

DOBZHANSKY, T., 1950. Evolution in the tropics. *American Scientist, 38:* 209–221.

EDDARD, D. G., 1979. The Signy Island terrestrial reference sites: XI. Population studies on the Acari. *British Antarctic Survey Bulletin,* No. *48:* 71–92.

FACLEAN, S. F., 1975. Ecological adaptions of tundra invertebrates. In F. J. Vernberg (Ed.), *Physiological Adaptation to the Environment:* 269–300. New York: Intext Educational Publishers.

FACLEAN, S. F., In press. The detritus-based trophic system. In J. Brown *et al.* (Eds), *An Arctic Ecosystem: the Coastal Tundra at Barrow, Alaska:* chapter 11. Philadelphia: Dowden, Hutchinson & Ross.

FELLER, L. K., 1978. Physiological studies of Arctic animals. *Comparative Biochemistry and Physiology, 59A:* 327–334.

FITCHELL, M. J., 1977. Life history strategies of oribatid mites. In D. L. Dindal (Ed.), *Biology of Oribatid Mites:* 65–69. New York: State University of New York, Syracuse.

FINKA, E. R., 1970. On 'r' and 'K' selection. *American Naturalist, 104:* 592–597.

FRECHT, H., CHRISTOPHERSON, J., HENSEL, H. & LARCHER, W., 1973. *Temperature and Life.* Berlin: Springer Verlag.

PROSSER, C. L., 1975. Physiological adaptations in animals. In F. J. Vernberg (Ed.), *Physiological Adaptation to the Environment:* 3–18. New York: Intext Educational Publishers.

SØMME, L., 1964. Effects of glycerol on cold-hardiness in insects. *Canadian Journal of Zoology, 42:* 87–101.

SOUTHWOOD, T. R. E., 1977. Habitat, the templet for ecological strategies. *Journal of Animal Ecology, 46:* 337–365.

STEARNS, S. C., 1976. Life history tactics: a review of ideas. *Quarterly Review of Biology, 51:* 3–47.

STEARNS, S. C., 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics, 8:* 154–171.

STRONG, J., 1967. Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. *Antarctic Research Series (American Geophysical Union), 10:* 357–371.

TILBROOK, P. J., 1973. *Terrestrial Arthropod Ecology at Signy Island, South Orkney Islands.* Unpublished Ph.D. thesis, University of London.

WALLWORK, J. A., 1973. Zoogeography of some terrestrial micro-Arthropoda in Antarctica. *Biological Reviews, 48:* 283–259.

WALLWORK, J. A., In press. Desert soil microarthropods: an 'r' selected system. In D. L. Dindal (Ed.), *Soil Biology as Related to Land Use Practices.* New York: State University of New York, (Soil Zoology Colloquium VII, Syracuse, New York, 1979).

WALTON, D. W. H., 1977. Radiation and soil temperatures 1972–74: Signy Island terrestrial reference sites. *British Antarctic Survey Data Report,* No. *1.*

WILLIAMS, G. C., 1966. *Adaptation and Natural Selection.* Princeton, New Jersey: Princeton University Press.

YOUNG, S. R., 1979a. Respiratory metabolism of *Alaskozetes antarcticus. Journal of Insect Physiology, 25:* 361–369.

YOUNG, S. R., 1979b. Effect of temperature change on the metabolic rate of an Antarctic mite. *Journal of Comparative Physiology, 131:* 341–346.

YOUNG, S. R. & BLOCK, W., 1980a. Experimental studies on the cold tolerance of *Alaskozetes antarcticus. Journal of Insect Physiology, 26:* 189–200.

YOUNG, S. R. & BLOCK, W., 1980b. Some factors affecting metabolic rate in an Antarctic mite. *Oikos, 34:*178–185.

SOIL BIOLOGY AS RELATED TO LAND USE PRACTICES

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ASPECTS OF THE ECOLOGY OF ANTARCTIC SOIL FAUNA

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INTRODUCTION

The Antarctic Region can be divided into ecological zones (Holdgate, 1964) including the sub-Antarctic, the maritime and continental zones. This paper is concerned with the maritime Antarctic zone south of 60° latitude. The majority of land habitats seasonally free of snow and ice occur here and hence its importance to the soil fauna. It is also an area in which much of the Antarctic soil biological work has been undertaken. The maritime Antarctic zone south of 60° latitude includes the South Orkney and South Shetland Islands, together with Adelaide Island and the west coast of the Antarctic (Graham Land) Peninsula and its offshore islands.

Apart from the microbial groups (fungi, yeasts and bacteria) in maritime Antarctic soils, there are eight invertebrate groups represented ranging from Protozoa to higher insects (Diptera). Table 1 presents the numbers of species found to date for these groups. Due to their wide distribution throughout the maritime Antarctic and the increasing body of information about them, this paper will concentrate on the arthropods in general and on the mites (Acari) and springtails (Collembola) in particular. Such soil micro-arthropods penetrate further south than most other invertebrates, and exhibit ecological features and adaptations to the environment, which may be considered typical of the Antarctic soil fauna generally. The soil fauna is the dominant terrestrial component, there being no permanent land dwelling vertebrates and above ground invertebrates are generally absent. There is considerable variation of terrestrial habitats within the maritime Antarctic, and Holdgate (1977) has discussed this in detail. Briefly, invertebrate soil communities are found in a range of habitats from exposed fellfield types (similar to the chalikosystem of Janetschek, 1967) to the closed moss dominated (bryosystem) in addition to relatively small areas covered by flowering plants (the grass Deschampsia antarctica Desv. and the cushion plant Colobanthus crassifolius (D'Urv.) Hook.f. Much of the information reviewed here has been collected from bryophyte communities on Signy Island in the South Orkney Islands, where arthropods occur in relatively large numbers and the fauna is comparatively diverse. Two sites have been investigated in detail: SIRS (Signy Island Reference Site) 1 and SIRS 2. The former is a fairly dry moss turf composed of Polytrichum alpestre Hoppe and Chorisodontium aciphyllum (Hook.f. et Wils.) Broth., whilst the latter is a relatively wet moss carpet composed of Calliergon sarmentosum (Wahlenb.) Kindb., Calliergidium austro-stramineum (C. Muell.) Bartr. and Drepanocladus uncinatus (Hedw.) Warnst.

TABLE 1

SOIL INVERTEBRATES OF MARITIME ANTARCTIC HABITATS

	No. of species recorded	Distribution	Reference
Protozoa	124	Ubiquitous	Smith, 1978
Rotifera	Number unknown but Adineta, other Bdelloidea, and Monogononta recorded	Mainly in wet moss communities	Jennings, 1976 a
Tardigrada	11	Wet moss communities	Jennings, 1976 b
Nematoda	40	Ubiquitous	Maslen, in press
Enchytraeidae	2 ?	Organic detritus in South Shetland Islands	Block, unpublished
Collembola	8	Ubiquitous	Wise, 1967; Wallwork, 1973
Diptera	2	South Shetland Islands, Antarctic Peninsula	Wirth & Gressitt, 1967
Acari	40	Ubiquitous	Gressitt, 1967; Wallwork, 1973
	Mesostigmata 9		
	Cryptostigmata 16		
	Astigmata 5		
	Prostigmata 10		

This review will consider aspects of the ecology and physiology of micro-arthropods living in these communities, which highlight their adaptations to the environment of the maritime Antarctic. These include features of their populations, life cycles, respiratory metabolism and cold tolerance.

ECOLOGY

Species composition

Consideration of the arthropod species list (Table 2) for the two moss sites at Signy Island shows a typical structure with the majority of the fauna comprised of prostigmatid mites, three collembolans, two cryptostigmatids and a single mesostigmatid predator. In general, a species poor and much simplified arthropod community than that found in temperate habitats.

Population density

The most numerous species present on the SIRS (Table 3) is the ubiquitous springtail Cryptopygus antarcticus Willem, which over a two year study period maintained a mean population of 48,296 individuals m^{-2}, six times as many as all the Acari. The Acari averaged c. 8,223 individuals m^{-2} for the same period. Between year differences occurred in two species of Prostigmata, Nanorchestes antarcticus (Strandtmann) and Ereynetes macquariensis (Fain), which showed over 50% decline in numbers during the second year. Eupodes minutus (Strandtmann) and Gamasellus racovitzai (Trouessart) maintained fairly constant numbers for 1972 and 1973.

Seasonal changes in mite population density were recorded (Figure 1, from Goddard, 1979) which followed a pattern of low numbers in winter with high summer numbers. G. racovitzai was the only species which had similar yearly cycles of abundance, which may be related to its predatory role in the community. Few seasonally related changes occurred in the collembolan population of this site (Tilbrook, 1977).

In terms of vertical distribution, most Acari and Collembola were found in the uppermost layer of the moss peat profile, except during winter when a reversal of the proportion of the total mite population in the 0-3 cm and 3-6 cm layers occurred. N. antarcticus was consistently (80-90% of its population) in the 0-3 cm stratum throughout the year, whilst E. macquariensis was found mainly at 3-6 cm. Deeper core samples collected on four occasions (Figure 2) revealed that Acari did not penetrate beyond 18 cm in the profile, and confirmed that E. macquariensis was a deeper dwelling form than the other species present. Little information exists on the horizontal distribution of the micro-arthropods on these sites, but they appear to be highly aggregated especially during spring and the early part of the austral summer.

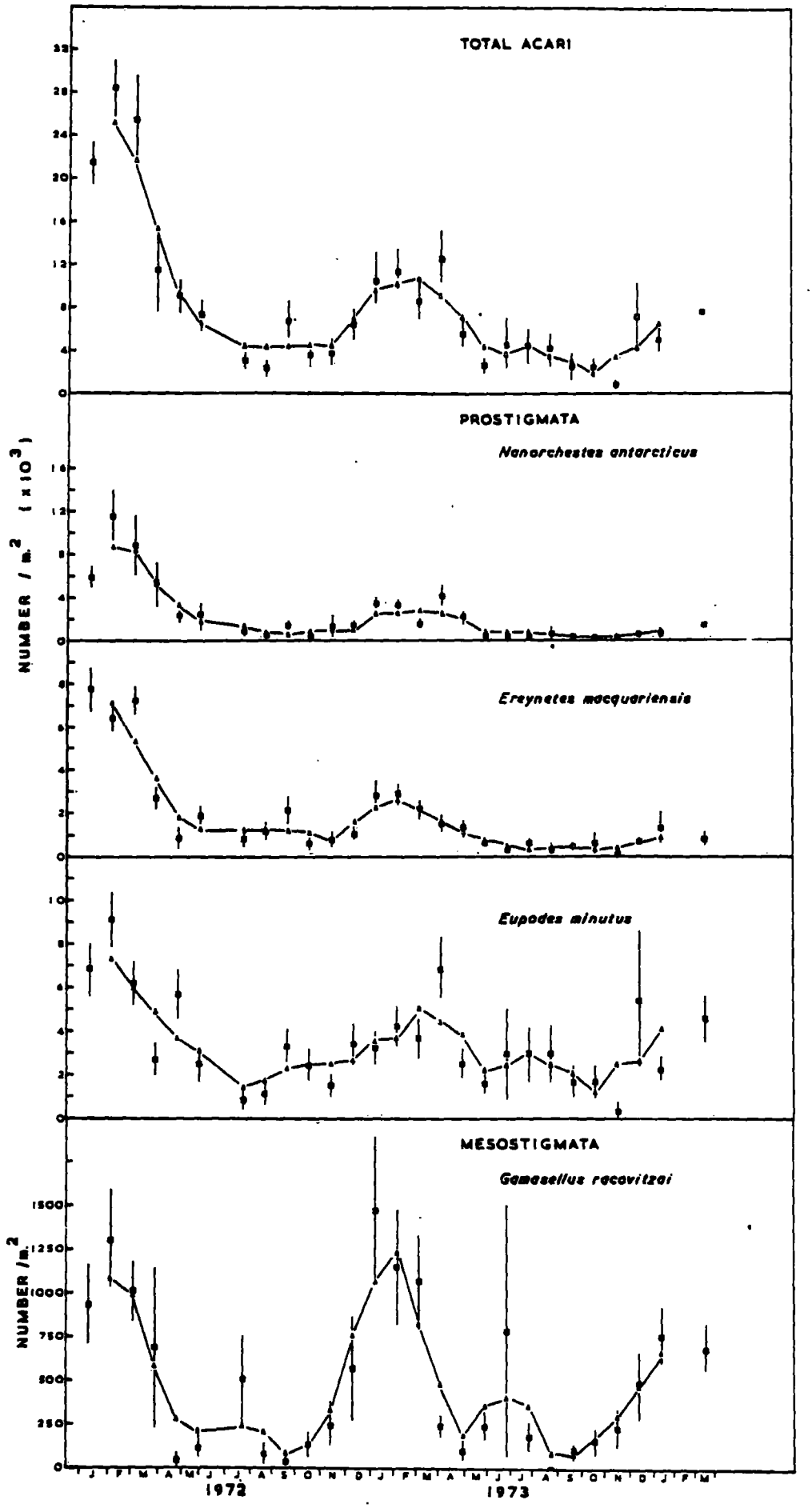

FIGURE 1. Seasonal fluctuations in mean population density ($x10^3$ ind m^{-2}) on SIRS 1 during 1972-74. Monthly mean values (±SEM) are plotted from Goddard, 1979.

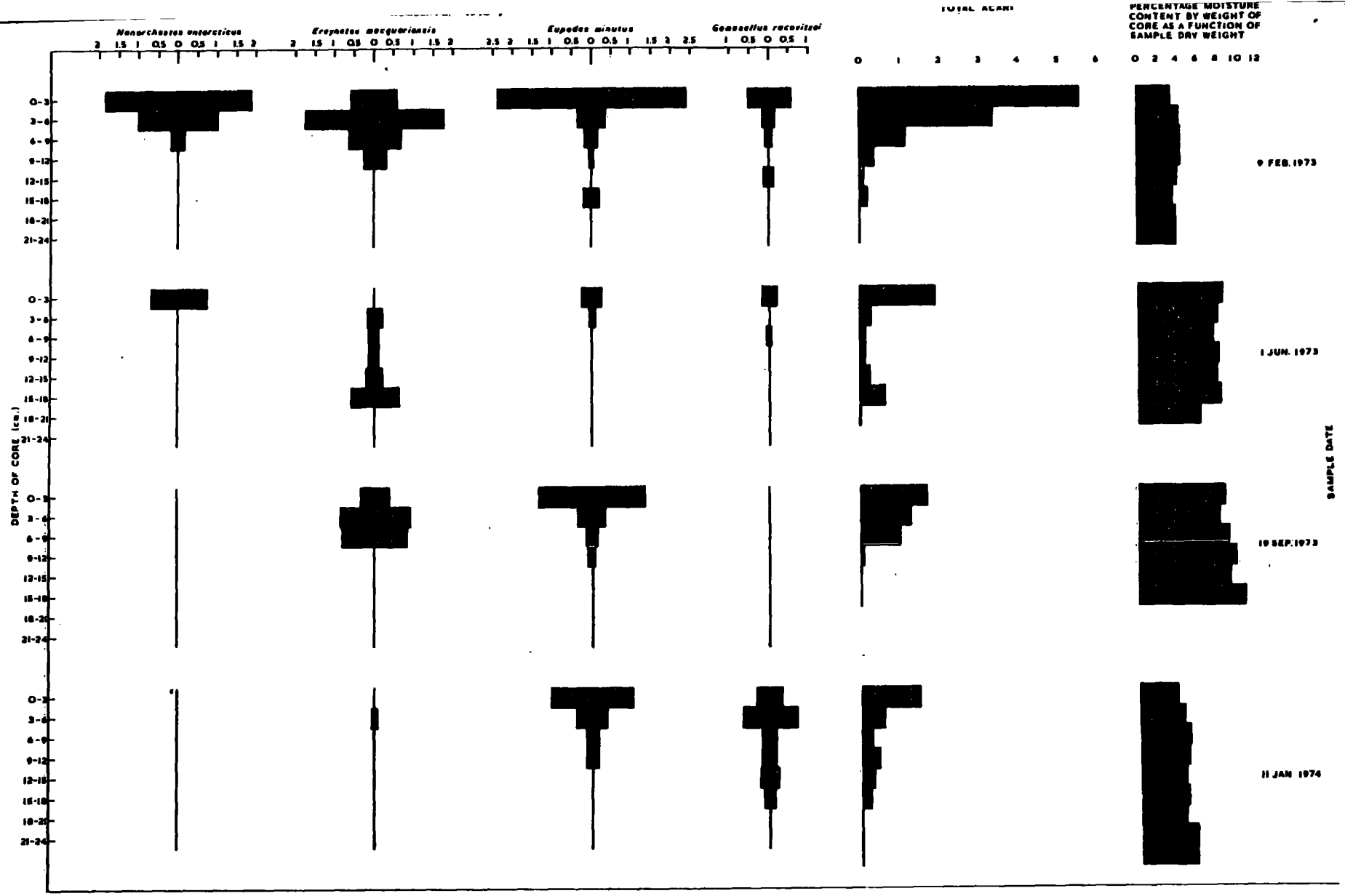

FIGURE 2. Vertical distribution of Acari in 24 cm deep cores on SIRS 1 (two winter and two summer samples) together with water content as percentage of core dry weight.

TABLE 2

SPECIES OF ACARI AND COLLEMBOLA RECORDED FOR TWO MOSS SITES AT SIGNY ISLAND, MARITIME ANTARCTIC

ACARI			
	Cryptostigmata	2 species	Alaskozetes antarcticus (Michael)
			Halozetes belgicae (Michael)
	Mesostigmata	1 species	Gamasellus racovitzai (Trouessart)
	Prostigmata	6 species	Nanorchestes antarcticus (Strandtmann)
			Eupodes minutus (Strandtmann)
			Halotydeus signiensis (Strandtmann)
			Ereynetes macquariensis (Fain)
			Stereotydeus villosus (Trouessart)
			Tydeus tilbrooki (Strandtmann)
	Astigmata	1 species	Neocalvolia antarctica (Hughes & Tilbrook)
COLLEMBOLA			
		3 species	Cryptopygus antarcticus Willem
			Frisea grisea (Schaffer)
			Parisotoma octooculata (Willem)

TABLE 3

ANNUAL MEAN POPULATION DENSITIES FOR FOUR COMMON SPECIES OF ACARI AND COLLEMBOLA FOUND IN THE SIRS 1 SAMPLES

Numbers of individuals m^{-2}

Year	*Nanorchestes antarcticus*	*Ereynetes macquariensis*	*Eupodes minutus*	*Gamasellus racovitzai*	Total Acari	Total Collembola*
1972	3,376	2,752	3,877	464	10,469	60,410
1973	1,278	1,086	3,144	469	5,977	36,182
1972 and 1973	2,327	1,919	3,510	467	8,223	48,296

* Entirely *Cryptopygus antarcticus*

Population biomass

Total acarine biomass varied from 23.0 to 38.2 mg live m^{-2} for the two year study. Of this G. racovitzai contributed 44 and 57% respectively, the remainder being made up of the three prostigmate species. Following the decline in population density, the live weight mite biomass decreased by c. 40% from 1972 to 1973 (Figure 3).

For C. antarcticus, live weight biomass varied from 432.5 to 1,124.8 mg m^{-2} during 1972, with an annual mean of 793.4 mg m^{-2}, which was 26 times greater than the Acari.

On an individual live weight basis the species ranged in the following order: E. minutus and E. macquariensis (0.3 - 2.0 µg), N. antarcticus (0.2 - 8.5 µg), Stereotydeus villosus (Trouessart) (2.8 - 37.1 µg), G. racovitzai (4.4 - 115.5 µg).

Population respiration

Calculations of annual species population respiration have been made by a computer programme using data for monthly population density, life stage composition, live weight biomass, mean daily field temperatures and the relation of metabolic rate (weight specific oxygen uptake) to temperature for each species of arthropod on SIRS 1. Daily population respiration values were calculated and summed for annual estimates (Table 4). Differences in respiratory activity occur between species and years, the former governed principally by the metabolism - temperature curve and the latter by population density levels. Between year changes are exhibited by the total Acari data, the 1972 estimate being 1.7 times higher than the 1973 level. The total oxygen consumed by the Acari was almost all used by the Prostigmata. The Collembola (entirely C. antarcticus) contributed 80-84% of the total soil arthropod respiration for both years.

Life cycles and feeding

Information on life stage composition (Figure 4) has been obtained by Goddard (1979) and other workers for mites and by Tilbrook (1977) for springtails in the maritime Antarctic. In the Acari, several species have been observed to lay batches of eggs in spring and early summer, whilst others oviposit throughout the summer period. Larvae are abundant only in summer, whilst large numbers of nymphs of all stages are found at all seasons. The duration of the nymphal stages is variable, even within a species, which results in a mixed stage nymphal component of the population. From such a nymphal pool, varying numbers of individuals mature to adult influenced primarily by environmental conditions. Nymphs have been found to be more cold tolerant than adults in the oribatid Alaskozetes antarcticus (Michael) by Young & Block (in prep.), and so nymphal mortality may be low. In terms of time, 12 to 18 weeks from egg to adult have been observed for Tydeus tilbrooki (Strandtmann) at laboratory temperatures (Goddard, 1979). Under field conditions it may take at least one year for A. antarcticus to reach sexual maturity with a further 9 to 12 months of adult life. Life cycles are therefore variable in duration dependent upon site and microclimate.

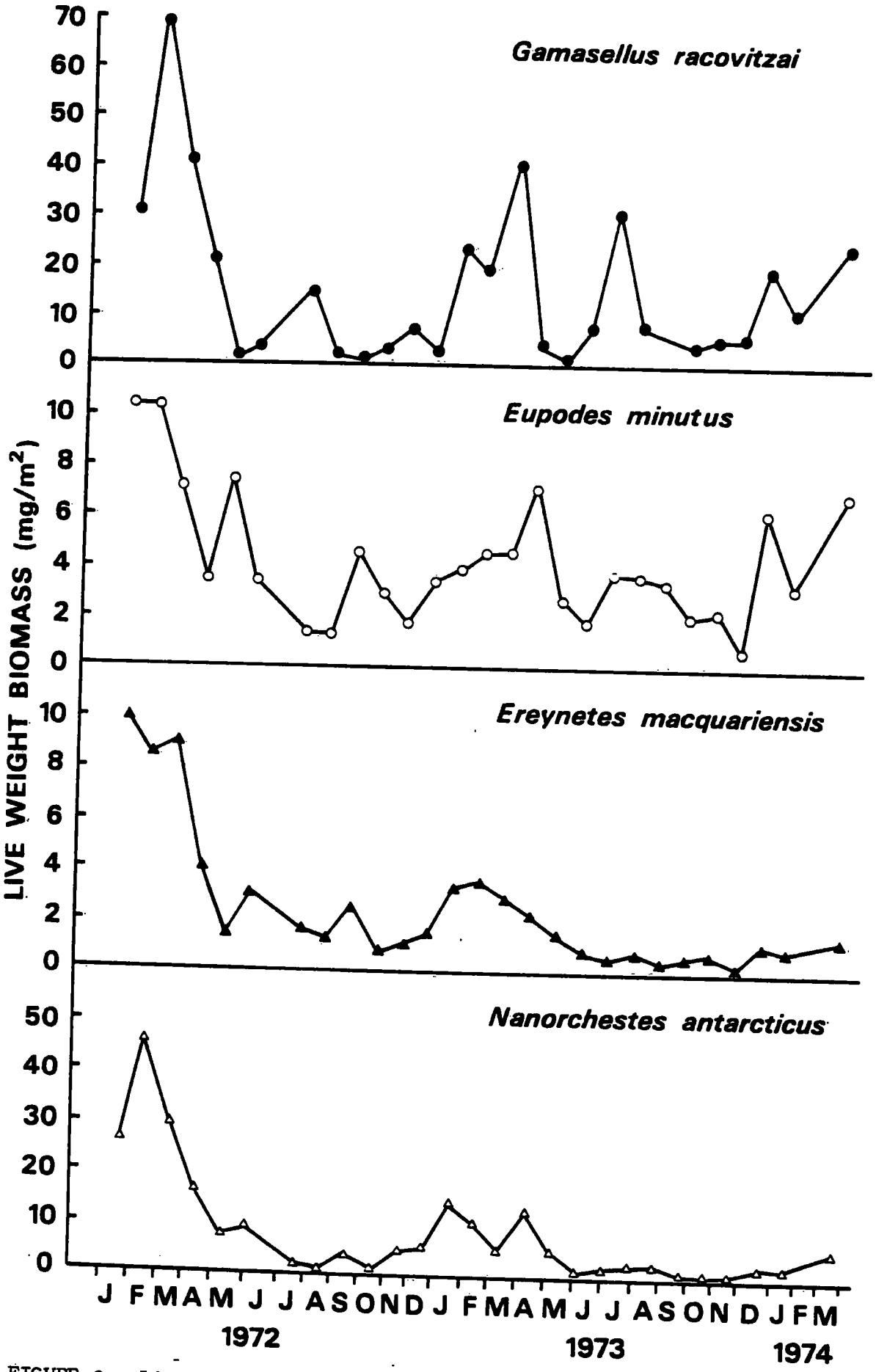

FIGURE 3. Live weight biomass changes in populations of four mite species on SIRS 1 during 1972-74.

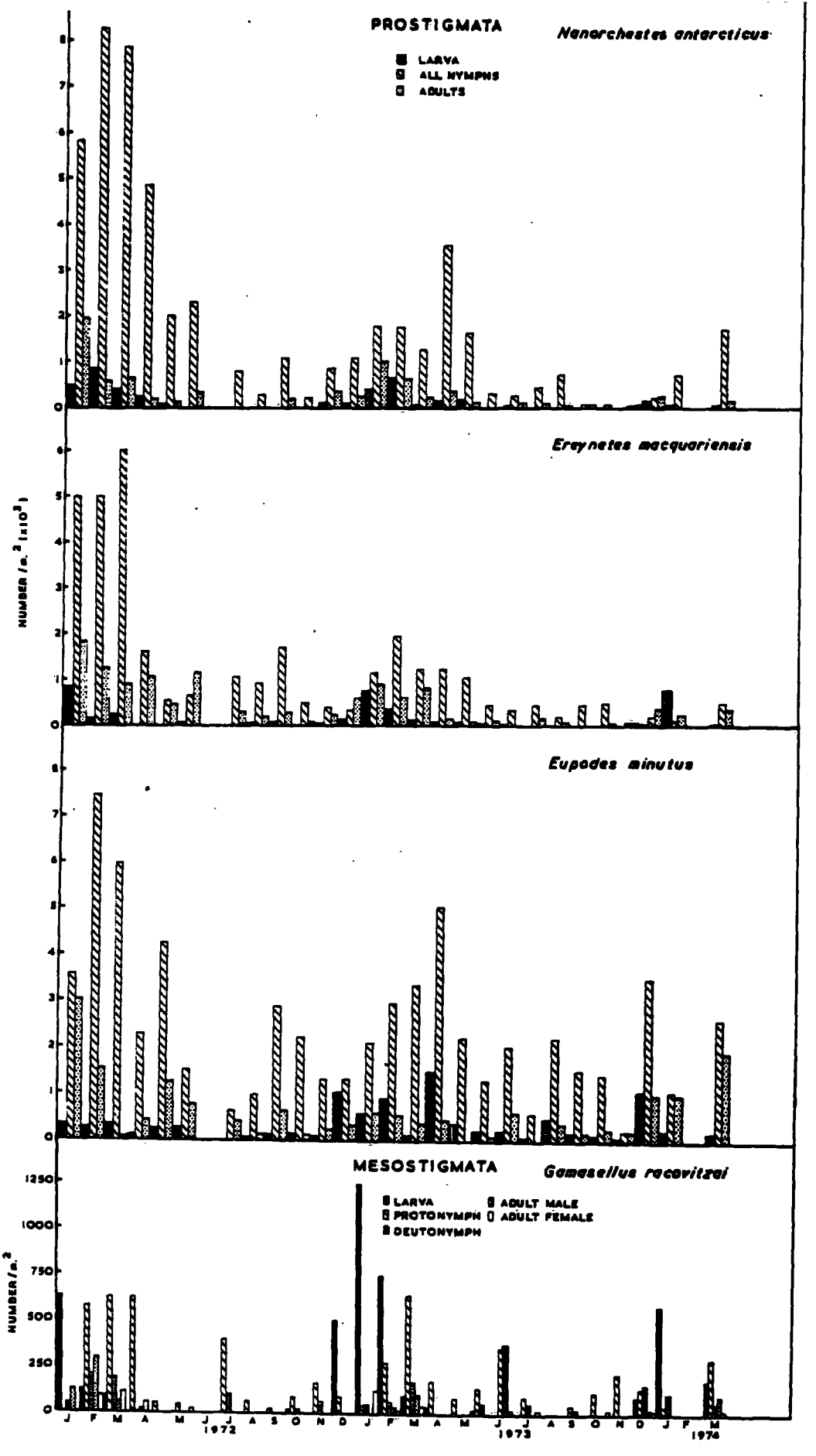

FIGURE 4. Life stage composition of four species of Acari on SIRS 1 during 1972-74.

TABLE 4

POPULATION RESPIRATION OF SIRS 1 ACARI AND COLLEMBOLA (ml O_2 m^{-2} y^{-1})

	Year	
Species	1972	1973
Ereynetes macquariensis	82.17	24.00
Eupodes minutus	43.87	29.94
Nanorchestes antarcticus	81.40	70.72
Gamasellus racovitzai	12.49	4.52
Total Acari	219.93	129.18
Total Collembola		
Cryptopygus antarcticus	893.35	685.84

For C. antarcticus, Tilbrook (1977) recorded a stable size class structure for the Signy Island population with few seasonal changes.

Few details of the feeding ecology of Antarctic soil arthropods exist. Observations at Signy Island suggest that algae and fungi are favoured by the majority of the Acari especially the prostigmatids (Table 5). Current work on C. antarcticus is to determine qualitative food preferences and measure ingestion and assimilation rates at field temperatures, whilst that on the predator, G. racovitzai, is investigating its interaction with various prey organisms.

Microclimate

Seasonal fluxes in solar radiation, air temperature and soil temperature at five points in the vertical profile of the SIRS moss peat have been given by Walton (1977). Temperature is a major determinant of arthropod activity, which on Signy Island is limited to c. five months of the year (November to March). The microclimate of the surface layer of the sites is characterized by short periods of high insolation with temperatures of up to +25° C being recorded in some situations, which are often associated with rapid temperature changes (1° C min^{-1} is common). Much longer periods of fairly constant low temperatures occur especially after a snow cover has been established (Figure 5). Snow depths vary between sites and between years, and up to 1 m may occur on bryophyte communities in the maritime Antarctic. At melt, greenhouse conditions may prevail locally, which encourage plant growth and invertebrate activity under the ice layer.

Of major importance for such communities are the frequent freeze-thaw cycles, which are a feature of both spring and autumn conditions. Substrate water content changes markedly with season particularly in peat sites. Annual water contents in respect of core dry weight were 609-666% (SIRS 1), and 1480-1842% (SIRS 2) for 1972 and 1973 respectively.

PHYSIOLOGY

The maritime Antarctic environment presents certain physiological problems to poikilotherms inhabiting it. Low temperatures may depress respiration rates, activity, feeding and growth, whilst wide thermal fluctuations may result in large variations in metabolic rates. Extreme winter temperatures may cause tissue freezing.

Respiratory metabolism

A considerable body of data now exists on the respiratory levels of many Antarctic arthropods. For Collembola, Block & Tilbrook (1975) and Block (1979) detail results for C. antarcticus and Parisotoma octooculata (Willem). In the Acari, Goddard (1977a, 1977b) gave information on G. racovitzai and the Prostigmata respectively, whilst Block (1977) and Young (1979a, 1979b) reported on the respiratory metabolism of the oribatid A. antarcticus in

TABLE 5

FOOD MATERIAL UTILIZED BY SPECIES OF ACARI AND COLLEMBOLA IN THE FIELD AND IN LABORATORY CULTURES AT SIGNY ISLAND

Species	Type of food material					
	Collembola	Acari	Algae	Fungal hyphae	Lichens	Organic debris
MESOSTIGMATA						
Gamasellus racovitzai	+	+				
CRYPTOSTIGMATA						
Alaskozetes antarcticus			+	+	+	+
Halozetes belgicae			+	+	+	+
ASTIGMATA						
Neohyadesia signyi			+			
PROSTIGMATA						
Eupodes minutus			+	+		
Ereynetes macquariensis			+	+		
Stereotydeus villosus			+			
Nanorchestes antarcticus			+			
Tydeus tilbrooki			+	+	+	
ISOTOMIDAE						
Cryptopygus antarcticus			+	+	+	+

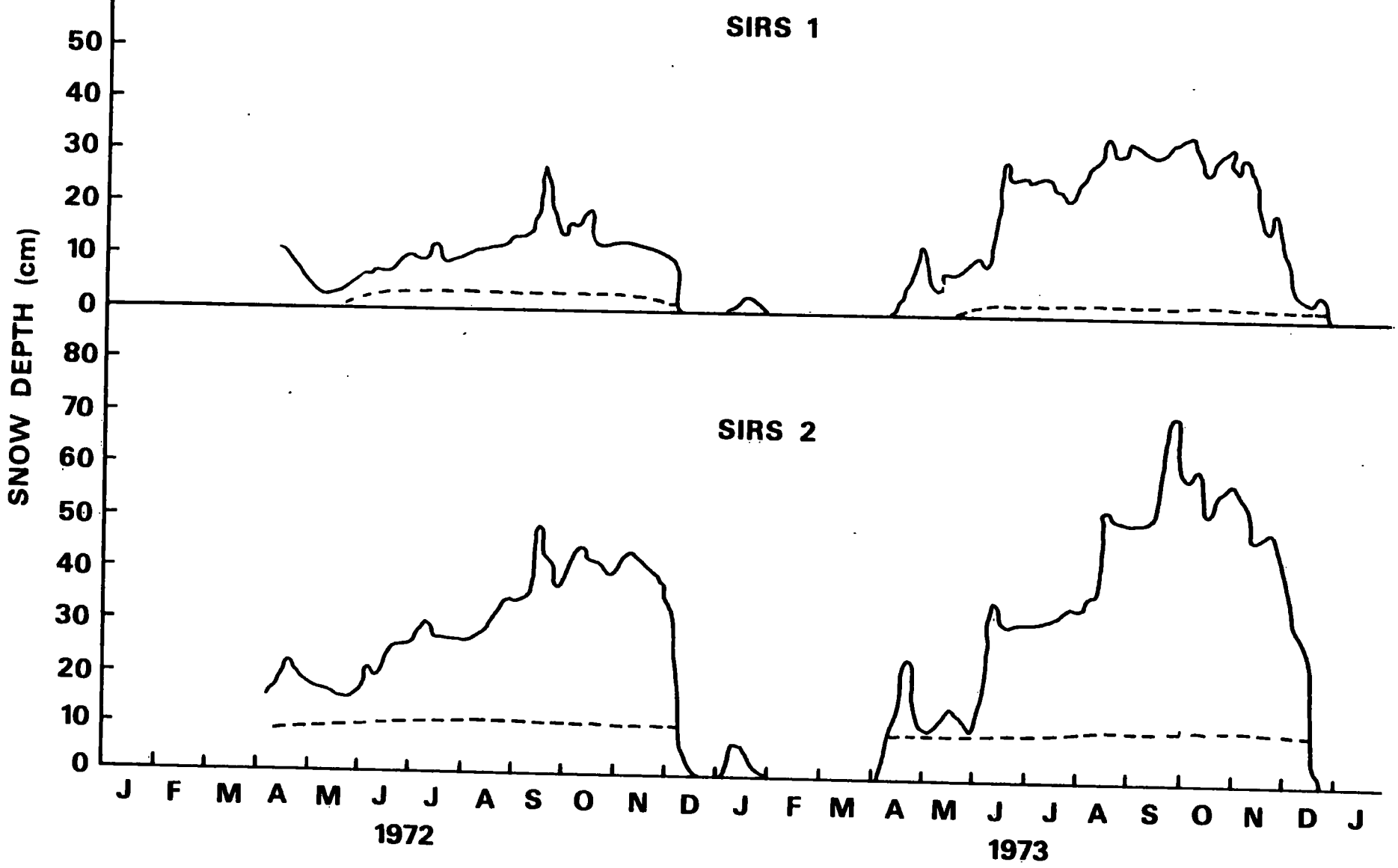

FIGURE 5. Mean snow depth of SIRS 1 & 2 during 1972-74. Dotted line represents approximate ice thickness.

field and culture. Data for this species supports the hypothesis of cold adaptation by metabolic rate elevation (Block & Young, 1978), in that its metabolic rate is higher than that of comparable temperate species measured at the same temperature. This enables the Antarctic mite to remain active at environmental temperatures that would immobilize those temperate forms. Such an adaptation is clearly of paramount use for this species, and similar metabolic phenomena may exist in other Antarctic species.

Overwintering survival

The limits of cold tolerance of several Antarctic mites have been examined (Block et al., 1978; Sømme, 1978), but a detailed investigation of the physiological and biochemical mechanisms involved has only been undertaken on a single species, A. antarcticus from Signy Island. Freezing is fatal in both juvenile and adult stages, and survival in the field takes place by means of the avoidance of freezing by supercooling (the maintainance of their body fluids as liquids below their freezing point). Food materials in the guts of individual mites has been shown to contain efficient ice nucleators and detract from supercooling ability (Young & Block, in prep.). Therefore animals with empty guts survive better under freezing field conditions. Glycerol aids supercooling in adult A. antarcticus, and this is supplemented by other polyhydric alcohols and sugars in the juveniles. Cold tolerance, as measured by glycerol concentrations and supercooling points, was increased to -30° C by exposure to low temperatures (0° to -10° C), and low relative humidity (40 to 60%), both of which can be related to its field habitat.

In Antarctic springtails, which are also freezing susceptible, similar limits of cold tolerance have been found (Block, et al., 1978), but sugars rather than glycerol appear to be the main factor for improving their supercooling ability.

CONCLUSIONS

The species considered in this short review are seen to be well adapted to their harsh maritime Antarctic environment, both in terms of their biology, ecology and certain of their physiological characteristics. The study of such Antarctic invertebrates is concerned essentially with the problems of adaptation, and the several facets of the adaptational strategy which are adopted by both the individual and the population. Much of what is known about the ecology of such forms suggest that they are ultimately controlled by environmental influences rather than interspecific competition. Until more information is available on the details of species biology, especially their trophic relationships, it is both difficult and dangerous to go further.

However, the physiological adaptations prompt various questions such as are these mechanisms novel and evolved in response to the polar environment, or are they merely extensions of pre-existing ones? Future work should be comparative, not only within the Antarctic Region, but also with similar forms from along climatic gradients such as cool temperate - sub-Antarctic - maritime Antarctic - Antarctic continental fringe. Such studies would indicate the ways in which

polar soil faunas have developed and colonized habitats, and suggest the possible dispersal mechanisms employed by soil invertebrates.

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LITERATURE CITED

Block, W. 1977. Oxygen consumption of the terrestrial mite Alaskozetes antarcticus (Acari : Cryptostigmata). J. exp. Biol. 68, 69-87.

Block, W. 1979. Oxygen consumption of the Antarctic springtail Parisotoma octooculata (Willem) (Isotomidae). Rev. Ecol. Biol. Sol. 16, 227-233.

Block, W. & Tilbrook, P.J. 1975. Respiration studies on the Antarctic collembolan Cryptopygus antarcticus. Oikos 26, 15-25.

Block, W. & Young, S.R. 1978. Metabolic adaptations of Antarctic terrestrial micro-arthropods. Comp. Biochem. Physiol. 61A, 363-368.

Block, W., Young, S.R., Conradi-Larsen, E.-M. & Sømme, L. 1978. Cold tolerance of two Antarctic terrestrial arthropods. Experientia 34, 1166-1167.

Goddard, D.G. 1977a. The Signy Island terrestrial reference sites: VI. Oxygen uptake of Gamasellus racovitzai (Trouessart) (Acari : Mesostigmata). Bull. Br. Antarct. Surv. No. 45, 1-11.

Goddard, D.G. 1977b. The Signy Island terrestrial reference sites: VIII. Oxygen uptake of some Antarctic prostigmatid mites (Acari : Prostigmata). Bull. Br. Antarct. Surv. No. 45, 101-115.

Goddard, D.G. 1979. The Signy Island terrestrial reference sites: XI. Population studies on the Acari. Bull. Br. Antarct. Surv. No. 48, 71-92.

Gressitt, J.L. 1967. Introduction. Pages 1-33 in J.L. Gressitt (Entomology of Antarctica), American Geophysical Union, Washington, D.C. (Antarctic Research Series, Vol. 10).

Holdgate, M.W. 1964. Terrestrial ecology in the maritime Antarctic. Pages 181-194 in R. Carrick, M.W. Holdgate & J. Prévost (Biologie antarctique), Hermann, Paris.

Holdgate, M.W. 1977. Terrestrial ecosystems in the Antarctic. Phil. Trans. R. Soc. Lond. B. 279, 5-25.

Janetschek, H. 1967. Arthropod ecology of South Victoria Land. Pages 205-293 in J.L. Gressitt (Entomology of Antarctica), American Geophysical Union, Washington, D.C. (Antarctic Research Series, Vol. 10).

Jennings, P.G. 1976a. The Tardigrada of Signy Island, South Orkney Islands, with a note on the Rotifera. Bull. Br. Antarct Surv. No. 44, 1-25.

Jennings, P.G. 1976b. Tardigrada from the Antarctic Peninsula and Scotia Ridge Region. Bull. Br. Antarct. Surv. No. 44, 77-95.
Maslen, N.R. In press. Additions to the nematode fauna of the Antarctic Region with keys to taxa. Bull. Br. Antarct. Surv. No. 51.
Smith, H.G. 1978. The distribution and ecology of terrestrial Protozoa of sub-Antarctic and maritime Antarctic Islands. Br. Antarctic Surv. Sci. Rep. No. 95, 1-104.
Sømme, L. 1978. Notes on the cold-hardiness of prostigmate mites from Vestfjella, Dronning Maud Land. Norw. J. Entomol. 25, 51-55.
Tilbrook, P.J. 1977. Energy flow through a population of the collembolan Cryptopygus antarcticus. Pages 935-946 in G.A. Llano (Adaptations within Antarctic ecosystems), Gulf Publishing Co., Houston, Texas.
Wallwork, J.A. 1973. Zoogeography of some terrestrial micro-Arthropoda in Antarctica. Biol. Rev. 48, 233-259.
Walton, D.W.H. 1977. Radiation and soil temperatures 1972-74: Signy Island terrestrial reference sites. Br. Antarct. Surv. data No. 1.
Wirth, W.W. & Gressitt, J.L. 1967. Diptera : Chironomidae (Midges). Pages 197-203 in J.L. Gressitt (Entomology of Antarctica), American Geophysical Union, Washington, D.C. (Antarctic Research Series, Vol. 10).
Wise, K.A.J. 1967. Collembola (Springtails). Pages 123-148 in J.L. Gressitt (Entomology of Antarctica), American Geophysical Union, Washington, D.C. (Antarctic Research Series, Vol. 10).
Young, S.R. 1979a. Respiratory metabolism of Alaskozetes antarcticus. J. Insect Physiol. 25, 361-369.
Young, S.R. 1979b. Effect of temperature change on the metabolic rate of an Antarctic mite. J. Comp. Physiol. B.
Young, S.R. & Block, W. In prep. Experimental studies on the cold tolerance of an Antarctic mite.

QUESTIONS and COMMENTS

K. RICHTER: Why do mites freeze more readily with a full gut content?

In extended constantly cool but not freezing weather the low gut content animal is favored. Can these animals survive with this limited food supply? If so, how? Wouldn't they have to extensively feed to build up reserves prior to brumation to survive the cold period?

W. BLOCK: Gut contents contain ice nucleation agents, especially small particles, and water which promote freezing of individual mites in the supercooled state.

No, the low gut content animal is only favoured during subzero temperatures. The Antarctic species studied to date are able to overwinter without much food being ingested, but reserves are probably built up during summer to allow this

to occur. We have some current research on this topic in the British Antarctic Survey.

M. HASSALL: With respect to those species which showed clear differences in population density between the two years studied could you please tell us what is the average life span of these species and could you speculate on the reasons for the observed differences in density?

Do the species with glycerol in the body fluids show seasonal differences in glycerol content? If so, do you know which stimuli trigger off the physiological response of glycerol production?

W. BLOCK: We have no information on the life span of these species. The between year differences (mainly a reduction in the second year) could have been due to a high winter mortality. Subsequent sampling suggests that the decline observed was not permanent.

We have some preliminary data which show seasonal fluctuations in glycerol levels in the mite Alaskozetes anarcticus. Low temperature, lowered RH levels both stimulate glycerol production in this species.

L. BENNETT: Is the cold adaptation of Anarctic mites aided by the sugar trehalose?

W. BLOCK: Trehalose has been found in both Collembola and mites from the Antarctic, but there is no quantitative information available. In general, juveniles of the cryptostigmatid mite Alaskozetes antarcticus appear to employ sugars as well as a variety of polyhydric alcohols in their cold tolerance physiology, whereas the adults rely almost entirely on glycerol.

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POPULATION ECOLOGY OF A TERRESTRIAL ISOPOD IN TWO BRECKLAND GRASS HEATHS

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SUMMARY

(1) Two superficially similar chalk grasslands in the Breckland of East Anglia provided ery different habitats for the abundant terrestrial isopod *Armadillidium vulgare* (Latreille). ıt Lakenheath Warren the site was a tussocky grassland, ungrazed, with *Festuca* spp. overing 65–80% of the area, and most of the isopod population was found in the litter ıyer (5 cm deep) of the large tussocks throughout the year. At Weeting Heath National lature Reserve, smaller *Festuca* tussocks comprised 25–30% of the site, and the isopods ıoved between the tussocks and the intervening grazed sward.

(2) Mean annual population density of *A. vulgare* on the grazed site at Weeting was ·4–1·6 times larger than that of the ungrazed site at Lakenheath, which increased to a .aximum of 2·8 times at other periods.

(3) Differences in population structure between the two sites were detected in terms of ;e structure, generation distribution and cohort composition.

(4) At Weeting each cohort bred once; whilst at Lakenheath each cohort participated two annual breeding seasons.

(5) There was a high mortality of new born young at both sites, and survivorship rves were similar being type 3 (Deevey 1947).

(6) Large variations occurred in the number of young produced per year at Weeting, ıilst annual recruitment was similar at Lakenheath. An alternation of high and low nsity generations occurred as a result at Weeting.

(7) Changes in the structure of the two populations of *A. vulgare* are discussed in ation to habitat structure, grazing effects and environmental heterogeneity.

INTRODUCTION

w studies of terrestrial invertebrate populations have investigated the dynamics of a :cies in closely related, but otherwise subtly different habitats. It is often assumed .t the main features of the population ecology of an invertebrate are fundamentally ıilar in equivalent habitats experiencing a similar climatic regime. Further, the variability numbers and seasonal dynamics of a species may be large between related habitats : to small differences in the architecture and micro-structure of part or whole of the ›itat. Some of these differences may be brought about by the activity of grazing animals ticularly sheep, cattle and rabbits. Such vertebrates have had a marked influence on ssland communities in lowland Britain, and it is widely accepted that much of the ssland below 300 m altitude owes its existence to the grazing animal. The effects ;razing on the insect community of such grasslands may be very significant (Morris

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1967, 1968), but there is little information on its effects on the litter invertebrates an on the biology and dynamics of individual species.

This paper presents the results of a study in which the terrestrial isopod *Armadillidiu vulgare* (Latreille) was used to investigate the variation in structure and dynamics o two populations inhabiting similar grasslands which differed in grazing pressure an experienced a common climate. An isopod was selected because they are poorly adapte to terrestrial life (Edney 1968), and therefore environmental conditions, especiall temperature and relative humidity, strongly affect their population densities. Few complet studies have been made of the population dynamics of individual species, but in some attempts were made to explain the mechanisms involved in the limitation of their numbers Brereton (1956) studied *Porcellio scaber* (Latreille); Paris (1963) worked on *Arma dillidium vulgare* (Latreille); Sutton (1968) on *Trichoniscus pusillus* (Brandt) an *Philoscia muscorum* (Scopoli); Sunderland, Hassall & Sutton (1976) on *P. muscorum* McQueen & Carnio (1974) on *Porcellio spinicornis* Say; McQueen (1976a, b) o *P. spinicornis* and *Tracheoniscus rathkei* Brandt, and Davis (1978) on *A. vulgare*. Thes studies have not offered a common explanation of isopod population dynamics and th problems of population limitation and variability between habitats remain largel unresolved.

A comprehensive study of the population ecology of *A. vulgare* was made in tw grass heaths in the Breckland, East Anglia. Two sites were selected, a chalk grassla at Lakenheath Warren with light grazing, and a similar grassland at Weeting Hea National Nature Reserve with heavy grazing pressure from rabbits, referred to Lakenheath and Weeting respectively. Field sampling continued for three years. Th objectives of this research were firstly, to provide information on the population dynami of *A. vulgare* in two closely related habitats and to determine the factors limiting the numbers; secondly, to provide evidence for the hypothesis that habitat structure a heterogeneity exerts a major influence on such terrestrial animals.

STUDY SITES

The Breckland is a well defined region of approximately 1100 km^2 in area lying betwe 15–55 m a.s.l. in southwest Norfolk and northwest Suffolk. The area is covered w varying depths of sand overlying chalk. Its climate approaches continentality with a me annual air temperature of 9·9 °C, low annual rainfall (45·9 mm) and with large diur temperature fluctuations in summer. Frosts may occur in any month of the year.

The ecology of Breckland is characterized by four plant communities dominated *Carex arenaria* L., *Calluna vulgaris* (L.) Hull, *Pteridium aquilinum* (L.) Kuhn a grasslands of *Festuca ovina* L. For the present study, the grass heath community w selected as it had relatively high populations of *A. vulgare*, similar floristic compositi and it was easy to sample. Two sites were established on chalk grassland, the first Lakenheath was a type C grassland and the second at Weeting was a type B grassl (*sensu* Watt 1940).

At Lakenheath, grassland C type was abundant and covered a larger area than a other type. *Festuca ovina* and *Festuca rubra* L. together covered between 65–80% the study site area. Under low grazing pressure from rabbits these species grew vigorou forming tussocks, which were evenly distributed forming a series of regular elevati and depressions on the site. The litter layer was 5–8 cm deep. The Weeting site ha similar vegetation cover to that for the grassland C type apart from differences cau

y heavy rabbit grazing and in the chalk content of the soil (pH of surface soil was ·2 at Weeting as compared to 6·4 at Lakenheath). *F. ovina* and *F. rubra* were dominant t Weeting, but lacked the luxuriant growth form of the other site. Tussocks were 0–30 cm high with *c.* 5 cm depth of litter and covered 25–35% of the site with an regular distribution. The remaining area was heavily grazed *Festuca* (<10 cm high and –1 cm depth of litter) with associated mosses and flowering plants. Further details of the story and ecology of these two areas may be found in Watt (1936, 1940) and Crompton Sheail (1975).

METHODS

eld sampling

Both sites were sampled at 28-day intervals. A grid was established at each site easuring 14 × 7·5 m. This was sub-divided into twenty strata each of 3·5 × 3·5 m with ch stratum being further divided into 49 sampling units of 0·25 m^2 each. For each mpling occasion twenty replicates were collected, one random sample per stratum, by eans of a circular metal corer 17 cm in diameter. The soil was sampled to a depth 5 cm. On each occasion, approximately one third of the replicates were of *Festuca* ssocks at Weeting, and two-thirds at Lakenheath, which reflected the area of each site vered by tussocks. Each replicate was transported separately in a labelled container the laboratory, where faunal extraction was started within 6 h of field collection. eld sampling commenced in April 1973 and terminated in August 1975.

pod extraction

An enlarged, modified split-funnel heat extractor (Murphy 1962) was used to recover fauna from the field sample. Isopods were collected into a saturated solution of odium orthophosphate (Sunderland, Hassall & Sutton 1976). The extraction efficiency s determined by hand searching a selection of replicates after extraction and was 30%.

fall trapping

An array of twenty pitfall traps (6 cm diameter and containing ethylene glycol) at 1 m ervals was maintained at Weeting throughout the study.

vironmental factors

A Grant automatic temperature recorder with thermistors was used to monitor hourly peratures in the upper soil and litter layers at both sites and integrated temperatures e derived by a sucrose inversion technique (Berthet 1960; Lee 1969) at Weeting. During ten month overlap period of the two methods at Weeting, integrated values were con-ntly higher (1·1° to 3·3 °C) than arithmetic means. The latter were transformed to grated values using the relationship:

$$T_i = 2{\cdot}399 + 0{\cdot}968\ T_a (r = +0{\cdot}99, SE_b = 1{\cdot}01\ ^\circ\mathrm{C})$$

re T_i is the integrated temperature and T_a is the arithmetic temperature. At Lakenheath grated temperature values were obtained throughout the study.

he water content of the field sample was determined from fresh and dry weights ach replicate, and expressed as a percentage of dry weight. Relative humidity in

the field at sampling was measured at three positions (air, litter and soil) with cob thiocyanate papers (Solomon 1957). The papers were exposed for 2 h (usually 11.0 13.00 hours) inside small, open-ended glass tubes (1 × 3 cm).

THE ENVIRONMENT

Litter layer integrated temperatures at the Weeting site ranged from 2·5° to 20 °C and from 4° to 18 °C at Lakenheath. Temperatures were generally lower in 1974 th in either 1973 or 1975 at Weeting, and a similar pattern was observed at Lakenheat The integrated temperatures were higher in summer and slightly lower in winter Weeting than at Lakenheath. Mean summer temperatures of the litter layers were 15·7 ° (Weeting) and 13·4 °C (Lakenheath). Such differences may reflect structural differenc of their plant cover and litter layer. The litter is much thicker and there is a complete closed vegetation cover at Lakenheath whereas the Weeting site is more exposed a without a litter layer.

The mean water content of the samples was generally low with maxima of 40% Weeting and 44% at Lakenheath. The poor water retention of these soils and low rainf for much of the study period accentuated the dryness of the substrate. The seasor pattern in water content was closely related to rainfall, and generally the Lakenhea soils were wetter than those at Weeting during winter.

Soil RH was >90% throughout the year with little variation at both sites (Fig.

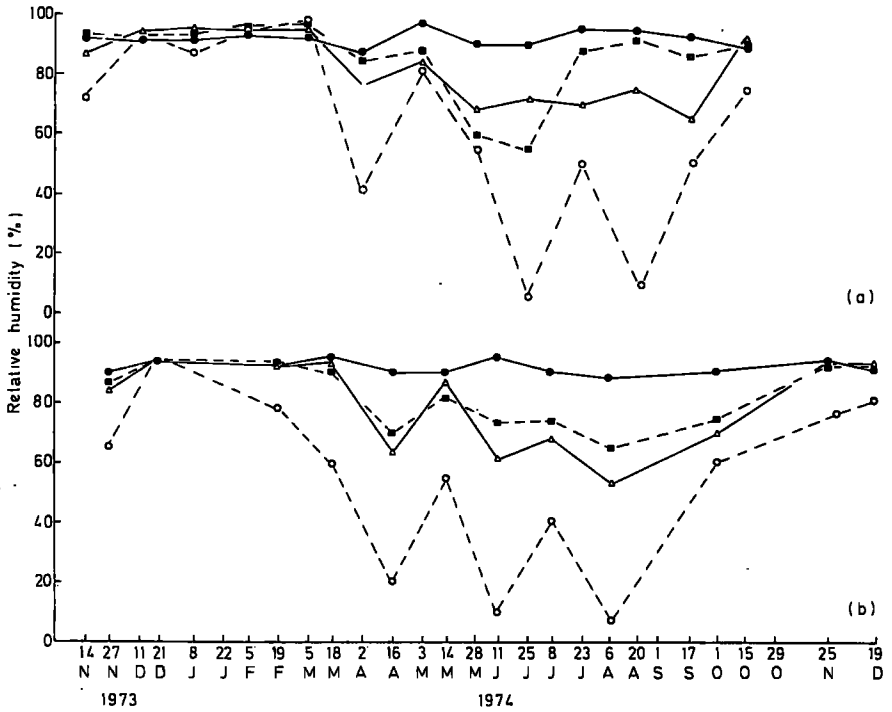

FIG. 1. Relative humidity at four positions in the air-litter-soil profile at (a) Weeting Heath and (b) Lakenheath Warren during the study period. O---O air; ●——● soil; ▲——▲ *Festuca* tussock; ■---■ short sward.

The higher RH values in tussock and short sward followed the same trends as the air, but the tussock bases were usually much drier than short sward during summer.

DISTRIBUTION AND ACTIVITY OF *A. VULGARE*

Seasonal variations in surface activity of the *A. vulgare* population at Weeting were examined over three years by pitfall trapping and analyses of heat extracted samples.

Despite the limitations of pitfall trapping (Mitchell 1963) the results (Fig. 2) showed a well defined seasonal activity. *A. vulgare* was inactive when the mean litter temperature was <6 °C during the winter months. Peaks of activity occurred in June and July when the mean monthly temperature was >16 °C (Fig. 3). No correlation was evident between the surface activity of *A. vulgare* and the monthly rainfall or the water content of field samples, and periods of high surface activity were in the driest part of the summer. There appeared to be a relationship between surface movement and the breeding condition of the isopods, as they became active in April with increasing numbers in pitfalls in May and June. Egg-carrying females were also active, with considerable movement of the population immediately after the release of young from the females. However, juveniles were collected

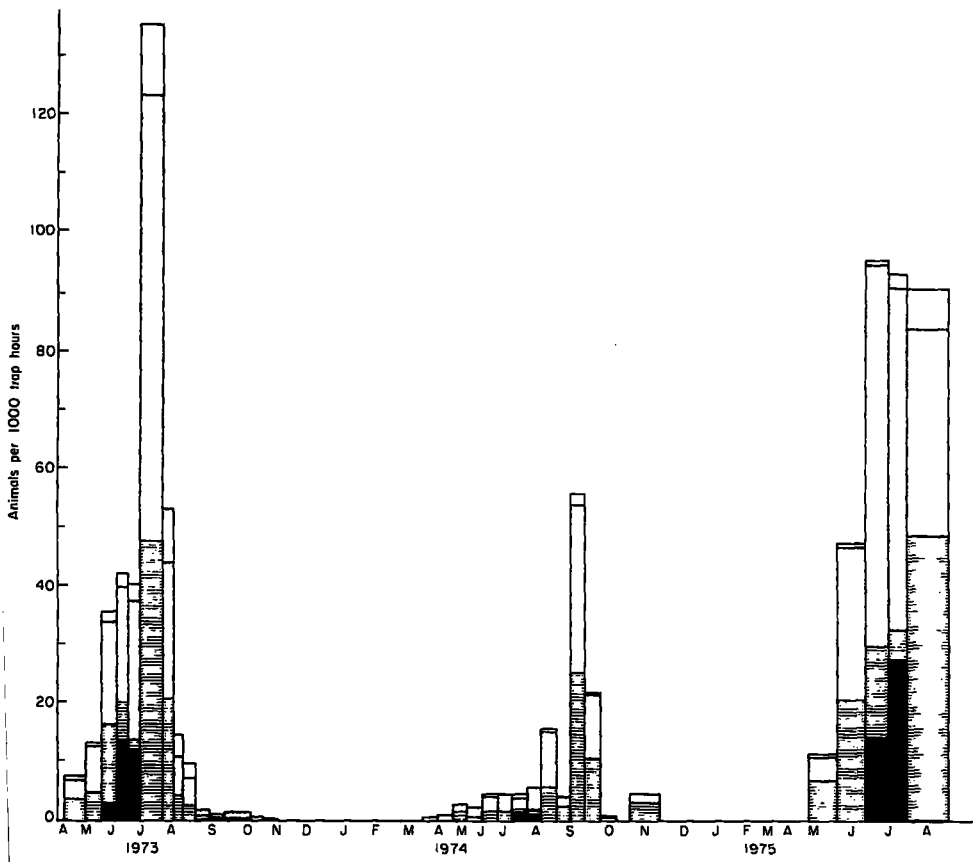

FIG. 2. Activity pattern of *Armadillidium vulgare* at Weeting Heath derived from pitfall trapping during the study period. □ juvenile; ▨ male; ▤ female; ■ gravid female.

in very small numbers in pitfalls, suggesting that only limited surface activity occurred in individuals less than one year old. Adult males and females appeared to be as active as each other.

Fewer individuals were captured at Weeting in 1974 compared to the other two years. Pitfall data suggested considerable horizontal movement of isopods through the grassland at certain times of the year, but no pronounced vertical movements in the soil-vegetation profile were observed. Horizontal dispersion of *A. vulgare* at Weeting was also monitored using the heat extraction samples. The 20 replicates of each sample were grouped into the habitat categories 'tussock' and 'short sward' (Fig. 3). The dispersion pattern varied with season and was related to periods of activity of the species (Fig. 2). From October to March, a large proportion of the population was located in tussocks, whereas during active periods (April–September) the isopods moved outside the *Festuca* tussocks and aggregated in short sward areas. This behaviour is the presumed response of the population to a combination of physical factors, especially temperature and relative humidity, mediated by the physiological tolerances of individual isopods. In winter, tussocks provided shelter with a relatively stable temperature regime and damped diurnal fluctuations (Workman 1978), together with equable humidity conditions (Fig. 1). Frost often occurred in the open sward. In summer, despite large temperature changes in the short sward *Armadillidium vulgare*

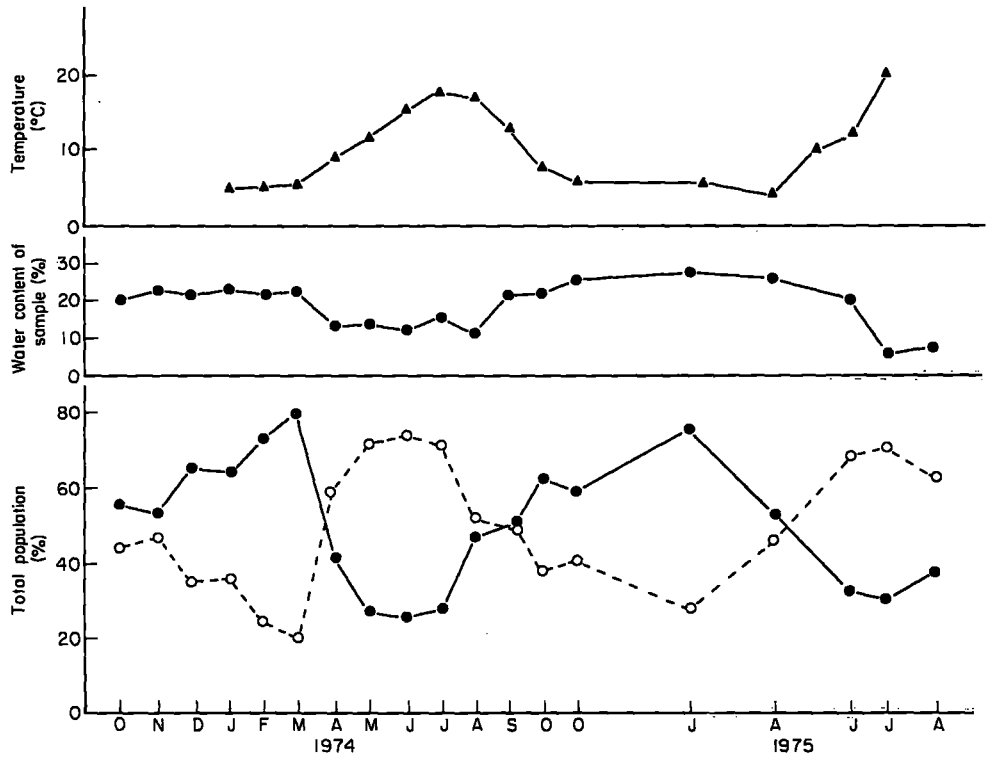

FIG. 3. Seasonal changes in the proportions of the *Armadillidium vulgare* population in tussocks (●——●) and short sward (○---○) at Weeting Heath during the study period. Data of sample water content and monthly integrated temperatures are also given.

preferred this to tussocks since it often provided a more humid atmosphere than elsewhere (Fig. 1).

POPULATION DYNAMICS

Population density

The numbers of *A. vulgare* at both study sites showed a well defined pattern of change during the period of study (Fig. 4). Population density was at its maximum after recruitment of the young in July–August, and only slight mortality occurred during

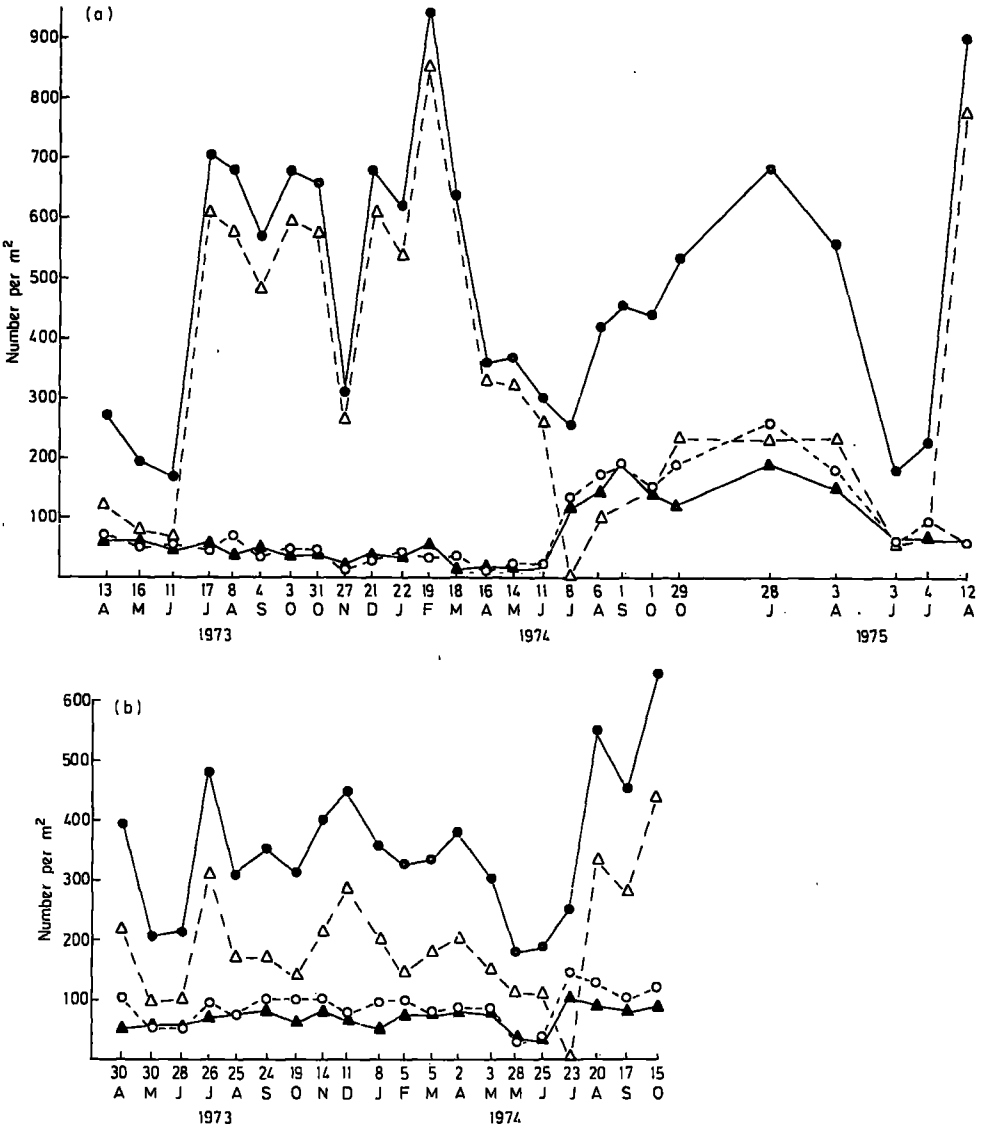

FIG. 4. Population density changes of *Armadillidium vulgare* at Weeting Heath (a) and Lakenheath Warren (b) during the study period. ●——● total population; △---△ juvenile; ▲——▲ male; ○---○ female.

winter. Numbers decreased gradually by April of each year and attained minimum levels in June–July prior to recruitment. The transformed data (Taylor 1961) confirmed that monthly estimates of the density within each site were not significantly different during the post recruitment period and throughout winter. Significant departures ($P < 0{\cdot}05$) of mean population density from the general overwintering level were observed mainly in June and July during breeding.

The Lakenheath population had similar recruitment patterns in 1973 and 1974, but at Weeting recruitment was different for the three years, being high in 1973 and 1975 but low in 1974. Notwithstanding these differences, the Weeting grassland supported a higher average density (1·4–1·6 times) of *A. vulgare*, than the Lakenheath site (mean annual densities were 488 and 353 individuals m^{-2} respectively). There is further evidence of the alternation of high and low numbers of *A. vulgare* from pitfall trap data for 1973–75 (Fig. 2) and for May–June during 1966–74 at Weeting (Dempster, pers. comm.). This pattern was especially evident after 1970, and it coincided with the changes in population density recorded in the present study.

There were clear differences in age structure of the population in the three years at Weeting in contrast to Lakenheath (Fig. 4). Juveniles comprised the main component of the population throughout 1973 and for the first half of 1974 but from July 1974 to June 1975 adults and juveniles were similar in density. In July 1975 a reversal to juvenile dominance had begun. During the two years when data are available for Lakenheath, the age structure remained relatively constant.

Size class analysis

A common feature revealed by the size class distributions for *A. vulgare* at Weeting (Fig. 5) and Lakenheath (Fig. 6) was the change in numbers of animals in each size class attributable to growth. This is seen clearly during April–September by the ascending waves of groups of animals through the size classes. During October–March growth ceased. The contraction in the proportion of certain size classes was due to mortality which was especially important in older animals after the breeding season. The data for both sites also suggest a generally low winter death rate.

At Weeting (Fig. 5), the population in April–June 1973 consisted mainly of older larger individuals, which were potentially able to breed (*c.* 60% of the monthly samples) and juveniles (*c.* 40%). This resulted in a substantial recruitment to the population in 1973 (Fig. 5). By July 1973, the new first size class was discernible and comprised *c.* 86% of the sample. This new group increased in size until the end of September 1973. The breeding individuals (head width > 220 micrometer units, 115 micrometer units = 1 mm) in 1973 suffered a marked reduction in numbers due to post breeding mortality. In summer 1974, the majority of the population was sub-adult (head width <220 micrometer units) and poor recruitment occurred. In the 1975 breeding season a high proportion of adults were in the older size classes and good recruitment occurred as in 1973.

At Lakenheath (Fig. 6), the size class distribution of *A. vulgare* was similar during the two breeding periods in 1973 and 1974. This resulted in an almost identical pattern of recruitment to the population in each year.

Generation distribution

Size classes belonging to each age group (cohort) were amalgamated to give the proportion of each in the total population (Fig. 7). Age groups were classified

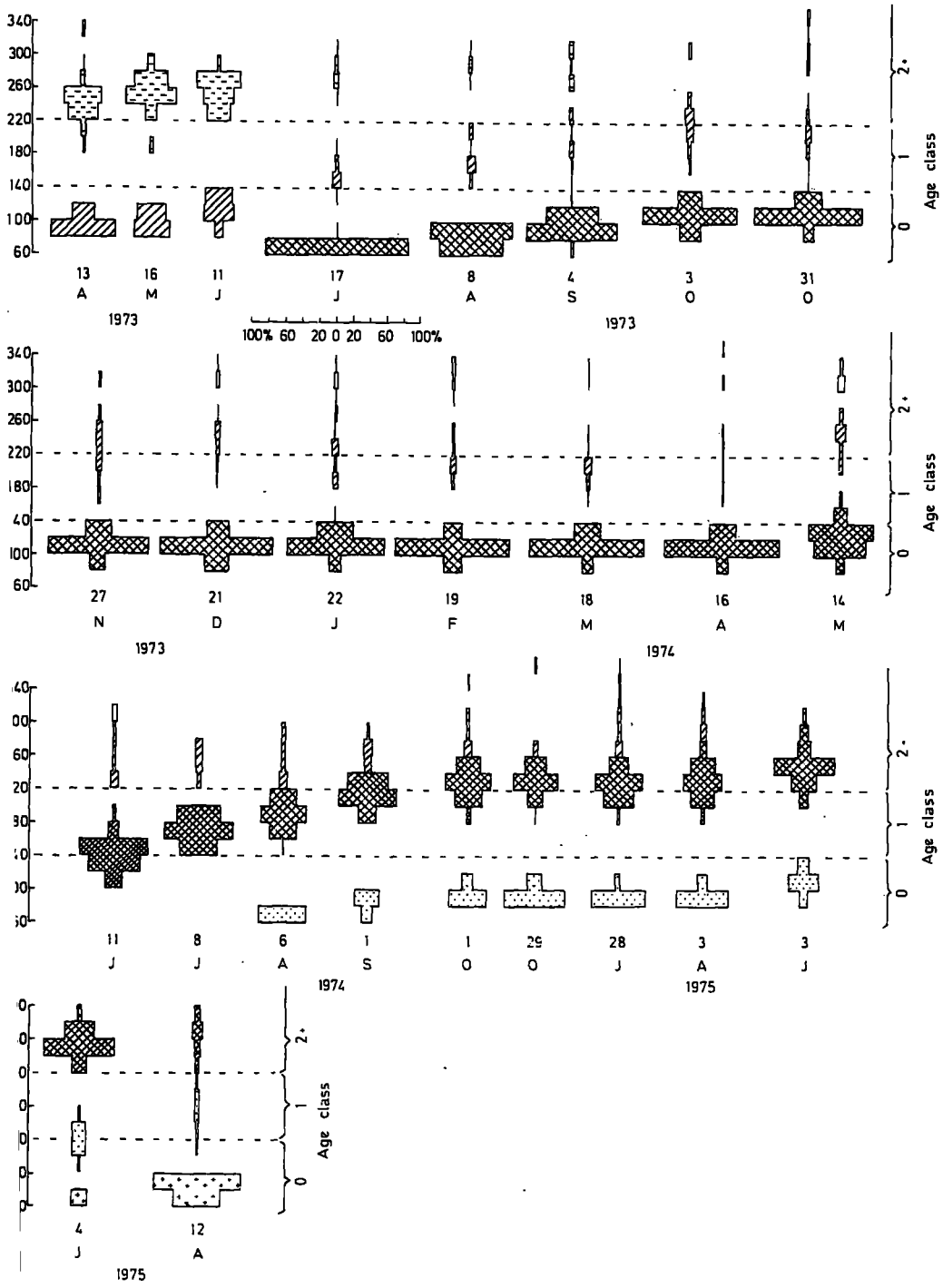

FIG. 5. Size class distribution in percentages of each cohort of monthly samples of the *Armadillidium vulgare* population at Weeting Heath during the study period. □ cohort 1970; ▤ cohort 1971; ▨ cohort 1972; ▩ cohort 1973; ▣ cohort 1974; ▦ cohort 1975.

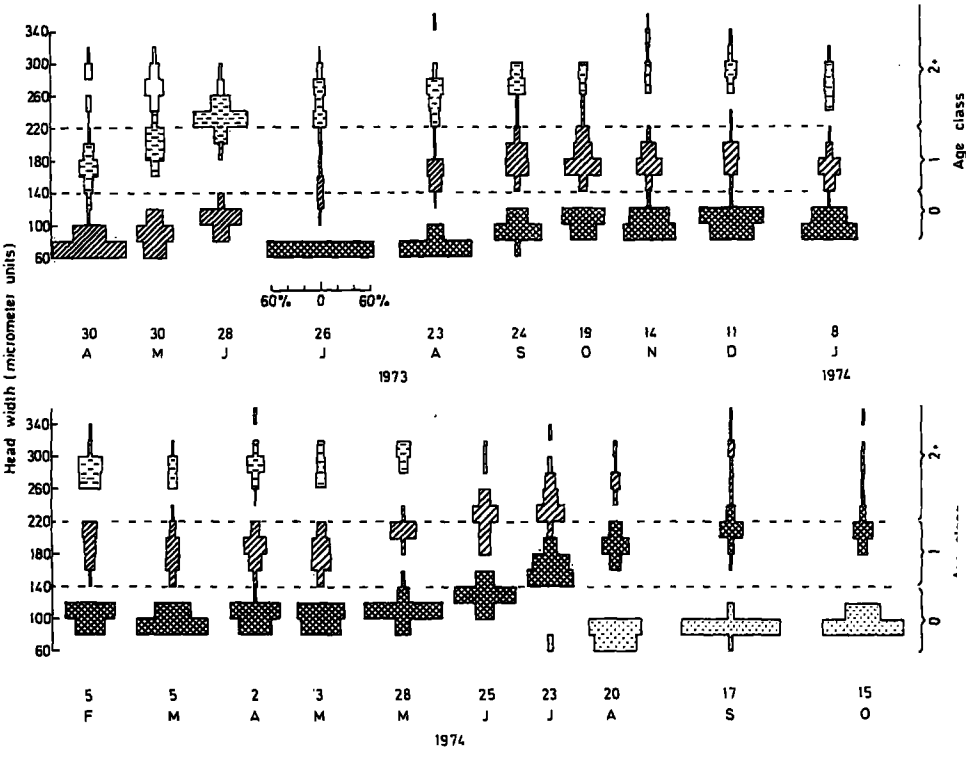

FIG. 6. Size class distribution in percentages of each cohort of monthly samples of the *Armadillidium vulgare* population at Lakenheath Warren during the study period. □ cohort 1970; ▤ cohort 1971; ▨ cohort 1972; ▩ cohort 1973; ⊡ cohort 1974.

generation 0 for those <1 year old, generation 1 for those 1–2 years old, generatio for those 2–3 years old, and so on. Little change occurred in the generation composit within years on both sites, and stability can be attributed to the highly synchroni breeding of *A. vulgare*, a single annual input of young to the populations and l mortality between breeding periods.

The two populations differed in their generation composition between study years. Weeting (Fig. 7(a)) the distribution suggested an alternation of dominance between ye (generations 0 and 1) brought about mainly by variations in the juvenile input into population during annual reproduction. At Lakenheath (Fig. 7(b)) there was no s alternation in generation dominance, as generation 0 comprised *c.* 50% of the *A. vulg* population throughout the years.

Breeding biology, natality and fertility tables

The breeding period of *A. vulgare* was short and highly synchronized. Females matu to adults and commenced breeding in their second year of life under Breckland conditi A single brood per female was produced annually. In Breckland, breeding activity sta in mid-May and continued to mid-August, extending over 2·5 to 3 months (Fig. Breeding commenced when the photoperiod was >15 h light and was maximal w litter temperatures were >16 °C. The developmental period from oviposition to releas young was *c.* 40–50 days.

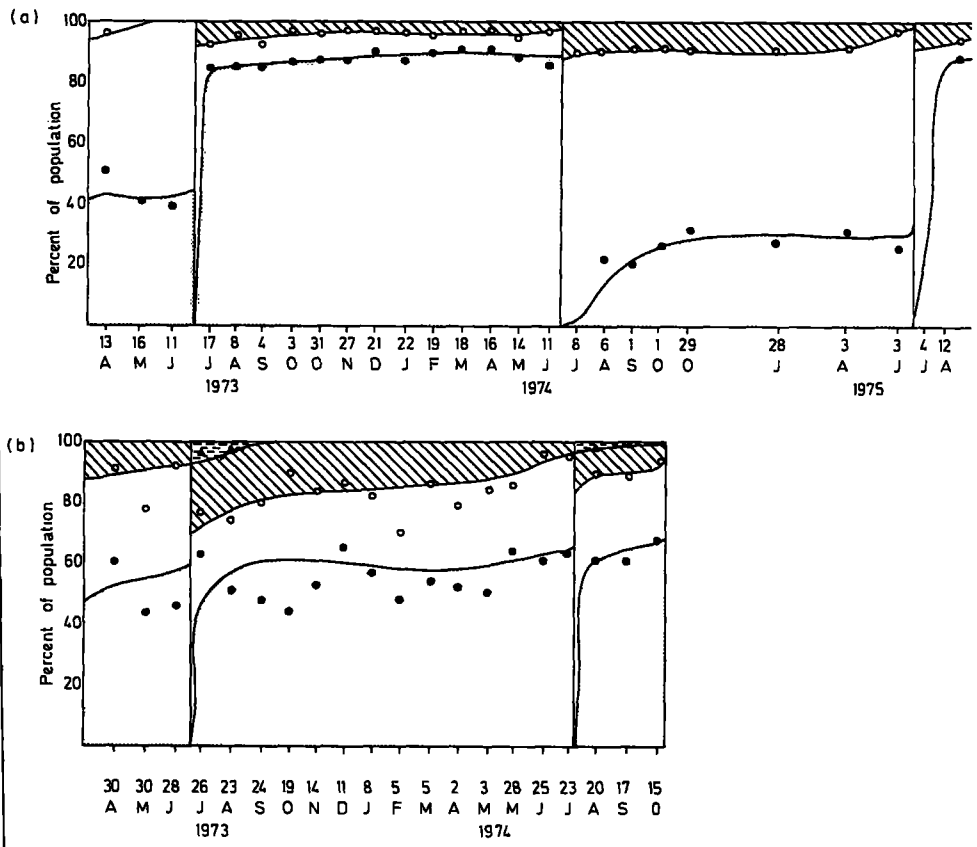

FIG. 7. Proportion of each generation in the *Armadillidium vulgare* population at Weeting Heath (a) and Lakenheath Warren (b) during the study period. □ generation 0; □ generation 1; ▨ generation 2; ▤ generation 3.

At Weeting, each generation or cohort bred once during its life span (Fig. 5), and ıe two-year-old generation was the main source of young in August of each of the ıree years. The three-year-old generation did not breed and died by July when repro-uction was at its maximum. Furthermore, the young forms (one year old) did not ıature in their first year. At Lakenheath (Fig. 6), adults reproduced at two years of ge and survived to participate in breeding in their third year and died thereafter. Thus single generation of *A. vulgare* at Lakenheath bred twice within its life span. Individual ngevity was estimated to be three years with the exception of one or two older males the Weeting population; whereas in the Lakenheath population the individual life span as 3·5 years.

Since abortion of young from the brood pouch can easily occur during extraction, e number of eggs or young carried by females was calculated from the relationship etween head width and the number of eggs carried in live field animals ($y = 0{\cdot}532x - 7{\cdot}225$; r: + 0·913, n: 50, $P < 0{\cdot}001$; where y is the number of eggs or young per brood uch, and x is the head width in micrometer units). This was used for the calculation of oduction of young by the population.

The total young produced by the *A. vulgare* populations (natality) are summarized

TABLE 1. Natality schedule of *Armadillidium vulgare* at Weeting Heath (three seasons) and Lakenheath Warren (two seasons)

	Number of individuals m^{-2}						
	Weeting Heath			Lakenheath Warren			
	1973	1974	1975	1973		1974	
				3 year-old	2 year-old	3 year-old	2 year-old
1. Adults entering the breeding stage	110	35	186	31	97	44	83
Sex ratio (%)	50	61	54	50	61	60	50
Number of females	55	22	100	15	59	26	41
2. Per cent gravid females	86	83	87	100	26	75	33
Number of females with brood pouches	47	18	87	15	15	20	14
3. Fecundity (eggs per female)	37	37	32	50	26	60	22
Maximum potential natality	2035	814	3200	770	1544	1584	913
Actual number carried by females (population fecundity)	1750	677	2784	770	401	1188	301
4. Brood pouch mortality %	6	6	6	6	6	6	6
Failure of eggs to hatch	105	41	167	46	24	71	18
5. Number of young released	1646	636	2617	724	377	1117	283
6. Number of female young (1:1)	823	318	1308	362	189	558	142
Age specific fertility (fertility rate) (mx)	14·9	14·4	13·1	23·5	3·2	21·5	3·4
Total young production	1646	636	2617	1102		1400	

in Table 1 for both Breckland sites, and these data emphasize the basic differences between the two populations. The Weeting population exhibited large variations in the number of young recruited in 1973–75, which resulted from the different densities of the breeding females. At Lakenheath, the recruitment was approximately similar with only comparatively slight variation in 1973 and 1974 in terms of the production of young. It appears that the contribution of the two generations (cohorts) to total natality had a stabilizing effect on the population.

Fertility tables (Table 2) were constructed based on the method of Birch (1948). At Weeting R_0 was 1·6 for the high density cohort and 1·2 for the low density cohort

TABLE 2. Fertility table for cohorts of *Armadillidium vulgare* at Weeting Heath and Lakenheath Warren

Age class years x	Number of females entering age class m^{-2}	lx	mx	vx Σlxmx	Ro = Σlxmx
Weeting Heath (high density cohort)					
0 (Immature stages)	823	1·0000			
2	100	0·1220	13·1	1·60	1·59
Weeting Heath (low density cohort)					
0 (Immature stages)	268	1·0000			
2	22	0·0820	14·4	1·19	1·18
Lakenheath Warren					
0 (Immature stages)	551	1·0000			
2	42	0·0762	3·4	0·26	
3	26	0·0472	21·5	1·01	1·27

ich was similar to R_0 of 1·3 at Lakenheath where the two generation (cohorts) ared the breeding.

Life tables and mortality

Age specific life tables (Deevey 1947) were derived by following the survival of each nort throughout the study period at 4-weekly intervals. At Weeting, the generation mposition of the *A. vulgare* population was different between alternate years, thus o life tables representing each of the high and low density cohorts were derived (Table At Lakenheath, where the generation composition of the population was relatively ble, a single life table represents the population dynamics of *A. vulgare* (Table 3). rvivorship curves derived from these three life tables were essentially of the same shape, l corresponded to the type 3 curve described by Deevey (1947).

A characteristic feature of both populations of *A. vulgare* in the Breckland was the y high death rate of new born young, perhaps due to desiccation, fungal attack and increasing number of predators, e.g. centipedes, lycosids and staphylinids. This urred within 2–3 weeks after birth and accounted for 65–77% of the high and low sity cohorts respectively at Weeting, and for 80% of the Lakenheath generations. age specific mortality rates of the two Weeting cohorts and the Lakenheath ort were U-shaped, indicating a low mortality during the first two years of life after initial high death rate period. Mortality increased considerably immediately after

TABLE 3. Life tables for *Armadillidium vulgare* at Weeting Heath (high and low density cohorts) and Lakenheath Warren

Age Class x	Number entering age class	Number surviving at start of age interval per 1000 lx	Number dying within age interval dx	Age specific mortality qx	Lx	Tx	Mean expectation of further life ex
eting Heath (high density cohort)							
	1646	1000	650	650	675	1404	1·40
	576	350	121	346	289	729	2·08
	377	229	58	253	200	440	1·92
	282	171	58	339	142	240	1·40
	186	113	80	708	73	98	0·87
	54	33	25	757	21	25	0·76
	14	8	8	1000	4	4	0·50
eting Heath (low density cohort)							
	636	1000	771	771	615	1195	1·19
	123	229	50	218	204	580	2·53
	96	179	73	408	143	376	2·10
	57	106	40	377	86	233	2·20
	35	66	0	0	66	147	2·23
	35	66	19	288	57	81	1·23
	25	47	47	1000	24	24	0·51
enheath Warren							
	1102	1000	808	808	596	1130	1·13
	212	192	56	292	164	534	2·78
	150	136	2	15	135	370	2·72
	148	134	59	440	105	235	1·75
	83	75	29	387	61	130	1·73
	51	46	6	130	43	69	1·50
	44	40	35	875	23	26	0·65
	6	5	5	1000	3	3	0·60

reproduction as shown by the high density cohort at Weeting and the Lakenheath coh after their second breeding. The latter did not show a marked increase in morta after their first breeding season at two years of age.

At Weeting, where a generation (cohort) bred only once during its life span, the specific mortality increased from 31% for the 0·5–1·5 years age classes to 71% for breeding age class. At Lakenheath mortality in the first season breeding age class, not differ from that of the juveniles, probably due to the low proportion of breed individuals (26% of breeding females). However, in the second breeding season, at th years of age, more than 80% of the adult population was in breeding condition, consequently the age specific mortality increased markedly to 86·5% as compared a mean of 25·0% for the first five age classes excluding juvenile mortality. It is not kno how the male components of the cohorts were affected by such breeding mortality.

DISCUSSION

The two Breckland populations of *A. vulgare* do not live in as similar habitats as supposed. Although the chalk grassland at the two sites was basically similar in domin plant species and general soil structure, the Lakenheath population inhabited a site v dense vegetation mainly due to low grazing pressure from rabbits whilst the Wee population occurred in a more open, often exposed, heavily grazed grassland. Expos habitat architecture including tussock structure and litter layer thickness were the esse differentiating features of the two habitats.

The Lakenheath population of *A. vulgare* had overlapping cohorts (generati characteristic of a more stable population, whilst at Weeting the population had separate components in the form of cohorts, which did not breed in the same year overlapped only temporally. Consequently a population with characteristics of instab developed, which had annual changes in density and age structure. Other population *A. vulgare* have been found to have overlapping generations similar to the Lakenh site (Paris 1963; Saito 1969; Davis 1978).

The fact that the population at Weeting had separate breeding cohorts may exp the alternation of high and low density generations. An almost catastrophic reduc in the numbers of one cohort would not easily be obliterated by recruitment from o cohorts. The causes and timing of such a crash affecting one cohort in the populatio unknown. A possible explanation in that a given cohort experienced severe environm conditions at the time of release from the female brood pouch, which killed a proportion of them due to their extremely high susceptibility to desiccation and rel immobility at this time. The older cohorts survived this period by their well devel behavioural responses including their ability to move to protected microhabitats suc tussocks within the habitat. Such a situation may not have occurred at Lakenheath if it did the reduction in numbers of a cohort would be dampened by the reprodu effort of the other cohort.

Despite basic differences between the two Breckland populations of *A. vulgare*, had similar patterns of age-specific mortality.

Several hypotheses have been proposed to explain the dynamics of terrestrial is populations. Brereton (1956) postulated that a *Porcellio scaber* population wa regulated through cannibalism of newly born young occurring at an optimum d level. Regulation in a density dependent manner was proposed by Paris (1963) population of *A. vulgare* in a Californian grassland through the interaction of we

nelter site availability and isopod numbers. *Trichoniscus pusillus* maintained its numbers a grassland habitat by its ecological flexibility, a capacity to avoid death by vertical ligration and an ability to compensate for lack of growth and poor recruitment by ktended breeding activity and improved survival of young (Sutton 1968). On the basis f a laboratory derived demographic model, McQueen & Carnio (1974) proposed that population of *Porcellio spinicornis* could be regulated by minor shifts in annual mean mperature and relative humidity. Later, McQueen (1976a) confirmed that temperature as responsible for population limitation in this species. However, studying *Tracheoniscus uhkei*, McQueen (1976b) concluded that temperature was not the limiting factor for lis species, and that two populations living together on the same site were not necessarily nited by the same factors. Sunderland, Hassal & Sutton (1976), working with *Philoscia uscorum* at Spurn Head, U.K., found that the population maintained a high degree of ability over several years by means of cohort-splitting. Each cohort could be divided to two size groups that differed on pre-reproductive period longevity, breeding pattern ld mortality. Davis (1978) stated that natality and mortality were primary determinants short term (seasonal) changes, and that migration and juvenile mortality were more portant in affecting long term density changes in *A. vulgare* at Spurn Head.

None of these hypotheses seem adequate to explain the changes in numbers of *A. lgare* under Breckland conditions. There was no evidence of cannibalism, high winter ortality, cohort-splitting or significant emigration. Weather would appear to be a ore likely limitation to numbers but no evidence was obtained of its effect in a density pendent manner as proposed by Paris (1963). Temperature was an important factor ecting individual growth rates and the structure of the two Breckland populations l-Dabbagh 1976), but this feature alone is not adequate to maintain the fairly constant pulation level at each site.

The use of grazing as a management tool to maintain the diversity of insect populations certain chalk grasslands has been advocated by Morris (1967, 1973). Rotational grazing s thought to conserve the characteristic fauna of grazed and ungrazed habitats. tending his study to the litter and soil fauna Morris (1968) recorded considerable erences in isopod numbers throughout the year for grazed and ungrazed areas from ich average populations of *A. vulgare* have been calculated: 292 individuals m^{-2} azed) and 7235 individuals m^{-2} (ungrazed). These population densities differed by a tor of 25 which is considerably greater and contrary to that found in the present dy where the grazed site possessed the larger population of this species. The contrast ween the two sites may have been due to fundamental differences in the grasslands died.

A study of a neutral grassland by Southwood & van Emden (1967) revealed contrasts ween the fauna, sampled by a vacuum technique, of cut and uncut plots. The short ss fauna had a marginally higher density than the long grass sward. The structural racteristics of habitats and their importance to the fauna in general were stressed by on & Miller (1954) in their classification scheme. More specifically Duffey (1966) discussed spider ecology and habitat structure. Some workers proposed terrestrial itat classifications based on the structural characteristics of the vegetation cover, nonstrated by Duffey (1968) for dune living spiders. It is clear that much remains to be ned of the relationships and interactions of a species within the spectrum of habitat s which is available to it under a generally similar climatic regime.

is suggested that the differences in habitat structure of the grasslands at Weeting and enheath are responsible for significant changes in the population structure and

dynamics of *A. vulgare*. Amongst these are the generally higher population density
Weeting, differences in age structure, generation distribution and cohort composition of t
two populations. At Weeting each cohort breeds once with large variations betwe
years in the number of young produced, whilst at Lakenheath each cohort breeds twi
and recruitment is similar from year to year. The microclimate of the two grass heat
clearly plays an important role in bringing about these differences, but ultimately t
physical structure of the habitat appears to be the major overall determinant. The stu
emphasizes the very real significance of habitat heterogeneity in understanding t
population dynamics of such relatively common terrestrial invertebrates.

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REFERENCES

Al-Dabbagh, K. Y. (1976). *Population dynamics and bioenergetics of the terrestrial isopod* Armadillidi
vulgare *(Latreille) in grassland ecosystems.* Unpublished Ph.D. thesis, University of Leicester.

Berthet, P. (1960). La mesure écologie de la température par détermination de la vitesse d'inversion
saccharose. *Vegetatio*, **9**, 197–207.

Birch, L. C. (1948). The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecol*
17, 15–26.

Brereton, J. Le G. (1956). *A study of factors controlling the population of some terrestrial isop*
Unpublished D.Phil. thesis, University of Oxford.

Crompton, G. & Sheail, J. (1975). The historical ecology of Lakenheath Warren in Suffolk, Engla
A case study. *Biological Conservation*, **8**, 299–313.

Davis, R. C. (1978). *Ecological studies of Isopoda and Diplopoda in dune grassland.* Unpublished Ph
thesis, University of Leeds.

Deevey, E. S. (1947). Life tables for natural populations of animals. *Quarterly Review of Biology*,
283–314.

Duffey, E. (1966). Spider ecology and habitat. *Senckenbergiana biologica*, **47**, 45–49.

Duffey, E. (1968). An ecological analysis of the spider fauna of sand dunes. *Journal of Animal Ecology*,
641–674.

Edney, E. B. (1968). Transition from water to land in isopod crustaceans. *American Zoologist*, **8**, 309–326.

Elton, C. S. & Miller, R. S. (1954). The ecological survey of animal communities with a practical sys
of classifying habitats by structural characters. *Journal of Ecology*, **42**, 460–496.

Lee, R. (1969). Chemical temperature integration. *Journal of Applied Meteorology*, **8**, 423–430.

McQueen, D. J. (1976a). *Porcellio spinicornis* Say (Isopoda) demography. II. A comparison between
and laboratory data. *Canadian Journal of Zoology*, **54**, 825–842.

McQueen, D. J. (1976b). The influence of climatic factors on the demography of the terrestrial iso
Tracheoniscus rathkei Brandt. *Canadian Journal of Zoology* **54**, 2185–2199.

McQueen, D. J. & Carnio, J. S. (1974). A laboratory study of the effects of some climatic factors or
demography of the terrestrial isopod *Porcellio spinicornis* Say. *Canadian Journal of Zoology*,
599–611.

Mitchell, B. (1963). Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trecus quadristri*
(Schrank). II. Studies on populations of adults in the field, with special reference to the techniqu
pitfall trapping. *Journal of Animal Ecology*, **32**, 377–392.

orris, M. G. (1967). Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. I. Responses of some phytophagous insects to cessation of grazing. *Journal of Applied Ecology*, **4**, 459–474.

orris, M. G. (1968). Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. II. The faunas of sample turves. *Journal of Applied Ecology*, **5**, 601–611.

orris, M. G. (1973). The effects of seasonal grazing on the Heteroptera and Auchenorhyncha (Hemiptera) of the chalk grassland. *Journal of Applied Ecology*, **10**, 761–780.

urphy, P. W. (1962). Extraction methods for soil animals. I. Dynamic methods with particular reference to funnel processes. *Progress in Soil Zoology* (Ed. by P. W. Murphy), pp. 75–114. Butterworths, London.

ris, O. H. (1963). The ecology of *Armadillidium vulgare* (Isopoda: Oniscoidea) in California grassland: food, enemies and weather. *Ecological Monographs*, **33**, 1–22.

to, S. (1969). Energetics of isopod populations in a forest of central Japan. *Researches in Population Ecology*, **11**, 229–258.

omon, M. E. (1957). Estimation of humidity with cobalt thiocyanate papers and permanent colour standards. *Bulletin of Entomological Research*, **48**, 489–506.

ithwood, T. R. E. & van Emden, H. F. (1967). A comparison of the fauna of cut and uncut grassland. *Zeitschrift für angewandte Entomologie*, **60**, 188–198.

iderland, K. D., Hassall, M. & Sutton, S. L. (1976). The population dynamics of *Philoscia muscorum* (Crustacea: Oniscoidea) in a dune grassland ecosystem. *Journal of Animal Ecology*, **45**, 487–506.

ton, S. L. (1968). The population dynamics of *Trichoniscus pusillus* and *Philoscia muscorum* (Crustacea: Oniscoidea) in limestone grassland. *Journal of Animal Ecology*, **37**, 425–444.

lor, L. R. (1961). Aggregation, variance and the mean. *Nature, London*, **189**, 732–735.

tt, A. S. (1936). Studies in the ecology of Breckland. I. Climate, soil and vegetation. *Journal of Ecology*, **24**, 117–138.

tt, A. S. (1940). Studies in the ecology of Breckland. IV. The grass heath. *Journal of Ecology*, **28**, 42–70.

rkman, C. (1978). Life cycle and population dynamics of *Trochosa terricola* Thorell (Araneae: Lycosidae) in a Norfolk grass heath. *Ecological Entomology*, **3**, 329–340.

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Terrestrial Arthropods and Low Temperature[1]

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Cold environments impose many constraints upon arthropods in terms of both their ecology and physiology. Low environmental temperatures will tend to reduce overall metabolic rate and restrict activity, and hence limit feeding. Slow growth rates may result, which in turn, lead to extended life cycles. Maturity and breeding conditions may not be attained in one season or a single year due to the restricted growing period, and there will thus be a requirement for winter survival of some stages. At subzero temperatures, the probability of freezing is greatly accentuated in such animals. Two strategies have been adopted by arthropods: they are either freezing susceptible (avoiding lethal freezing by extensive supercooling) or freezing tolerant (being able to withstand ice formation in their tissues). Such constraints, in conjunction with the geographical isolation of the south polar region, are of considerable importance in determining the relatively low level of species diversity found in the terrestrial communities of this region.

This paper examines in detail the ways in which a typical representative of the Antarctic land fauna, an oribatid mite *Alaskozetes antarcticus* (Michael), has solved the constraints presented by the environmental regime of the south polar region. In particular, some of the physiological problems posed by low temperatures on such small poikilotherms are discussed in relation to its life cycle. It is concluded that *Alaskozetes*, in common perhaps with other freezing susceptible arthropods, ensures its survival and the maintenance of its populations in habitats of the maritime Antarctic by what is termed a bipartite adaptational strategy. This allows the maximal use of above-zero conditions when they occur during the austral summer, and survival of subzero microclimatic conditions in all seasons by an efficient system of cold hardiness.

Data are presented of the survival of this species under desiccating conditions and on the influence of body water content on cold hardiness as assessed by supercooling points and glycerol concentration.

ACTIVITY AND FEEDING

The effect of temperature on the activity of *Alaskozetes* has been studied in the laboratory to determine optimum and threshold temperatures for locomotion. Randomly selected adults of both sexes were used from cultures maintained at 5°C. Activity was measured on the surface of tap water agar (pH 7) in a petri dish, which provided a solid substrate with a high humidity (ca. 85%). The track described by each mite was traced onto the petri dish lid. The length of the track was measured by transferring the pattern to tracing paper, magnifying it with a microscope and mirror attachment, and following this with an opisometer. A range of temperatures from 4 to 32°C was achieved with a thermogradient bar. Agar surface temperatures were monitored by a Grant copper–constantan thermocouple, the agar being allowed to equilibrate at each

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ew temperature for 150 min. Mites were pt at each experimental temperature for a)-min equilibration period prior to track easurements.

Alaskozetes shows a sigmoid response irve of activity to temperature over the nge 4 to 24°C (Fig. 1) with peak activity curring between 16 and 24°C. The op- num temperature for activity (defined as at at which activity is most sensitive to mperature change) occurs between 12 and °C, whilst the lower threshold for activity suggested, by extrapolation, to be ca. 8°C. The curve suggests that these mites ay have considerable locomotory func- ns at subzero temperatures, which would mobilize temperate species. Addition- y, the optimal level for activity is lower an that of warm conditioned arthropods. ie mean chill-coma temperature (temper- ire at which locomotion is inhibited by ld) of summer field *Alaskozetes* adults s been measured as −4.6°C (range −3.5 −7.0°C) at Signy Island, maritime Ant- tic (3), which in part supports the labo- ory observations on activity rates.

If locomotory activity for such a species inhibited below 0°C, it is estimated that only ca. 137 days per year, on average, will provide thermal conditions suitable for movement at Signy Island. By possessing the potential for locomotion down to −4.6°C, this increases the active period to 251 days per year. If activity is possible to ca. −8°C, this period will only be increased to 274 days per year compared to 0°C. It may be that juvenile stages of *Alaskozetes* remain mobile at lower field temperatures, thereby conferring an advantage on these instars.

Alaskozetes is a herbivore and detritivore (8, 12). It has been recorded as feeding on algae especially the foliose *Prasiola crispa* (Lightf.) Menegh., on crustose lichens (at least four species) and organic debris from vertebrate sources (penguins and seals). Food intake and assimilation rates in adult *Alaskozetes* have been measured (9), and 78% of the energy content of ingested food was respired during maintenance metabolism. In terms of energetics, the species has several features of an obligate polar animal, in which respiratory energy loss may increase faster with rising temperature than does the rate of energy assimilation (2). In such forms, a positive energy

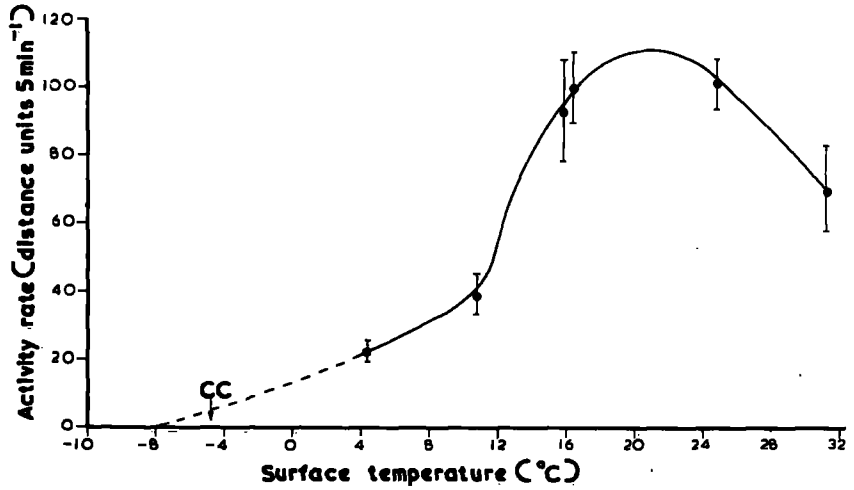

FIG. 1. Mean (±SEM) activity rates at various temperatures of adult *Alaskozetes antarcticus*. $n = 9$ in each case except at 10.5 and 15.6° where it was 4 and 6, respectively. CC: mean temperature of chill-coma measured on field fresh adults at Signy Island.

balance (where respiration energy is less than assimilated energy) may be achieved only at low temperatures.

The gut is characterized in *Alaskozetes* by a pair of elongated, lateral, digestive caecae in the midregion, in which food boluses may be observed. The presence of food in the alimentary system of the mite has been correlated with considerable loss of supercooling power in cultured animals (6, 19), and in field specimens (3). Starvation has been shown to increase the cold hardiness of all life stages by reducing the possibility of ice nucleation in gut contents. Gut clearance is of considerable survival value to overwintering mites and other arthropods which consume solid material.

It is concluded that *Alaskozetes* is well able to maximize its activity in the field when small temperature increases occur, especially during spring and autumn when several (up to 23 per year) freeze–thaw transitions have been monitored (7). These times are also periods of intense microbial activity in soil habitats of the maritime Antarctic (16), and food may become rapidly available to mites at these low temperatures. For a herbivore such as *Alaskozetes* whose diet will include at times, a substantial microbial component, mobility at temperatures in the zone −5 and 5°C will be advantageous in this respect. The adults are able to feed at around 0°C, but a balance has to be reached between the metabolic advantages of such activity and freezing due to gut content ice nucleation.

RESPIRATORY METABOLISM

Temperature is second only to live weight in influencing individual respiratory rates of *Alaskozetes* measured by the Cartesian Diver technique. Metabolic rate (measured as oxygen uptake unit^{-1} live weight hr^{-1}) has been used to compensate for variations in live weight and to facilitate comparison of *Alaskozetes* with other Antarctic soil invertebrates and with temperate oribatid mites (1). Ten species of Antarctic invertebrates had the metabolic rate to temperature (−4 to 22°C) relationship l $O_2 = 2.287 + 0.048\,T$ (where O_2 = μl O_2 g hr^{-1}, T = temperature in °C, and numb of observations (n) = 24) from which overall Q_{10} of 3.04 was derived. Oxyg consumption is measurable down to −4° in *Alaskozetes* (20). Comparison with sim lar data for 109 temperate oribatid mites r vealed no significant differences betwe the slopes of the metabolism–temperatu curves, but demonstrated that the Antarct forms had metabolic rates between three five times higher than temperate speci over the range 0 to 20°C. This phenomen is termed cold adaptation (1, 4, 17), and allows *Alaskozetes* to function in a l temperature environment. The mechanis behind such an elevation is unknown, b activation energies for whole anim metabolism of polar and temperate mi show that the former have significantly < 0.01) lower values, which may constitu part of the basis for cold adaptation (17)

Other studies have shown that *Alas zetes* does not regulate its oxygen uptake response to diurnal or seasonal temperat changes (18). This is surprising, since thermal variability experienced in the fi is extensive with maximum habitat temp atures reaching near 30°C, albeit for v short periods in the austral summer at Sig Island (14). The ability to compens metabolically for temperature changes frequently well developed in animals periencing such regimes (10), but this d not apply in the case of *Alaskozetes*. It m be advantageous for this species not utilize reserves for metabolic homeost during long periods of low temperature, to become relatively quiescent, and to crease its metabolic rate at higher temp tures. Such metabolic conformity will mit maximal exploitation of resources du warmer conditions, but does not con with elevation of its metabolism relativ temperate species.

Alaskozetes therefore, appears to sess an opportunistic metabolic stra with the ability to exploit relatively s

ermal increments as and when they occur its Antarctic environment. In addition, e species has an elevated or cold-adapted etabolic rate which allows it to remain tive at temperatures which would im-obilize nonpolar forms.

COLD HARDINESS

The overwintering physiology of *Alaskozetes* has been extensively investigated. eezing is fatal and survival of low temratures depends on avoiding ice formaon in the body by supercooling (6, 19). eding detracts from its supercooling ility as food contaminants initiate ice mation at relatively high subzero temratures. Cold hardiness may be improved perimentally by starvation (3, 19), but in field it is likely that feeding is much reced and gut contents voided before temratures below −15°C are reached. *Alaszetes* synthesizes glycerol and a linear ationship exists between its concentran in the body fluids and mean superling point. Concentrations of up to 45 μg $^{-1}$ body water (equivalent to 103 μg mg^{-1} weight less glycerol) have been reted (19), and these depress the mean ercooling point to below −30°C and rly is of great survival value in the field ere temperatures of this order may occur . Experimental results have demonted that acclimation to low temperature −5, and −10°C) results in increased erol levels, while photoperiod is ineive.

f considerable ecological interest is the ing that glycerol production is stimud by low relative humidity (40%) and/or ccation in *Alaskozetes* (19). The body r contents of animals maintained under % (9 weeks at 0°C) and 40% (4 weeks at relative humidity were 70.6 and 59.7% resh weight, respectively. Assuming a solute was present in the same proion of dry weight in both groups, its entration would be 1.6 times greater in 40% relative humidity group. But the mean (±SEM) glycerol concentration was significantly ($P < 0.002$) greater (by 3 times) in the low humidity group (35.9 ± 1.6 μg mg^{-1} water) than in the 100% control group (11.5 ± 0.8 μg mg^{-1} water). There was a concomitant lowering of the mean supercooling point of unfed animals from −27.5 ± 0.4 to −28.8 ± 0.4°C; significant at $P < 0.05$.

Examination of data for body water contents of *Alaskozetes* at Signy Island during 1979 (Fig. 2) shows considerable variation with season. Male and female adults had similar patterns with high mean water contents (>75%) in January followed by a sharp reduction to ca. 64% in March–April. A steady increase in percentage water then occurred during winter to near 70% in both sexes. Tritonymphs (third nymphal instars) had a more variable water content together with the other juvenile stages. Data for the previous year and 1980 indicate an overall similarity both of levels and fluctuations. Water contents determined for animals during desiccation and relative humidity experiments (19) thus lie within the range observed for field mites. Using the relationship between body water content (y: percentage of fresh weight) and glycerol concentration (x: μg mg^{-1} body water) derived from these experiments: $y = 75.75 - 0.44x$, and assuming for the moment that relative humidity is the major factor influencing glycerol synthesis in *Alaskozetes* under field conditions, field glycerol levels have been calculated from the water content data (Fig. 2). It is found that adults may have concentrations ranging from 0 to ca. 31 μg mg^{-1} body water, and tritonymphs of 11 to 42 μg mg^{-1} body water. It is predicted that these concentrations, using the relation of mean supercooling points of unfed mites (y: °C) to mean glycerol concentrations (x: μg mg^{-1} body water) as $y = -26.71 - 0.07x$ (19), will enable temperatures of −26 to −30°C (adults and tritonymphs) to be reached before freezing. Recent work at Signy Island during the 1979–1980 Antarctic summer confirm these predictions as mean supercooling points ranged from −24 to

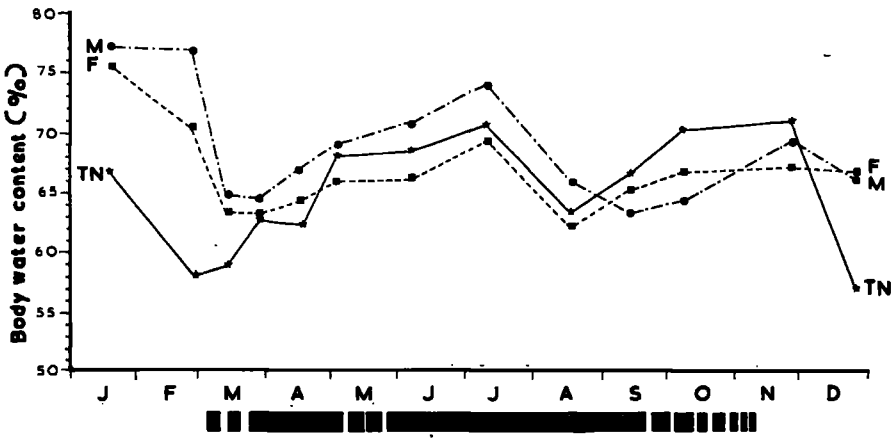

FIG. 2. Seasonal changes in individual water contents of adults and tritonymphs of *Alaskozetes antarcticus* at Signy Island during 1979. F (■): female, M (●): male, TN (★): tritonymph. n = 80–100 individuals per stage per monthly sample. ▬: ground surface frozen.

−31°C (3). Current fieldwork at Signy Island is investigating these seasonal changes in cold hardiness.

It is perhaps premature to place emphasis on glycerol concentrations affecting supercooling ability in *Alaskozetes*, even though it is the main polyol detected in its body fluids. However, despite the behaviour of aqueous solutions, the supercooling of biological systems such as *Alaskozetes* may be lowered by more than twice the melting point depression at any given glycerol concentration (5). This is of considerable adaptive value in freezing susceptible arthropods, and it may account for the widespread occurrence of glycerol, often in conjunction with other polyhydroxy compounds, in mites which experience subzero conditions for much of the year.

The water relations of *Alaskozetes* have been studied as they relate to its cold hardiness. The aims were to establish the rates of individual water loss in saturation deficits which prevail in its natural environment, to determine the level of water loss which it could survive and its capacity to absorb water. Water loss was measured as fresh weight loss using a Beckman electrobalance (LM 500) coupled to a Rikadenki continuous pen recorder. An accuracy of 0.25 μg for a 250-μg mite was achieved. Desiccating atmospheres and low relative humidit were obtained using silica gel in both c ture and weighing chambers. Adult mi collected in March of 1978 and 1979 Signy Island were used, and no food w provided during the experiments. Satu tion deficits of 5.2 and 12.3 mm Hg w achieved by relative humidities of 25% 5°C and 40% at 20°C, respectively.

Experiment 1. The weight losses of f groups of five mites each and of four mi kept individually were monitored over days. Adult *Alaskozetes* survived ca. 3 loss in live weight due to desiccation (i to ca. 65% of their initial live weight). 40% of initial live weight over half the a mals had died at both saturation defic After the initial 20% weight loss, the m lose water at the low saturation deficit slower rate (0.95 $\mu g\,hr^{-1}\,mg^{-1}$ mite) tha the high saturation deficit (10.2 μg mg^{-1} mite), but the change in rate of w loss declines more rapidly in the latter (3). Loss rates are consistently higher a than at 5°C and rates decrease as desi tion proceeds, the most marked rate cha occurring between 65 and 40% of its in live weight (saturation deficit: 12.3 mm when death occurs.

Experiment 2. Thirteen groups of mites each were desiccated to ca. 80

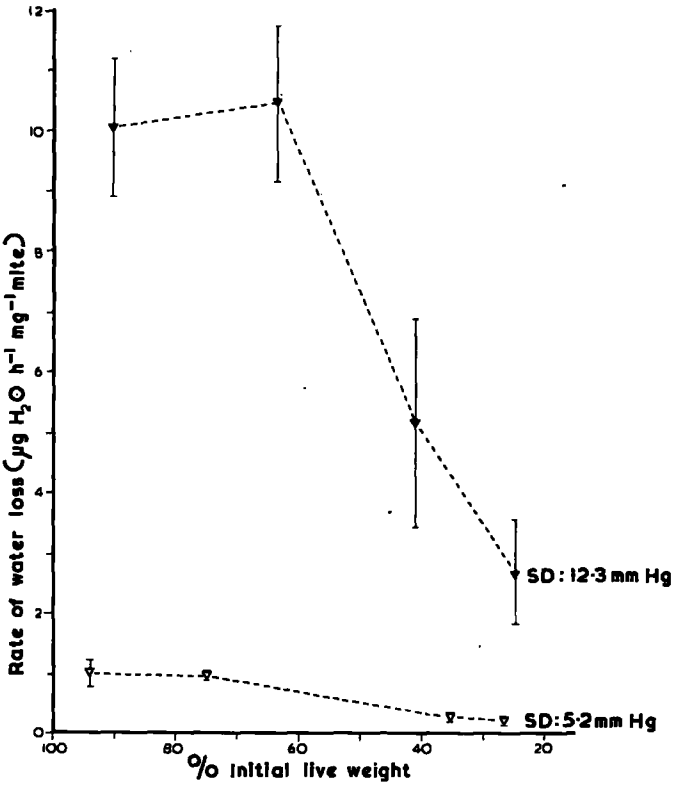

FIG. 3. Variation in rates of water loss by adult *Alaskozetes antarcticus* under desiccation at saturation deficits (SD) of 12.3 mm Hg (40% relative humidity at 20°C) (▼) and 5.2 mm Hg (25% relative humidity at 5°C) (▽) in relation to live weight.

ir initial live weight by placing them for 6 's at 5.2 mm Hg saturation deficit. Dif- ent groups were then subjected to the owing treatments.

Four groups (n = 20), mean (±SEM) initial live weight: 223.0 ± 11.5 μg, were placed on wet filter paper in contact with free water to test their ability to absorb moisture.

Five groups (n = 25), mean initial live weight: 198.8 ± 6.8 μg, were placed in a nearly saturated atmosphere (95% relative humidity, SD: 0.1 mm Hg), but did not have direct contact with free water.

Four groups (n = 20), mean initial live weight: 204.7 ± 9.9 μg, were desiccated continuously at 5.2 mm Hg saturation deficit.

mites were weighed in groups at approximately 3-day intervals over 24 days at 5°C. Initially, mean rate of water loss was 1.33 μg hr^{-1} mg^{-1} mite under the experimental conditions, and 20% weight loss required five days (Fig. 4A). Mites in treatment (a) recovered their initial live weight within 3 days, they therefore gained water faster than they lost it. The animals in a saturated atmosphere (treatment b) continued to lose water, but at a much reduced rate compared to those which were continually desiccated (treatment c). In treatment (c), the mites continued to lose weight at a constant rate and after 30% weight loss about one-third of the animals were dead, at 40% half had succumbed and at 60% weight loss mortality had increased to 85% (Fig. 4B).

Comparison of live and dead mites from treatments b and c showed that there was an increase in weight loss after death. The

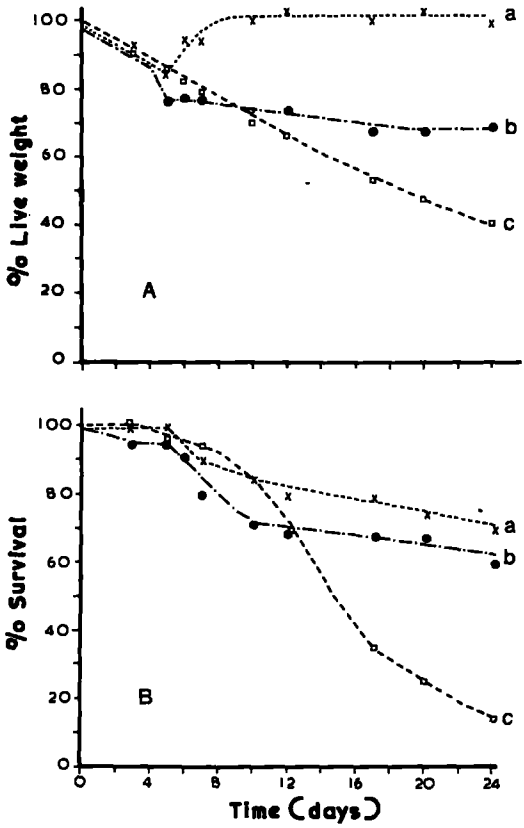

FIG. 4. Changes in mean live weight as a percentage of initial weight (A) and survival (B) of *Alaskozetes antarcticus* after 6 days of desiccation at a saturation deficit of 5.2 mm Hg followed by three different treatments: (a) in contact with free water (X---X); (b) at a relative humidity of 95% (SD: 0.1 mm Hg) (●-·-·-·-●); (c) continued desiccation at a saturation deficit of 5.2 mm Hg (□---□).

sigmoid curve (Fig. 4B) for survival of desiccated mites, when compared with the almost constant rate of water loss suggests that water loss of live specimens declines with increasing desiccation to compensate for the increase in weight loss of dead animals. Survival was in excess of 60% for treatments a and b over the period of the experiment. *Alaskozetes* is unable to absorb water vapour from a nearly saturated atmosphere, and the results indicate that free water must be available for the maintenance of body weight. In contrast, other mites such as the Acaridei are able to use water vapor from unsaturated air to r plenish lost body water (15). The increas in postdeath water loss suggests that t cuticle has an active role in water retentic in *Alaskozetes*.

In summary, *Alaskozetes* employs exte sive supercooling to avoid freezing at su zero temperatures in the maritime Anta tic. Food nucleators may detract from ability to avoid freezing in this wa Glycerol plays a major role in enhanci supercooling powers, and the environme tal cues for its synthesis are low tempe tures and decreased atmospheric relati humidity. Examination of the water cc tents of field mites shows that these va seasonally, with a reduction of at least 1(of live weight occurring during Februar April, at the end of the austral summ This is probably linked to glycerol synthe in the field population. Calculations of fi glycerol and supercooling levels based water contents of *Alaskozetes* show si larity with recent field measurements. P liminary studies on the water relations this species indicate that individuals are a to lose up to 20% of body weight (i.e., suming an initial water content of 60–7 of live weight, a decrease to 40–50% wa content). Reduction of body water, gether with the associated production glycerol in the body, may well be an i gral feature of the increased cold hardi observed for *Alaskozetes* during late s mer. As half the experimental animals vived when desiccated to 60% of their tial live weight (i.e., 40% weight loss), species is seen as extremely hardy in b able to resist desiccation and its physiol cal effects. Individual mites imbibe water to restore water losses and op tunities for this could occur during sh local melt periods in their microhabitat winter.

CONCLUSIONS

The major features of the ecophysio of *Alaskozetes* have been defined and it be viewed as a bipartite strategy. The

)mponents, metabolic adaptation and cold ırdiness, have evolved in response to the lverse nature of its terrestrial habitats roughout the maritime Antarctic. Clear- such a strategy has arisen from the evo- tionary "trade offs" of costs versus ben- its in the process of adaptation to hab- its (11). *Alaskozetes* is adapted not only survive freezing temperatures in all sea- ns of the year, but also to exploit, op- rtunistically, warmer conditions when ey occur. It has survived in its present bitats by having the capacity to function, equately, in the −5 to 5°C temperature nd.

Individuals of this species remain mobile temperatures near 0°C, movement ceas- ; around −5°C. As *Alaskozetes* is the ly herbivore of its kind in the maritime tarctic zone, competition for food and ıer resources is likely to be only intra- cific. It appears to metabolize ingested terials at low temperatures, and enzyme ıtems may have evolved accordingly. :h functioning overall is closely related its relatively high rate of respiratory tabolism from 0 to 15°C, and its reported k of metabolic compensation. In habitats ich experience a low annual temperature ., mean annual air temperature at Signy ınd during the 40 years 1947–1977 ged from −1.2 to −5.9°C with an overall ın of −3.7°C), a metabolism which re- nds directly to temperature changes will serve resources and may be selectively eficial. Studies of growth rates and de-)pment of *Alaskozetes* and other micro- ıropods are now being undertaken to ify this aspect.

s habitat temperatures decline below , a capacity to resist freezing rather ı compensate metabolically becomes ımount. Freezing is lethal to all stages *laskozetes*, and this is avoided as far as iible by supercooling, a capacity for :h is present all the year. A spectrum of potential cryoprotectants have been tified from the body fluids of *Alasko-* ; in particular the juvenile stages, and glycerol is the major polyhydroxy compound detected. Glycerol promotes supercooling, but only develops its full potential in the absence of gut contents. As activity ceases at relatively high subzero temperatures, feeding is suppressed and the full protective action of glycerol to ca. −30°C is realized. The species appears to possess the capacity to resist freezing at temperatures several degrees below the levels normally encountered in its maritime Antarctic habitats, and this is especially evident in the nymphal stages which are well adapted for overwintering.

These two adaptations lend support to the zoogeographical evidence (13) that the Family Podacaridae to which *Alaskozetes* belongs, has experienced a long evolutionary history in the Antarctic, and that its representatives inhabited the south polar region before continental drift occurred. However, optimal adaptation of such a species as *Alaskozetes antarcticus* must not be assumed, as the constraints both of ecology and physiology which have been placed on the animal by the environment may have resulted in a reduced evolutionary rate.

SUMMARY

Cold environments impose several ecological and physiological constraints upon arthropods, including reduction of metabolic rate, locomotory activity, and feeding. These result in slow growth rates and extended life cycles. Additionally, the probability of freezing is accentuated at subzero temperatures. Using data for Antarctic mites, the interplay of such constraints is examined, and the resultant ecophysiological adaptations outlined for a common oribatid mite (*Alaskozetes antarcticus*) of the maritime Antarctic. The synthesis suggests that its survival strategy is comprised of two components. First, the utilization of above-zero temperatures during the short austral summer to maximize growth and production, and thereby reproduce. These processes are aided

by an elevation of its standard metabolic rate, commonly termed cold adaptation. Second, the tolerance of freezing temperatures by supercooling of all its post-ovum life stages throughout the entire year. Its supercooling potential is enhanced by the presence of glycerol and other polyols in the body fluids, the production of which is mediated by environmental temperature and desiccation at low relative humidities. Thus this species, in common perhaps with many other freezing susceptible arthropods, has ensured its survival in southern polar habitats by the evolution of a bipartite adaptational strategy.

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REFERENCES

1. Block, W. Oxygen consumption of the terrestrial mite *Alaskozetes antarcticus*. *J. Exp. Biol.* 68, 69–87 (1977).
2. Block, W. Survival strategies in polar terrestrial arthropods. *Biol. J. Linn. Soc.* 14, 29–38 (1980).
3. Block, W., and Sømme, L. Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. *Oikos* 37. (In press).
4. Block, W., and Young, S. R. Metabolic adaptations of Antarctic terrestrial micro-arthropods. *Comp. Biochem. Physiol.* 61A, 363–368 (1978).
5. Block, W., and Young, S. R. Measurement of supercooling in small arthropods and water droplets. *Cryo. Lett.* 1, 85–91 (1979).
6. Block, W., Young, S. R., Conradi-Larsen, E.-M., and Sømme, L. Cold tolerance of two Antarctic terrestrial arthropods. *Experientia* 34, 1166–1167 (1978).
7. Chambers, M. J. G. Investigations of patterned ground at Signy Island, South Orkney Islands: II. Temperature regimes in the active lay *Bull. Br. Antarct. Surv.* No. 10, 71–83 (196
8. Goddard, D. G., Ecological studies on the ter trial Acari of Signy Island, South Orkney lands, in the maritime Antarctic. Unpublis Ph.D. thesis, University of Leicester, Engla 1977.
9. Marsh, J. B. Radioisotopic determination of ingestion rates of three species of Antarctic thropods. Unpublished M.Sc. thesis, Univ sity of California, Davis, 1973.
10. Prosser, C. L. Physiological adaptations in mals. *In* "Physiological adaptation to the e ronment" (F. J. Vernberg, Ed.), pp. 3–18. text Educational Publishers, New York, 19
11. Southwood, T. R. E. Habitat, the templet ecological strategies? *J. Anim. Ecol.* 337–365 (1977).
12. Strong, J. Ecology of terrestrial arthropods Palmer Station, Antarctic Peninsula. *Anta Res. Ser.* (*Amer. Geophys. U.*) 10, 357– (1967).
13. Wallwork, J. A. Zoogeography of some terrest micro-Arthropoda in Antarctica. *Biol. Rev.* 233–259 (1973).
14. Walton, D. W. H. Radiation and soil temperatu 1972-74: Signy Island terrestrial refere sites. *Brit. Antarct. Surv. Data* 1, (1977).
15. Wharton, G. W. Uptake of water vapour by m and mechanisms utilized by the Acaridei "Comparative physiology: water, ions and f mechanics" (K. Schmidt-Nielsen, L. Bolis S. H. P. Maddrell, Eds.), pp. 79–95. Cambr Univ. Press, London, England, 1978.
16. Wynn-Williams, D. D. Seasonal fluctuation microbial activity in Antarctic moss peat. *J. Linn. Soc.* 14, 11–28 (1980).
17. Young, S. R. Respiratory metabolism of *Ala zetes antarcticus*. *J. Insect Physiol.* 361–369 (1979a).
18. Young, S. R. Effect of temperature change o metabolic rate of an Antarctic mite. *J. Co Physiol.* 131, 341–346 (1979b).
19. Young, S. R., and Block, W. Experime studies on the cold tolerance of *Alasko antarcticus*. *J. Insect. Physiol.* 26, 189 (1980a).
20. Young, S. R., and Block, W. Some factor fecting metabolic rate in an Antarctic *Oikos* 34, 178–185 (1980b).

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upercooling points of insects and mites on the Antarctic Peninsula

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ABSTRACT. 1. Mean supercooling points of eleven species of arthropods (three Collembola, seven Acari and one Diptera) ranged from −6.2 to −9.4°C (high group), and from −17.7 to −31.0°C (low group). The majority of individuals in the high group had food in their gut systems.

2. Freezing was lethal to all species examined except larval *Belgica antarctica* Jacobs (Chironomidae).

3. Glucose, glycerol and mannitol were found in low concentrations in extracts of *Cryptopygus antarcticus* Willem (Collembola) and larvae of *B.antarctica*; it is unlikely that these substances had a major effect on the supercooling of either species.

4. Two Collembola species possessed significantly ($P < 0.05$) lower supercooling points at locations on the Antarctic Pensinsula than at Signy Island, South Orkney Islands. The converse was observed for two species of Acari.

5. It is suggested that whilst gross climatic and also micro-habitat conditions may influence the cold hardiness of such arthropods, especially seasonally, their full supercooling ability is rarely tested.

Key words. Supercooling, Antarctic, Acari, Collembola, Chironomidae, cold hardiness, freezing susceptible, freezing tolerant.

oduction

rmation on the cold tolerance of Antarctic ropods in terrestrial habitats is limited. l studies on Collembola have been confined Bouvetøya (Sømme, 1978a, 1981) and y Island in the South Orkney Islands ime & Block, 1981), whilst those on i have been undertaken in the Vestfjella, ining Maud Land (Sømme, 1978b) and at y Island (Block & Sømme, 1981). Field es of the Antarctic midge (*Belgica antarc-* Jacobs) were made at Anvers Island off Antarctic Peninsula (Baust & Edwards, ; Baust, 1980). Laboratory experiments on cold hardiness have been conducted on both Acari and Collembola (Block *et al.*, 1978; Young & Block, 1980) particularly in respect of acclimatory responses to low temperatures. All the species of micro-arthropods investigated have proved to be susceptible to freezing, i.e. they die at their supercooling point, whereas the larvae of the Antarctic midge are tolerant of freezing, i.e. they live after freezing and subsequent thawing (Salt, 1961).

Extensive comparative data exist for northern arthropod species particularly insects (e.g. Miller, 1969; Baust & Miller, 1970; Block, 1979) and there is a need for a wider survey of the Antarctic fauna in this respect. In addition, Antarctic field studies will form a baseline against which future laboratory

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studies may be compared. This research was therefore undertaken using arthropods collected at two locations on the west coast of the Antarctic Peninsula with the following aims: (a) to determine the levels of cold hardiness in terms of individual supercooling ability of a variety of terrestrial arthropods acclimatized to summer conditions in the maritime Antarctic; (b) to analyse body fluid samples for the presence of possible cryoprotective substances; and (c) to compare these data with other Antarctic locations.

The two locations for this study were Galindez Island in the Argentine Islands (65° 15′ S, 64° 16′ W) and Rothera Point on Adelaide Island (67° 34′ S, 68° 08′ W).

Methods

Two techniques for sampling arthropods in the field were employed. Micro-arthropods were collected by aspirator from various vegetation types when the substrate was not frozen. At Galindez Island these included relatively dry lichen-encrusted moss turf, the main moss species being *Polytrichum alpestre* Hoppe, shallow, wet, moss carpets composed almost entirely of *Drepanocladus uncinatus* (Hedw.) Warnst. and algal dominated areas with *Prasiola crispa* (Lightf.) Menegh. Larval *Belgica antarctica* were obtained by hand-sorting samples of *D.uncinatus* from Galindez Island in the laboratory. This was undertaken in the biological laboratory of the RRS *Bransfield*, whilst work at Rothera Point was done at the British Antarctic Survey station on shore. Arthropod collections at Rothera Point were made from small patches of *D.uncinatus* only, no fauna being found in the lichens (*Usnea*, *Alectoria* and *Umbilicaria* spp.) and small tufts of other mosses. When the ground was frozen, samples of moss and peat *c.* 20 cm^3 were cut by knife, transported in polythene bags to the laboratory where they were thawed at 2–4°C and then placed in a Tullgren extractor in an unheated room. The arthropods left the samples upon very low, gentle heating; they were collected immediately and stored in vials on ice in a thermos flask until required. Field collections were made on 22–26 March and 2–5 April 1980 at Galindez Island and 28–31 March 1980 at Rothera Point.

Individual supercooling points (lo body temperature reached before spontan freezing) of arthropods were determined a cooling rate of *c.* 1°C min^{-1} using a C battery driven recorder and the techni described by Block & Sømme (1981). A ture (1:1.5 v/v) of $CaCl_2.6H_2O$ and crushe and snow was utilized for cooling, and in dual animals were attached with thin sn of vaseline to copper–constantan the couples for monitoring body tempera Supercooling point data were separated high group (HG) and low group (LG) v on the basis of gut contents (Block & Sø 1981).

Sufficient material of two species was lected for polyol and sugar analyses: collembolan *Cryptopygus antarcticus* W from both locations and the chironomid m *Belgica antarctica* from Galindez Island Samples of 5.0–7.4 mg fresh weight (20- individuals) were homogenized and extr in 70% ethanol, and stored frozen for s quent GLC analyses using a Pye-Un GCD chromatograph in the United King Samples were derivitized using a trimethy reagent with pyridine (Sigma Sil-A); stan ization techniques were as described in & Sømme (1981).

Significance of differences between values was determined by *t*-test (Bailey, 1

Results

Supercooling points

A total of eleven species of arthr (three Collembola, seven Acari and one tera) was examined. Only two species (*C pygus antarcticus* and *Stereotydeus v* (Trouessart)) were found at both locatio the Antarctic Peninsula (Table 1). Wit exception of the cryptostigmatid mite *M zetes antarcticus* (Michael), the rem (eight species) were found only at the no location (Galindez Island). Mean superc points ranged from −6.2 to −9.4°C (HG from −17.7 to −31.0°C (LG). Species biting both HG and LG showed, on scopic examination, that the majority individuals contained food in their guts, was probably responsible for ice nucl

.BLE 1. Comparison of mean high group (HG) and low group (LG) supercooling points of field specimens of ects and mites from two sites on the Antarctic Peninsula during March–April 1980. *R*: number in LG/ mbers in LG + HG; figure in parentheses: *n*; n.d.: not determined.

ecies	Site and substrate	*R*	Mean (± SD) supercooling point (°C)	
			HG	LG
lembola:				
Cryptopygus antarcticus Willem	Galindez Island, *Polytrichum* moss	0.33	−7.9 ± 2.7 (76)	−23.9 ± 3.1 (37)
C.antarcticus	Rothera Point *Drepanocladus* moss	0.82	−9.4 ± 2.5 (21)	−26.0 ± 2.1 (96)
Parisotoma octooculata (Willem)	Galindez Island, *Polytrichum* moss	0.03	−6.5 ± 1.2 (66)	−20.8 ± 5.8 (2)
Friesea grisea (Schäffer)	Galindez Island *Polytrichum* moss	0.17	−8.8 ± 2.4 (15)	−24.4 ± 2.7 (3)
ari:				
Stereotydeus villosus (Trouessart)	Galindez Island, *Polytrichum* moss	0.0	−7.6 ± 1.2 (30)	n.d.
S.villosus	Rothera Point, *Drepanocladus* moss	1.0	n.d.	−31.0 ± 1.2 (2)
Rhagidia gerlachei (Trouessart)	Galindez Island, *Polytrichum* moss	0.0	−7.2 ± 1.5 (28)	n.d.
Eupodes minutus (Strandtmann)	Galindez Island, *Polytrichum* moss	0.0	−8.2 ± 1.9 (7)	n.d.
Vanorchestes antarcticus Strandtmann	Galindez Island, *Polytrichum* moss	1.0	n.d.	−23.1 ± 2.1 (21)
Gamasellus racovitzai (Trouessart) deutonymphs	Galindez Island, *Polytrichum* moss	0.0	−6.6 ± 1.1 (12)	n.d.
Oppia loxolineata Wallwork	Galindez Island, *Polytrichum* moss	0.15	−9.6 ± 2.2 (11)	−17.7 ± 2.4 (2)
Magellozetes antarcticus Michael)	Rothera Point, *Drepanocladus* moss	1.0	n.d.	−23.2 ± 9.9 (2)
era:				
Belgica antarctica acobs	Galindez Island, *Drepanocladus* moss	0.0	−6.2 ± 1.0 (61)	n.d.

ing supercooling (Salt, 1968). The propor- of animals (*R*) which constituted the LG ach sample varied greatly (Table 1), but se species which had the lowest mean ercooling points contained a high percen- of LG individuals.

There were differences in cold hardiness, as rmined by mean supercooling points, be- en the populations of both *C.antarcticus* *S.villosus* at Galindez Island and Rothera t (Table 1), but these differences were statistically significant. In the latter ies, only two LG individuals were found Rothera Point, which contrasts with data Signy Island (60° 43′ S, 45° 36′ W), re only HG animals occurred (Block & me, 1981).

Comparison of the Collembola supercool- point data from the Antarctic Peninsula locations with those from Signy Island, South Orkney Islands (Fig. 1) shows a similar proportion of LG individuals in the populations of *C.antarcticus* at Galindez and Signy Islands. There was, however, a 3.1°C difference in LG mean supercooling points between these population samples. Furthermore, the Rothera Point LG mean supercooling point was 2.1°C lower than the Galindez Island value, making a total difference of 5.2°C ($P < 0.05$) between Signy Island and Rothera Point animals. No data are available for *Friesea grisea* (Schäffer) other than that from Galindez Island (Fig. 1), which precludes comparisons. For *Parisotoma octooculata* (Willem), almost all individuals at Galindez and Signy Islands were in the HG, the HG mean supercooling point being slightly lower ($P < 0.05$) at the Antarctic Peninsula site.

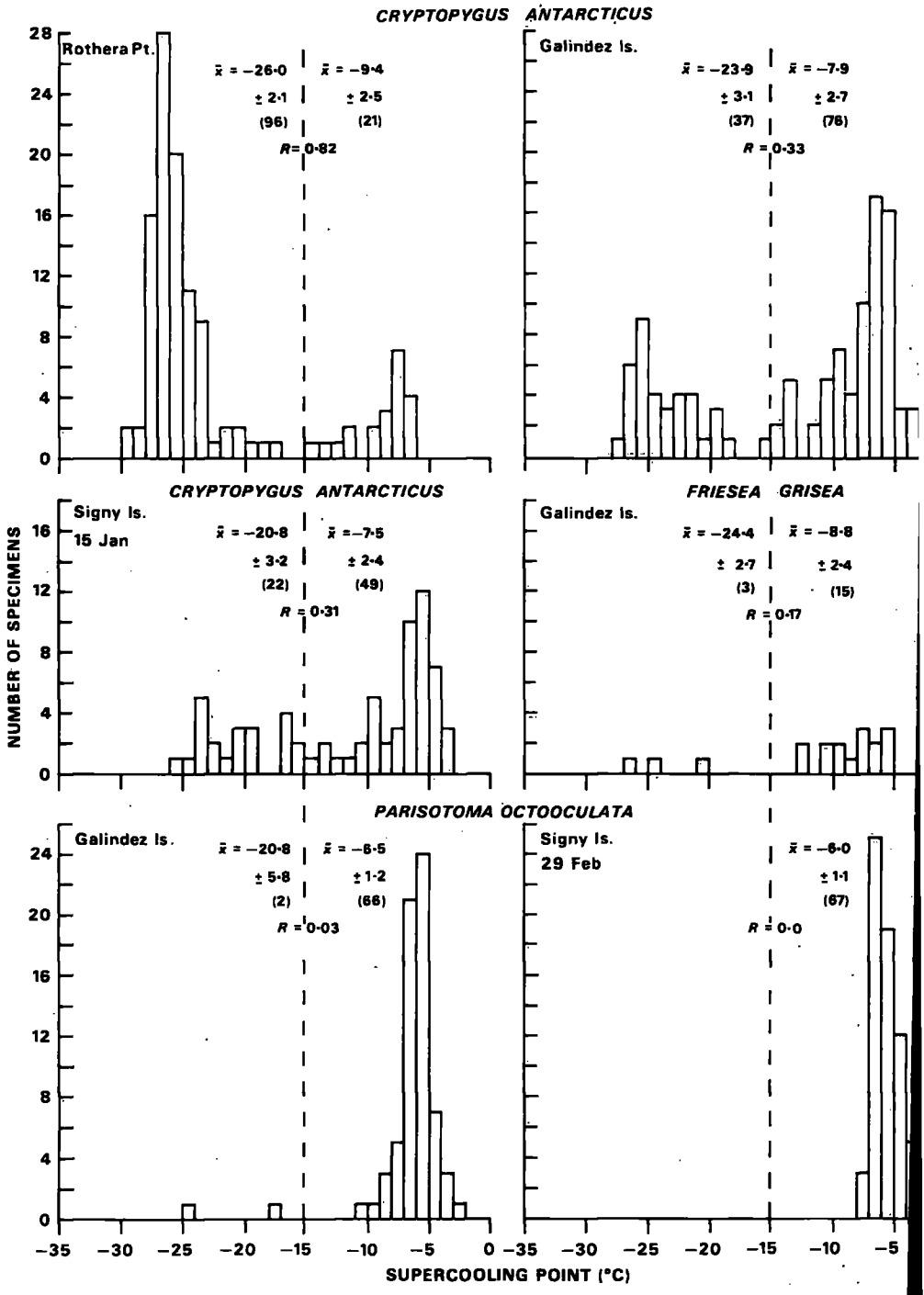


FIG. 1. Supercooling point distribution histograms for Collembola at Rothera Point and Galindez (Antarctic Peninsula), compared with those at Signy Island, South Orkney Islands. x̄: mean (± SD); fig parentheses: number of specimens; *R*: LG/(LG + HG) ratio with the division between the HG and LG −15°C.

For three species of Acari, the situation ffers from that of the Collembola studied. In *norchestes antarcticus* Strandtmann, the mean supercooling point was similar (no nificant difference) for Galindez and Signy nds (Fig. 2), and a high proportion of tes occurred in both LGs. For *S.villosus*, ly HG animals were found at both locations, l the Signy Island population had a LG an supercooling point 2°C lower than the lindez Island sample (significant at $P < 0.01$). omparable picture was shown by the deuto-nphs of the predatory mesostigmatid mite, *nasellus racovitzai* (Trouessart) (Fig. 2), h the Signy Island animals being more cold dy in terms of mean supercooling points < 0.02). The data for *Rhagidia gerlachei* ouessart), another prostigmatid mite, are ilar to those for *S.villosus* at Galindez nd.

All the Collembola and mites examined e susceptible to freezing, i.e. they died n frozen at their supercooling point. Larvae he midge, *Belgica antarctica*, on the other d, were tolerant of freezing and many indi-uals recovered when thawed after freezing . −6°C. These insects are relatively poor ercoolers compared with the micro-arthro-s studied. This may be due to nucleators heir bodies causing them to freeze at rela-y high sub-zero temperatures, which ces damage during freezing (Baust & ards, 1979).

protective substances

he mean concentrations of sugars and ols were low in the two species examined le 2). Glucose was found in the highest entrations of the three substances identified in extracts of *C.antarcticus* together with small amounts of two polyols, glycerol and mannitol. Even with the most concentrated glucose (0.34% in *C.antarcticus* at Rothera Point) the expected freezing point depression is only −0.05°C, compared with an actual LG mean supercooling point of −26.0°C (Fig. 1). This suggests the possibility of a protein anti-freeze because both sugars and polyols were present in such low concentrations. There were no major differences between the Galindez Island and Rothera Point samples of *C.antarcticus*, but both differed from analyses of the same species at Signy Island (Sømme & Block, 1981). A high mean concentration (*c.* 43 μg mg^{-1} fresh weight) of glycerol was determined in the latter animals, together with fructose (6 μg mg^{-1} fresh weight), and glucose (similar to Antarctic Peninsula samples, Table 2). Mannitol was not detected in *C.antarcticus* at Signy Island. The quantities of these substances were too small to exert a profound influence on the supercooling points of either mites or Collembola at the Antarctic Peninsula sites.

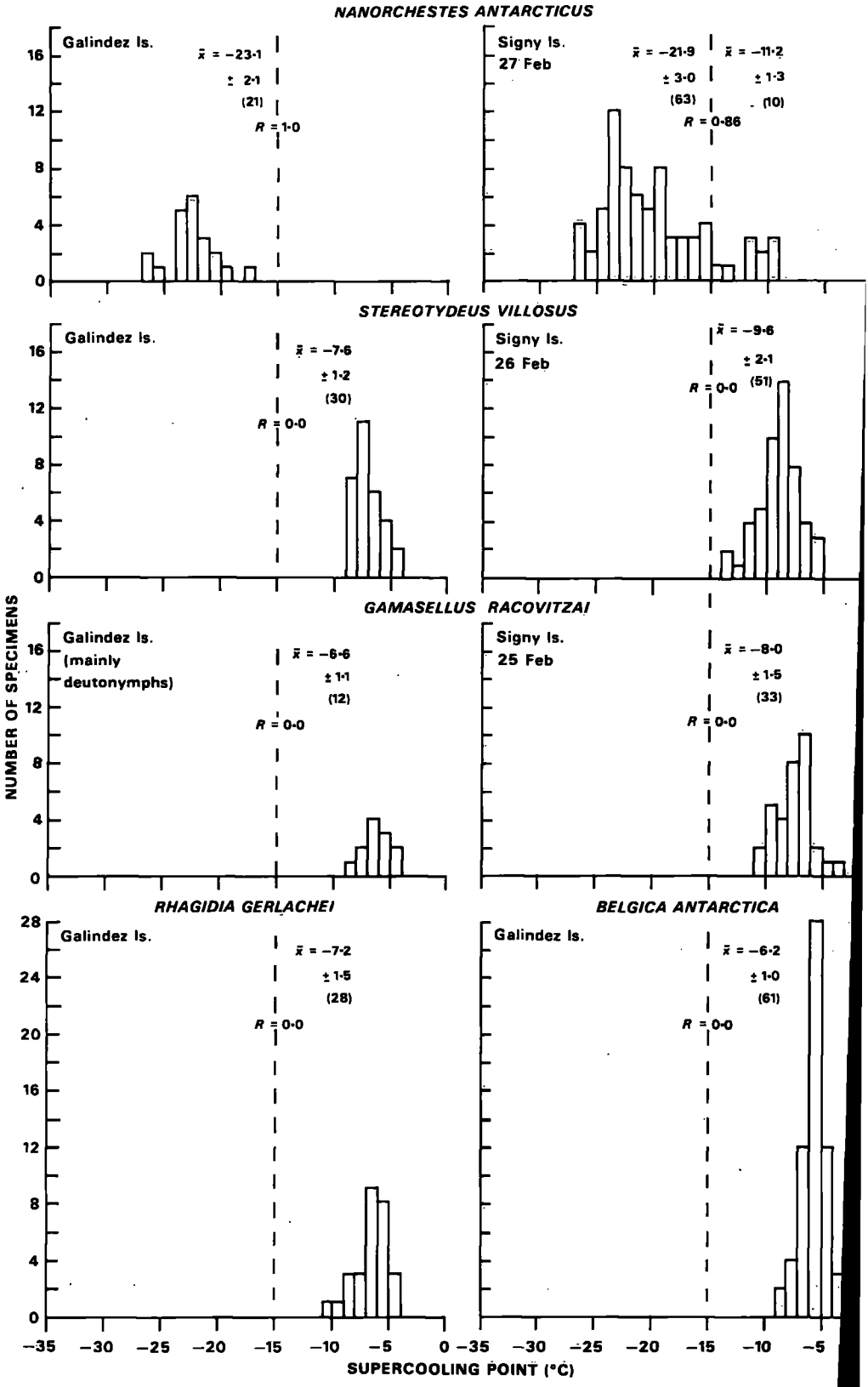
Mannitol was the only substance present in significant amounts in larval *B.antarctica* from Galindez Island (Table 2). This contrasts with the findings of Baust & Edwards (1979) for this species at Anvers Island (64° 46′ S, 64° 03′ W), in which three sugars and erythritol were the main components during summer. This may be due to differences in analytical technique and sampling or to habitat and microclimate changes.

Discussion

Considerable variation in cold hardiness was found in eleven species of arthropods examined

LE 2. Mean concentrations of sugars and polyols in field samples of *Cryptopygus antarcticus* and larval *a antarctica* from two sites on the Antarctic Peninsula during March–April 1980. *n*: number of samples.

es	Site and substrate	*n*	Mean (± SD) concentrations (μg mg^{-1} fresh weight)		
			Glucose	Glycerol	Mannitol
opygus antarcticus, s	Galindez Island, *Prasiola* alga	4	2.62 ± 2.30	0.31 ± 0.22	0.85 ± 0.64
rcticus	Rothera Point, *Drepanocladus* moss	2	3.37 ± 1.23	0.46 ± 0.17	0.38 ± 0.10
a antarctica	Galindez Island, *Drepanocladus* moss	4	0.47 ± 0.05	0.35 ± 0.11	2.97 ± 0.64


NANORCHESTES ANTARCTICUS
Galindez Is.
$\bar{x}$ = −23·1
± 2·1
(21)
R = 1·0
Signy Is.
27 Feb
$\bar{x}$ = −21·9
± 3·0
(63)
$\bar{x}$ = −11·2
± 1·3
(10)
R = 0·86
STEREOTYDEUS VILLOSUS
Galindez Is.
$\bar{x}$ = −7·6
± 1·2
(30)
R = 0·0
Signy Is.
26 Feb
$\bar{x}$ = −9·6
± 2·1
(51)
R = 0·0
GAMASELLUS RACOVITZAI
Galindez Is.
(mainly
deutonymphs)
$\bar{x}$ = −6·6
± 1·1
(12)
R = 0·0
Signy Is.
25 Feb
$\bar{x}$ = −8·0
± 1·5
(33)
R = 0·0
RHAGIDIA GERLACHEI
Galindez Is.
$\bar{x}$ = −7·2
± 1·5
(28)
R = 0·0
BELGICA ANTARCTICA
Galindez Is.
$\bar{x}$ = −6·2
± 1·0
(61)
R = 0·0
NUMBER OF SPECIMENS
0
4
8
12
16
20
24
28
−35 −30 −25 −20 −15 −10 −5 0
SUPERCOOLING POINT (°C)

two locations on the Antarctic Peninsula
nge of LG mean supercooling points from
7.7 to −31.0°C). The three substances (one
ar and two polyols) identified from extracts
two species were unlikely to affect indivi-
al supercooling ability due to their low con-
trations. In the Collembola two species
ibited significant increases in cold hardiness
m Signy Island to the Antarctic Peninsula,
the converse was true for some of the
es. In two species of Acari, field samples
icated that Signy Island animals were signi-
ntly more cold hardy than those at Galindez
nd. It is interesting that neither of these
cies formed a LG in their supercooling
nt distributions (Fig. 2), and therefore the
parison is restricted to the HG (i.e. those
ing food in their gut systems) in both cases.
sonal studies of arthropod cold hardiness
ently in progress at Signy Island show that
form during winter conditions in these
ies.

antarcticus from Bouvetøya, also in the
itime Antarctic zone (Holdgate, 1977),
ibited supercooling points between −24
−26°C (Sømme, 1978a), similar to the
es obtained in the present study. Only a
t lowering of the LG mean supercooling
t to −27.4°C occurred after 4 weeks accli-
on to −5 and −10°C in this species
nme, 1981). Three species of prostigmatid
s in Dronning Maud Land showed super-
ing points between −20 and −30°C
me, 1978b), with LG means ranging
−22.6 to −26.9°C and an absence of HG
als. *S.villosus* at Rothera Point showed a
tly deeper level of supercooling to −31.0°C
le 1).

oth the South Orkney Islands and the
coast of the Antarctic Peninsula to about
ide 70°S are included in the maritime
rctic zone (Holdgate, 1977). This zone
riences a cold, maritime climate with
monthly air temperatures exceeding 0°C
in midsummer and rarely falling below
C in winter. Clearly, differences in lia-
to supercooling will be brought about
easonal climatic changes, especially of
temperature and snow cover, affecting the microclimate of the moss-peat in which these arthropods live. The data for animals from the Antarctic Peninsula locations were obtained in March–April 1980, towards the end of the austral summer, whilst the Signy Island experiments were undertaken in midsummer. Slight differences in microclimatic conditions, particularly around the phase change of water at 0°C, may therefore have influenced the physiological state of the fauna, which might explain the collembolan data. Such factors would not explain the converse situation found in the Acari. Further experimental work is needed to show whether different triggers for cold hardening may be operating in these two groups of micro-arthropods.

It is possible that the extreme low levels of cold hardiness measured for individual mites and Collembola in the present study are not normally utilized in the field. If micro-habitat conditions, especially temperature, remain approximately constant at around 0°C for much of the year, their ability to supercool extensively may be tested only rarely. Thus, such species may possess relict adaptations while existing under relatively optimal conditions, as has been postulated for *B.antarctica* (Baust, 1980).

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References

Bailey, N.T.J. (1959) *Statistical Methods in Biology*. English Universities Press, London.

. Supercooling point distribution histograms for four species of Acari and larvae of the midge, *Belgica tica*, at Galindez Island (Antarctic Peninsula), compared with those at Signy Island, South Orkney s. $\bar{x}$: mean (±SD); figure in parentheses: number of specimens; *R*: LG(LG + HG) ratio with the division en the HG and LG being −15°C.

Baust, J.G. (1980) Low temperature tolerance in an Antarctic insect: a relict adaptation? *Cryo-Letters*, 1, 360–371.

Baust, J.G. & Edwards, J.S. (1979) Mechanisms of freezing tolerance in an Antarctic midge, *Belgica antarctica*. *Physiological Entomology*, 4, 1–5.

Baust, J.G. & Miller, L.K. (1970) Variations in glycerol content and its influence on cold hardiness in the Alaskan carabid beetle *Pterostichus brevicornis*. *Journal of Insect Physiology*, 16, 979–990.

Block, W. (1979) Cold tolerance of micro-arthropods from Alaskan taiga. *Ecological Entomology*, 4, 103–110.

Block, W. & Sømme. L. (1981) Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. *Oikos* (in press).

Block, W., Young, S.R., Conradi-Larsen, E.-M. & Sømme, L. (1978) Cold tolerance of two Antarctic terrestrial arthropods. *Experientia*, 34, 1166–1167.

Holdgate, M.W. (1977) Terrestrial ecosystems in the Antarctic. *Philosophical Transactions of the Royal Society of London*, 279 (963), 5–25.

Miller, L.K. (1969) Freezing tolerance in an adult insect. *Science*, 166, 105–106.

Salt, R.W. (1961) Principles of insect cold-hardin *Annual Review of Entomology*, 6, 55–74.

Salt, R.W. (1968) Location and quantitative asp of ice nucleators in insects. *Canadian Journa Zoology*, 46, 329–333.

Sømme, L. (1978a) Cold-hardiness of *Cryptop antarcticus* (Collembola) from Bouvetøya. *Oi* 31, 94–97.

Sømme, L. (1978b) Notes on the cold-hardines prostigmate mites from Vestjella, Dronning M Land. *Norwegian Journal of Entomology*, 51–55.

Sømme, L. (1981) Supercooling in two Anta terrestrial arthropods from Bouvetøya. *N Polarinstitut Skrifter* (in press).

Sømme, L. & Block, W. (1981) Cold hardines Collembola at Signy Island, maritime Antar *Oikos* (in press).

Young, S.R. & Block, W. (1980) Experimental stu on the cold tolerance of *Alaskozetes antarcti Journal of Insect Physiology*, 26, 189–200.

Accepted 8 July 1981

OS 38: 157–167. Copenhagen 1982

ld hardiness of terrestrial mites at Signy Island, maritime ıtarctic

am Block and Lauritz Sømme

Block, W. and Sømme, L. 1982. Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. – Oikos 38: 157–167.

(1) The cold hardiness of four species was studied in respect of supercooling ability, cryoprotective substances, chill-coma temperatures and survival under anaerobiosis. The effects of low temperature acclimation and starvation on cold hardiness were examined experimentally.
(2) Mean supercooling points of field animals ranged from –6.1° to –28.8°C during Jan–Mar 1980. In *Nanorchestes antarcticus* (Strandtmann) and *Alaskozetes antarcticus* (Michael), a bimodal distribution of individual supercooling points occurred with the low group (LG) consisting of animals without gut nucleators. In *Stereotydeus villosus* (Trouessart) and *Gamasellus racovitzai* (Trouessart) only a high group (HG) was present in the supercooling-point distributions.
(3) In all species, except the predatory *G. racovitzai*, starvation combined with low temperature exposure for various time periods lowered the mean supercooling point. This was associated with increased concentrations of glycerol in the body fluid. Glucose, ribitol and mannitol together with straight chain hydrocarbons were also detected in the extracts by GLC techniques.
(4) Chill-coma temperatures varied from –4.5° to –8.0°C.
(5) Under anoxia at 0°C, survival of *A. antarcticus* was greater than that of *G. racovitzai*, with the later nymphal stages being slightly more resistant than adults.

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1. Исследовали холодовое оцепенение у 4-х видов с точки зрения их способности к переохлаждению, наличия морозоустойчивых компонентов, температурной точки наступления холодового анабиоза и выживаемости в анаэробных условиях. Экспериментально проверяли воздействие акклимации к низким температурам и голодания при анабиозе.
2. Средние точки переохлаждения животных, взятых из природных условий, -6,1 - - 28,8°C в период с января по март 1980 г. У *Nanorchestes antarcticus* (Strandtmann) и *Alaskozetes antarcticus* (Michael) наблюдалось бимодальное распределение индивидуальных точек переохлаждения, при этом группа с более низкими показателями (LG) включала животных, не имеющих кишечных кристаллогенных соединений у *Stereotydeus villosus* (Trouessart) и *Gamasellus racovitzai* (Trouessart) отмечена лишь группа с высокими температурами переохлаждения (HG).
3. У всех видов, кроме хищного *G. racovitzai* голодание при низких температурах разной продолжительности приводит к снижению средней температуры переохлаждения. Это связано с повышением концентрации глицерола в полостной жидкости. Гликоза, рибитол и маннитол, вместе с неароматическими углеводородами также обнаружены в экстрактах методом GLC. Температура холодового оцепенения колеблется от -4,5° до -8°C. При анаэробных условиях и температуре 0°C выживаемость *A. antarcticus* выше, чем у *G. racovitzai*, причем, поздние нимфальные стадии несколько более устойчивы, чем взрослые.

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1. Introduction

The survival of individuals in a population of a poikilotherm species at low temperatures is a basic component of its adaptational strategy. The ability of land invertebrates, which have colonized polar regions, to resist freezing temperatures has received increasing attention in recent years. In the Antarctic, research has been concentrated on the relatively abundant micro-arthropods (mites and springtails), the majority of which resist freezing, which is generally fatal, by supercooling (thereby being termed freezing susceptible). One of the few higher insects of the Antarctic, the chironomid *Belgica antarctica* (Jacobs), is able to survive body freezing in the larval stage and has been described as freezing tolerant (Baust and Edwards 1979).

Using cultured material, Block et al. (1978) and Sømme (1978a, 1981) demonstrated that the common maritime Antarctic collembolan *Cryptopygus antarcticus* (Willem) survived temperatures as low as –30°C by supercooling. Similar levels of supercooling may be achieved by the oribatid mite *Alaskozetes antarcticus* (Michael) (Block et al. 1978, Young and Block 1980, Sømme 1981). In both species, a bimodal distribution of individual supercooling points (temperatures of spontaneous freezing) resulted from ice nucleation by food in the guts of animals that had fed (Block et al. 1978). Glycerol was detected in mites acclimated to 0°C. Detailed investigations (Young and Block 1980) revealed that there is an inversely proportional relationship between glycerol concentration and supercooling point in *A. antarcticus*, and confirmed that feeding detracts from individual supercooling ability. Additionally, low temperature acclimation and desiccation increases glycerol concentrations, and juvenile instars have a greater degree of cold resistance than adults. An increase in the ability of both *C. antarcticus* and *A. antarcticus* to supercool, following acclimation at temperatures of 0° to –10°C, was confirmed by Sømme (1981).

Research on field-fresh micro-arthropods in the Antarctic by Sømme (1978b) showed that three species of prostigmate mites from Dronning Maud Land had levels of supercooling similar to the above species.

Consequently, the aims of the research reported here were: (1) to determine individual supercooling points for a range of Antarctic micro-arthropods under summer field conditions; (2) to measure levels of polyhydric alcohols in extracts of these species; (3) to examine experimentally the effects of low temperature and starvation on supercooling ability and polyol levels; and (4) to record chill-coma temperatures and to estimate survival under anaerobic conditions.

The work was undertaken at the British Antarctic Survey station on Signy Island, South Orkney Islands (60° 43′S, 45° 38′W) in the maritime Antarctic during Jan – Mar 1980. The free-living, terrestrial arthropod fauna indigenous to Signy Island comprises four species of Collembola and ten species of Acarina (Tilbrook 1973, Goddard 1979), of which six species are comm The work was concentrated on these six species (each of mesostigmatid and cryptostigmatid mites, prostigmatid mites and two isotomid collembola The results for the four species of mites are prese here, and those for the two species of Collembola presented in a separate paper (Sømme and B 1982).

2. Methods

2.1. Field collection and culture

All animals were collected by hand and micro-aspi from several contrasting terrestrial habitats at Sign land including rocky fellfields, moss banks, the sid melt streams, guano enriched areas near penguin and elephant seal wallows, snow margins and liche algal covered sites. For tests on field-fresh animal dividuals were collected on the day of measure whilst larger collections for experimental animals made over two days. In the laboratory all live ma was stored in glass vials on snow/ice at 0°C pri sorting under a binocular microscope at ×10 to magnification. Food was provided in the form of tions of their natural substrate, algae or mosses, a the case of the predatory mesostigmatid mite, se springtail prey were included also.

2.2. Temperature acclimation and starvation

For longer experiments, micro-arthropods were s into single-species groups and 25–100 individuals placed, without food, in 15 ml vials, the tops of were covered by nylon mesh gauze to prevent the cape. These vials, placed in 250 ml glass jars with caps, were situated in controlled (±1°C) temper cabinets at various temperatures (–5°, 0°, 5° and for varying time periods.

2.3. Supercooling points

Supercooling points were measured by monitoring temperature of individual arthropods with a fine (swg) copper-constantan thermocouple, whose was recorded on a chart by a Ni-Cd battery op Grant recorder. This enabled four temperature urements to be recorded every three seconds at a speed of 38 cm h^{-1} over a temperature range of 3 –70°C. Cold junction compensation was automa the single thermocouple used. Animals were cons either singly or in groups of up to eight individu run, and were attached to the thermocouple by a spot of vaseline. The thermocouple was enclosed or two air filled glass tubes and suspended in a th flask containing a mixture of granular snow and $6H_2O$ in the proportion 1.5:1 v/v which pr

mum temperatures of –50° – to –55°C. By adjusting insertion depth of the thermocouple unit in the , a cooling rate of ca. 1°C min $^{-1}$ was achieved, and was used throughout all the experiments. Two re- ers utilized one freezing mixture. Supercooling s were measured as the point of origin of the small, ignificant, temperature rise which accompanied the t heat emission during freezing of the animal in the rcooled state.

ter each run, the thermocouple unit was slowly ied to room temperature in order to reduce con- ation of water vapour on the cold surfaces and pre- inoculative freezing of animals in later runs. After ing, animals were observed for signs of possible ery at room temperature before confirming their ification. At least 30 and often up to 70 individuals run for each sample, but in a few cases this was not ved due to poor survival during previous treat- s. Individual supercooling points were plotted as ency histograms and the mean (± S.D.) calculated. e case of bimodal distributions of supercooling s, mean values were derived for each distribution gh group and a low group). The distribution of als in the two supercooling-point groups was ex- ed as the ratio R = LG/(LG + HG), where LG IG are the numbers of individuals in the low group igh group, respectively.

high and low groups of each species, supercooling data recorded after each treatment were subjected ne-way analysis of variance, and the variance ratio d was used to test for homogeneity of mean val- sing a computer program (Statistical Package for cial Sciences) on the Cambridge University IBM 65. If homogeneity was present ($P < 0.05$), pairs an values were subjected to t-tests using 'mean within groups' values from the previous analysis rall estimates of variance (Sokal and Rohlf 1969). icance of differences between means was further igated by a least significant range test in the Stu- Newman-Keuls procedure (Sokal and Rohlf . If variance homogeneity was lacking, t-tests onducted according to Bailey (1959).

yoprotective substances

ts for chromotographic analyses were prepared cerating 20–200 individuals (fresh weight meas- n a Cahn microbalance ranged from 1–13 mg) in thanol for each sample or treatment. Such ex- were stored at 0°C before analysis.

e preliminary determinations of glycerol con- tions were performed at Signy Island using mensional separation and an ascending solvent of l-ol : acetic acid : water (12:3:5) on paper atograms. Extracts were treated as described by and Block (1980), the relationship between the of glycerol applied and the spot area being linear a wide range (Sømme 1964). Confirmatory analyses for glycerol and the identification of other polyhydroxy compounds in the mite extracts were undertaken using gas-liquid chromatography at the British Antarctic Survey laboratories in Cambridge. A trimethylsilyl reagent with pyridine (Sigma Sil-A) was used to prepare derivatives of the polyhydroxy compounds in sample extracts (Sweeley et at. 1963). The derivatives were chromatographed directly using a Pye-Unicam GCD chromatograph and a Chrompack SE – 30 capillary column with helium as the carrier gas and standardization with pure sugars and polyols. Integration of areas under the curves and corrections were achieved using a Hewlett-Packard Integrator 3380A. Three determinations were made for each sample and the mean polyol and sugar concentrations in μg mg^{-1} fresh weight were derived.

Identification of sugars and polyols were made on a Varian combined gas chromatograph-mass spectrometer (MAT, Bremen) at the Univ. of Oslo.

2.5. Chill-coma temperature

Chill-coma temperature, defined as the temperature at which walking activities cease, although small movements of legs and other appendages may still be observed, was determined for groups up to five individuals. As described by Sømme (1976) the animals were observed directly in a cylindrical, perspex chamber with an inner diameter of 4 cm, cooled by a Peltier module on a binocular microscope stage at X10 to X25 magnification. The temperature of the chamber floor near the test animals was monitored by a copper-constantan thermocouple and recorded on a Grant miniature temperature recorder (see below for details). The arthropods was either collected from the field on the day of the experiment or acclimated at –5°C for 10–14 d. Each experiment commenced at 0°C and by adjustment of the degree of cooling a rate of ca. 1°C min^{-1} temperature decrease was obtained. The behaviour of individual animals was noted and the mean temperature at which chill-coma occurred was determined.

2.6. Anoxia experiments

Anaerobic conditions were produced in glass tubes (inner diam. 5 mm) filled with nitrogen, containing 20–50 ind of one species (Sømme and Conradi-Larsen 1977). A moist atmosphere was provided by six drops of distilled water placed on a small, loose pad of tissue paper in each capillary. After flushing with nitrogen gas for two minutes, the capillary was sealed at both ends by melting the glass in a small flame, and when cool they were placed at 0°C for various time intervals. At sampling, each capillary was broken open, the animals removed to a normal atmosphere in a dish, their recovery within 24 h observed at 15°C and the percentage survival calculated.

3. Results

3.1. Supercooling

Stereotydeus villosus: Individual supercooling points from field and acclimated animals ranged from –5.5° to –21.8°C for this species (Fig. 1), with no low group being identified. Field specimens in January and February 1980 had mean supercooling points between –8°C and –10°C, with an individual maximum of –5.9° and a minimum of –18.0°C. Depression of the mean supercooling point was obtained by acclimation both after –5°C/14 d and –5°C/20 d preceded by 8 d at 0°C (significant at $P < 0.001$). Intermediate responses in terms of lowering of the mean supercooling point were observed in three other low temperature treatments (Fig. 1).

Nanorchestes antarcticus: This species exhibited a variation in individual supercooling ability ranging from –3.8° to –30.8°C with both high and low groups being present. The majority of individuals had supercooling points in the LG, while few specimens froze above –15°C (Fig. 1). Low temperature acclimation at 0° and –5°C increased the proportion of the mites in the LG concomitant with a significant depression of their mean supercooling points from ca. –22°C in field collected specimens to –24.6°C after acclimation at 0°C/7 d and –5°C/21 d.

Gamasellus racovitzai: Only the HG was present in this species. The range of individual data differed slightly between adults (–3° to –9.8°C) and deutonymphs (–4.2°

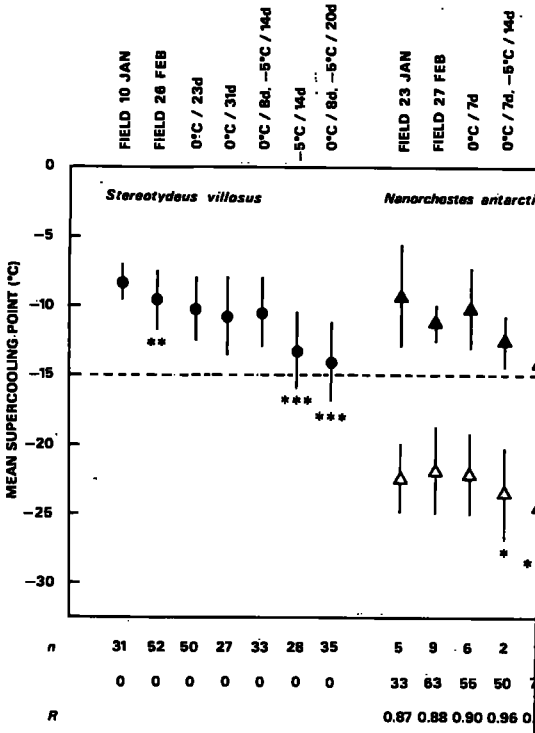

Fig. 1. High group (HG) and low group (LG) mean (± supercooling points of mixed samples of adults and nym the two prostigmatid mites, *Stereotydeus villosus* (● *Nanorchestes antarcticus* (△ ▲), collected from the field and Feb 1980, and others acclimated to 0° and –5°C for v time. *n:* number of specimens in the HG and LG, *R:* LG + LG) ratio with the division between the HG and LG –15°C. Comparisons by t-test of mean supercooling po specimens from both field collections and specimens mated to 0° and –5°C compared to 0°C/23 d are given *villosus*, whilst for *N. antarcticus* comparisons were with d. Significance levels are *: $P<0.05$, **: $P<0.01$ $P<0.001$. Other comparisons were not significant.

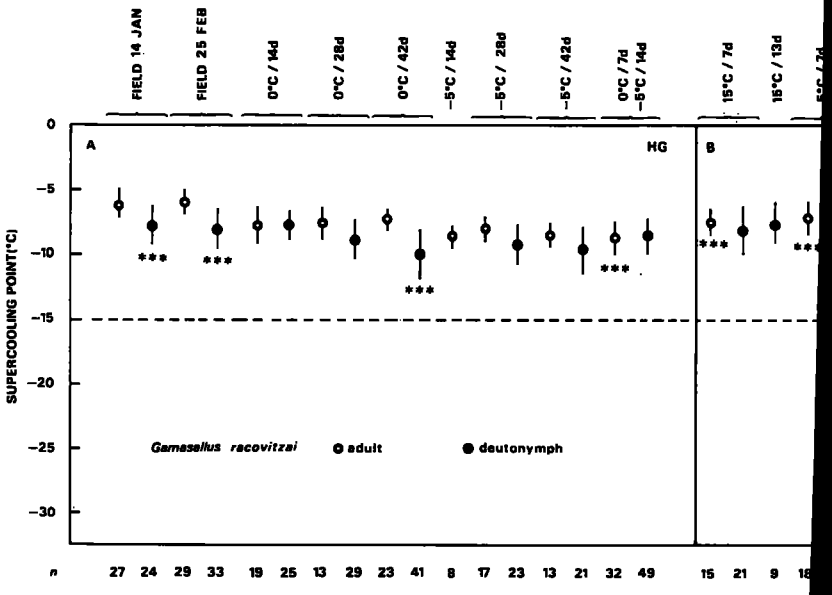

Fig. 2. High group (HG) mean (± SD) supercooling points of adults (○) and deutonymphs (●) of the mesostigmatid mite *Gamasellus racovitzai. n:* number of specimens in the HG. A: specimens acclimated at 0° and –5°C are compared to field animals collected in Jan and Feb 1980. Significance of differences by t-test in mean supercooling points between deutonymphs and adults within each field collection are indicated, and between other treatments and field data for 14 Jan 1980. B: specimens starved at 5° C and 15°C. Significance of differences by t-test in mean supercooling points of both life stages between starved specimens and field collected animals on 25 Feb are indicated. Significance levels are *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$.

14.6°C). Field collected deutonymphs had signifi-
y ($P < 0.001$) lower mean supercooling points than
ts (Fig. 2A), and this was also true for four out of
even experimental treatments. In general, acclima-
to 0°C and –5°C or to a combination of these two
eraures did not lower the mean supercooling point
ther life stage very much. Acclimation at 0°C/42 d produced the lowest mean supercooling point of –10.1°C, comparable to that of –9.7°C produced after acclimation at –5°C/42 d.

An attempt was made to improve the cold hardiness of *G. racovitzai* by experimentally starving the mites at 5° and 15°C. It was hoped that gut clearance would occur at a faster rate at higher acclimation tempera-

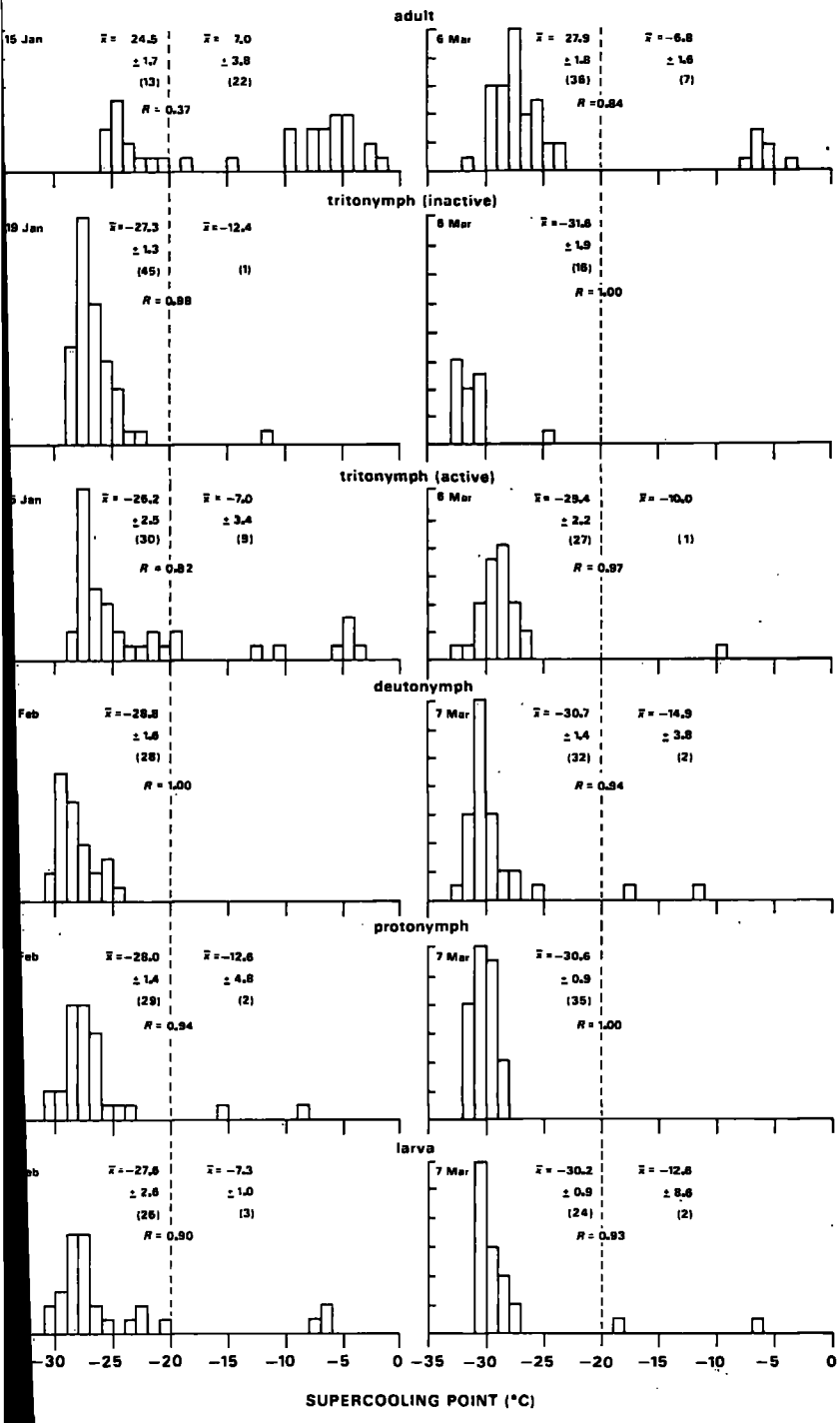

Fig. 3. Supercooling point distribution histograms for all life stages of the cryptostigmatid mite *Alaskozetes antarcticus* collected in the field in Jan and Feb compared to those collected in Mar 1980. $\bar{x}$: mean (± SD), figure in parentheses: number of specimens, *R*: LG/(HG + LG) ratio with the division between the HG and LG being –20°C.

tures, and thus potential nucleators would be voided. The results (Fig. 2B) show only a minor influence of starvation at these higher temperatures, but significant differences were detected in mean supercooling points between starved and field specimens collected on 25 February. This supports the hypothesis that such a predator feeding mainly on a liquid diet from prey will not contain gut nucleators which promote freezing when supercooling. However, prolonged starvation of *G. racovitzai* deutonymphs at low temperatures suggests that a small number of mites can develop a capacity to supercool to below –20°C. Cultures of *G. racovitzai* were transported from the Antarctic to the Univ. of Oslo in Mar 1980, where they were starved for 3–4 months at 0°C. No change in their mean supercooling point occurred after acclimation of these mites initially to 0°C followed by –5°C for 7 d and 14 d compared with the field animals (Fig. 2A), but a small group of mites placed at –5°C for 14 d contained four out of eight individuals whose supercooling points ranged from –27.3° to –30.5°C. At the same time, data collected at Signy Island during the 1980 austral winter showed that between 31% (adult) and 52% (deutonymph) were capable of supercooling to around –24°C. The factors controlling such an increase in cold hardiness are not clear and further experiments are in progress.

Alaskozetes antarcticus: It was possible to study supercooling ability of all the free-living stages, inc ing larva, of this species. Most of the nymphal stag field collections were composed of both active an active mites, the latter being completely immobile pre-moult/ecdysial condition. The distribution of vidual supercooling points was bimodal with HG LG components for adults and most of the juv stages. The HG was present mainly in active mite

Field animals of all stages collected in Jan – Mar exhibited a range of individual supercooling points HG being from –2.0° to –18.9°C, and the LG –20.0° to –33.4°C. Comparison of the samples coll in January and February with those of early Mar for the various life stages of *A. antarcticus* (Fig shows changes in supercooling ability and the pr tion of the total number of individuals in the LG. sideration of the mean supercooling points of LG mals indicates a depression over the 6–8 wk perio all stages (significant at $P<0.001$ in all cases). HG data showed a similar tendency but only for larva active tritonymphs, as the HG were absent from o the field samples for each of the protony deutonymphs and inactive tritonymphs. These ch were accompanied by an increase in the number of viduals comprising the LG of five out of six stages

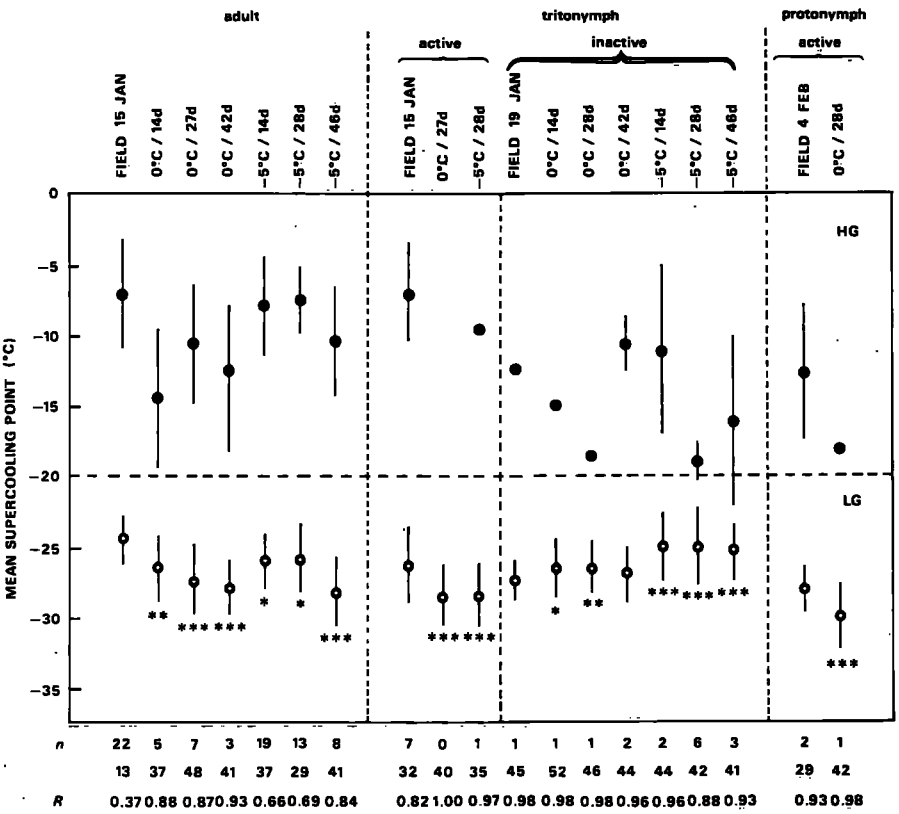

Fig. 4. High group (H and low group (LG, C mean (± SD) superco points of adults, active inactive tritonymphs, protonymphs of the cryptostigmatid mite *Alaskozetes antarcticu* acclimated at 0° and – for various times com to data obtained from specimens collected i and Feb 1980. *n:* nu specimens in the HG LG, *R:* LG/(HG +L ratio.
For each life stage, r t-test comparisons of supercooling points c specimens after low temperature acclima compared to field sp are indicated. Signifi levels are *: $P<0.05$ $P<0.01$, ***: $P<0.0$

ılation. In this respect, the maximum change rred in the case of adults where the proportion of ıals in the LG increased from 37% to 84%. This ests that for *A. antarcticus*, an important stage in cold-hardening process in the field is the cessation eding and the clearance of the gut to reduce the ibility of ice nucleation in the autumn period. In ion, this is accompanied by a lowering of the mean rcooling point as evidenced by the non-feeding, in-e, tritonymphs (Fig. 3).

order to induce experimentally cold-hardening, s, tritonymphs, and deutonymphs were acclimated o temperatures: 0° and –5°C for 14 d to 46 d. Fig. 4 s the results of these experiments, the mean super-ng points of the HG being more variable than the In the case of adults and active tritonymphs, mean supercooling points decreased significantly with at both acclimation temperatures. A similar de-ion of the mean LG supercooling point occurred in nymphs after 0°C/28 d compared with field indi-ls ($P<0.001$). In the case of inactive tritonymphs, ver, mean supercooling points were significantly r after low temperature exposure compared to specimens (Fig. 4). In general, mean HG super-g points of acclimated mites were lower than of field animals, but due to the small number of ates and large variations, the means are not sig-ntly different. Undoubtably, the important com-t of the population for survival at low tempera-will be the unfed LG. Under field conditions, it is that natural acclimatization to these and lower ratures would occur over a longer time period.

evels of supercooling: When supercooling points ed for the various life stages of the four species of during the austral summer 1980 at Signy Island mpared (Tab. 1), considerable variation is seen in G values as expected, but the LG values differed by only 6.4°C between species. The highest LG mean supercooling point was for *N. antarcticus* and the lowest for the active deutonymphs of *A. antarcticus*. HG mites were absent for both active and inactive deutonymphs of *A. antarcticus*, and LG mites were not found in either life stage of *G. racovitzai* or in *S. villosus*. In stages where both HG and LG occurred, 82–100% of the individuals sampled were in the LG except for adult *A. antarcticus* (37% in LG). Further work on the factors which determine the bimodal separation of supercooling points in these species is required to link with current observations on their food and feeding habits before final conclusions can be drawn.

3.2. Sugar and polyol content

Stereotydeus villosus: Glucose and glycerol were found in both the field and acclimated animals, glucose being high and glycerol low in concentration for field mites (Tab. 2). During acclimation at 0° and –5°C, the glycerol concentration increased compared to field levels and reached its maximum after 0°C/7 d followed by –5°C/21 d.

Nanorchestes antarcticus: Only glycerol was recorded in field samples of this species (Tab. 2). Experimental acclimation revealed glucose and mannitol in addition to glycerol, the latter increasing in concentration by up to four times after exposure to –5°C.

Gamasellus racovitzai: Glucose and glycerol were detected in extracts of this mite, the former being found in the highest concentration (Tab 3). Field specimens of both adults and tritonymphs possess very small amounts of glycerol with deutonymphs having three times the level of glucose found in field adults. Glycerol increased in concentration during acclimation at –5°C in both adults and deutonymphs, but a similar trend was not

Comparison of mean high group (HG) and low group (LG) supercooling points of field-collected mites at Signy Island an and Feb 1980. Data for active and inactive individuals of *Alaskozetes antarcticus* are given together with the ratio R = in LG/(numbers in LG + HG), + : not found.

	Stage	R	Date	Mean (± SD) supercooling point (°C)	
				HG	LG
llus racovitzai	adult	0	14 jan	– 6.1±1.2	+
	deutonymph	0	14 Jan	– 7.7±1.5	+
etes antarcticus	adult, active	0.37	15 Feb	– 7.1±3.8	–24.5±1.7
	tritonymph, inactive	0.98	19 Jan	–12.4	–27.3±1.4
	tritonymph, active	0.82	15 Feb	– 7.0±3.4	–26.2±2.6
	deutonymph, inactive	1.00	4 Feb	+	–27.7±2.6
	deutonymph, active	1.00	4 Feb	+	–28.8±1.6
	protonymph, active	0.93	4 Feb	–12.6±4.8	–28.1±1.5
	larva, active	0.89	4 Feb	– 7.3±1.0	–27.6±2.7
leus villosus	adults + nymphs	0	10 Jan	– 8.3±1.3	+
estes antarcticus	adults + nymphs	0.87	23 Jan	– 9.2±3.7	–22.4+2.5

Tab. 2. Concentrations of sugars and polyols in samples of two prostigmate mites acclimated to low temperatures and for animals at Signy Island during Feb 1980. All samples were mixtures of adults and juveniles. n = number of samples.

Species	Temperature acclimation/ Date of field collection	n	Mean (±SD) concentrations (μg mg^{-1} fresh weight)		
			Glucose	Mannitol	Glycero
Stereotydeus villosus	0°C/28 d	2	0.6±0.8	–	6.8±1.4
	–5°C/14 d	3	3.5±0.2	–	6.1±1.
	0°C/7 d, –5°C/21 d	2	2.2±0.5	–	10.1±0.4
	26 Feb	2	14.1±2.3	–	0.8±0.
Nanorchestes antarcticus	0°C/7 d	3	3.2±0.9	0.6±1.0	3.9±0.
	0°C/7 d, –5°C/14 d	3	2.1±0.7	1.5±1.1	16.7±2.(
	26 Feb	4	–	–	3.5±2.(

Tab. 3. Concentrations of sugars and polyols in samples of *Gamasellus racovitzai* acclimated to low temperatures and fo animals at Signy Island during Feb 1980. n = number of samples.

Stage	Temperature acclimation/ Date of field collection	n	Mean (±SD) concentratio (μg mg^{-1} freash weight)	
			Glucose	Glycer
Adult	0°C/7 d	1	2.4	0.5
	–5°C/14 d	3	1.7±1.0	2.8±1
	–5°C/28 d	4	2.6±1.3	3.0±1
Deutonymph	0°C/7 d	2	9.6±10.0	2.2±0
	0°C/28 d	2	1.9±0.7	0.9±0
	0°C/42 d	4	2.2±0.6	0.8±(
	–5°C/14 d	3	9.3±2.7	5.9±1
	–5 C/28 d	5	9.0±6.9	7.9±1
Adult	25 Feb	3	5.8±1.3	0.7±0
Deutonymph	25 Feb	3	17.6±0.8	0.6±0

Tab. 4. Concentrations of sugars and polyols in samples of *Alaskozetes antarcticus* acclimated to low temperatures and f animals at Signy Island during Feb and Mar 1980. n = number of samples.

Stage	Temperature acclimation/ Date of field collection	n	Mean (± SD) concentrations (μg mg^{-1} fresh weight)		
			Glucose	Ribitol	Glyce
Adult	0°C/14 d	3	4.3±0.6	2.1±0.5	5.0±(
	0°C/28 d	3	4.1±2.0	3.0±0.8	6.4±2
	0°C/42 d	3	3.6±1.2	4.6±0.7	8.2±
	–5°C/14 d	1	7.2	1.4	8.6
	–5°C/28 d	3	3.9±0.9	1.8±0.3	9.7±
	–5°C/46 d	4	2.2±0.7	2.6±1.7	8.8±
Inactive tritonymph	0°C/14 d	3	4.3±0.8	6.7±1.1	2.1±
	0°C/28 d	3	2.3±1.1	6.7±1.2	4.1±
	0°C/42 d	3	1.6±0.8	4.1±0.5	4.4±
	–5°C/14 d	3	3.7±0.4	6.6±0.6	3.4±
	–5°C/28 d	3	5.3±1.8	6.6±1.4	5.8±
	–5°C/46 d	2	2.0±0.1	6.1±4.2	11.7±
Active tritonymph	0°C/28 d	2	7.6±1.5	2.7±0.6	4.6±
	–5°C/28 d	2	8.5±1.1	2.6±0.6	10.8±
Adult	6 Mar	3	5.6±1.0	3.5±0.8	5.9±
Active tritonymph	6 Mar	2	7.2±6.5	4.9±5.2	6.0±
Deutonymph	6 Mar	3	8.3±0.7	5.2±0.9	6.6±
Deutonymph	7 Feb	4	12.2±5.6	1.8±0.6	3.0±
Protonymph	6 Mar	3	4.8±2.5	7.0±2.0	4.6±
Larva	8 Feb	2	9.7±4.1	0.8±0.4	2.4±

5. Chill-coma temperatures of field-collected mites at Signy Island and of *A. antarcticus* and *G. racovitzai* acclimated at –5°C 0 to 14 d. n = number of animals.

ies	Stage	Treatment	n	Chill-coma (°C) mean	range
ozetes antatcticus	adult	field	14	–4.6	–3.5 to –7.0
	adult	–5°C/10 d	15	–4.5	–
sellus racovitzai	adult	field	9	–7.6	–6.5 to –8.0
	deutonymph	field	14	–7.0	–6.0 to –8.0
	adult	–5°C/14 d	6	–7.3	–6.5 to –8.0
	deutonymph	–5°C/14 d	11	–6.8	–6.0 to –8.0
tydeus villosus	mixed	field	8	–7.6	–4.5 to –9.5
rchestes antarcticus	mixed	field	6	–8.9	–8.0 to –11.0

ved at 0°C. Similarly, higher levels of glucose were ured in both stages after 14 d and 28 d at –5°C after acclimation at 0°C.

ozetes antarcticus: Ribitol was identified in addi- o glycerol and glucose in all samples of this species 4). Glycerol concentrations differed slightly be- the four life stages in field samples collected in nd Mar 1980, as did ribitol, which may have been seasonal effects. In adults and in both active and ve tritonymphs, glycerol concentrations increased time during acclimation at 0° and –5°C. The nt of ribitol increased slightly in adult *A. ant- s* but did not change markedly in the active and ve tritonymphs with low temperature exposure. cose appeared to change inversely with glycerol ntration especially in the adults and inactive mphs at 0° and –5°C. Of particular interest was e in glucose concentration in inactive tritonymphs -5°C/46 d, which was associated with the highest ol synthesis. Conversely, the highest concentra- glucose was recorded in field deutonymphs at the ime as a small amount of glycerol (7 Feb 1980). It cluded that the three substances identified from s of *Alaskozetes* changed during low temperature ation, and that reduced glucose levels were as- d with glycerol synthesis.

compounds: In extracts of field samples for the ite species, the mass spectral data revealed the ce of straight chain, unsaturated hydrocarbon unds. These may be lipid storage products or leton components and work is in progress to e the significance of such compounds in the ogy of these arthropods.

ll-coma temperature

or field collected specimens of the four Acari are given in Tab. 5, together with those for *A.* cus and *G. racovitzai* acclimated to low temper- There were no differences apparent between and deutonymphs of the latter species. Low temperature acclimation did not produce observable changes in chill-coma temperatures of the two species examined. *N. antarcticus* had the lowest chill-coma temperature of all the field animals, whilst *A. antarcticus* had the highest chill-coma temperature. In the latter species, however, difficulty was experienced in determining the chill-coma temperature due to its usual sluggish movements. *S. villosus* stored at –5°C for 14 d walked with irregular, shaking movements, and although all specimens moved their legs between 0° and –2.5°C, none were able to walk. It is likely that desiccation or other adverse conditions affected these fragile mites during storage at –5°C.

3.4. Anoxia

The mortalities of two species of mites during 28 d in nitrogen are shown in Fig. 5. Adults and tritonymphs of *A. antarcticus*, with a maximum mortality of 40% after 28 d, generally showed a lower mortality than adults and deutonymphs of *G. racovitzai*. There were no dif-

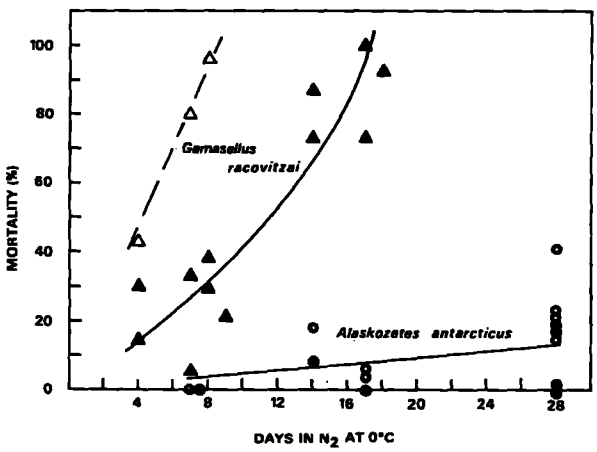

Fig. 5. Mortality of adults (△) and deutonymphs (▲) of *Gamasellus racovitzai* compared to adults (●) and tritonymphs (○) of *Alaskozetes antarcticus* when stored in nitrogen at 0°C for various times. Each point represents a separate sample of 20–40 specimens.

ferences in survival between adults and tritonymphs of *A. antarcticus*. *G. racovitzai* deutonymphs survived about twice as long as adults in nitrogen (16 d as compared to 8 d for 100% mortality).

4. Discussion

The contrast in supercooling ability shown by the two prostigmate mites, *Stereotydeus villosus* and *Nanorchestes antarcticus*, may reflect major differences in their life styles and ecology. The absence of a LG in the supercooling point distribution of *S. villosus* (Fig. 1) and the locomotory activity of *N. antarcticus* down to –8.0°C (Tab. 5) suggests that the latter species is better adapted to cold conditions than the former. However, this striking difference in their supercooling ability may have been brought about by their feeding on material containing differing proportions of potential nucleators. This has been demonstrated experimentally for the collembolan *Cryptopygus antarcticus* feeding on moss turf homogenate and purified green algae, both obtained from a single field site (Sømme and Block 1982). Glycerol was detected in field samples of both prostigmates in the present study, it increased in concentration during low temperature acclimation (Tab. 2) in association with a lowered mean supercooling point. The only other data for cold hardiness of Antarctic Prostigmata are from Vestfjella, Dronning Maud Land (Sømme 1978a), where supercooling points between –20°C and –30°C were recorded for *Eupodes tottanfjella* Strandtmann and two *Nanorchestes* spp. This range corresponds to the LG observed for *N. antarcticus* at Signy Island.

The supercooling characteristics of both adult and deutonymph *G. racovitzai* remained unchanged in the region of –6° to –10°C even after low temperature acclimation (Fig. 2A), and although relatively high concentrations of glucose were found, particularly in the deutonymph samples (Tab. 3), neither this nor glycerol showed a pattern of change. The high supercooling points may be attributed to nucleating agents in the gut, either obtained from its mainly liquid food as a predator of other micro-arthropods and invertebrates, or being synthesized for this purpose. Starvation did not improve the supercooling ability of *G. racovitzai*, although deutonymphs were marginally better than adults (Fig. 2B). The question arises of how this species overwinters at Signy Island, as both stages are found throughout the year, albeit sometimes in small numbers (Goddard 1979). Possibly as a predator, gut content nucleation may not be so frequent during winter as compared to herbivorous and detritivorous species, and in summer *G. racovitzai* is active to ca. –7.3°C (Tab. 5). On the other hand, if anaerobic conditions occur in its overwintering sites for more than 16 d, survival even of *G. racovitzai* deutonymphs is likely to be severely affected (Fig. 5).

Alaskozetes antarcticus, with the lowest LG supercooling points recorded (Tab. 1) of all the sp examined, was the most cold hardy arthropod at Island. Field data on supercooling points were parable to those for cultured *A. antarcticus* (Youn Block 1980) and for populations at other Antarcti (Sømme in press). In the Signy Island observa there was a significant depression of the mean s cooling point of LG individuals associated wit clearance during autumn (Fig. 3). This was supp by experimentally induced depression of the supercooling point of adults, tritonymphs deutonymphs (Fig. 4). Ribitol was found in additi glucose and glycerol in extracts of *A. antarcticus* the concentrations of the latter two compounds cha inversely with time at 0°C and –5°C. The effect c hydration on glycerol synthesis in field-fresh *A. a ticus* was not examined at Signy Island, as had done for cultured animals (Young and Block 1980) likely that desiccation occurring under field cond will exert a considerable influence on the time cou cold-hardening in this species. *A. antarcticus* is als to tolerate an anaerobic environment for upwa 28 d (Fig. 5) with low mortality, which clearly c tutes another facet of its overwintering strategy.

The occurrence of straight chain hydrocarbons four Acari species but not in the Collembola in gated during this study suggests a basic bioche difference between the two micro-arthropod grou in the ways in which they have adapted their phys to polar conditions. The significance of this, to with seasonal changes in polyol and lipid conc tions, is presently under study at Signy Island.

In conclusion, it can be seen that at low temper different survival abilities are exhibited durin short, Antarctic summer by various members terrestrial mite fauna in the maritime Antarcti present evidence, this variability does not seem directly related to taxonomic groups, life stages o of life. As the data presented here are for summe of cold hardiness, as exemplified by supercooling and levels of potential cryoprotective substanc trapolation to other seasons must be attempte caution. However, due to the severe environ conditions (mean annual air temperature over 29 –3.7°C at Signy Island) compared with sub-A areas (eg. South Georgia whose mean annual a perature over 68 yr was 1.8°C), it is thought t levels of cold hardiness measured in this study a resentative of much of the year. It is significant the species examined are freezing susceptible a upon extensive supercooling to avoid ice form their tissues. It is suggested from the present d only *N. antarcticus* and *A. antarcticus* may sur thermal conditions in their habitats during the winter. It is possible that the predator, *G. ra* being more active than the other species, may to more favourable micro-sites in such cold pe

at survival occurs mainly in protected microhabitats ch as beneath accumulated snow. During over-ntering, *G. racovitzai* and possibly *S. villosus,* may ve the ability to lower their mean supercooling points levels comparable to the low groups of other species. ch cold survival mechanisms, however, must be ;wed in the perspective of the species' life cycle lock 1980), and the need for such information is now ›riority.

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ferences

ley, N. T. J. 1959. Statistical methods in biology. – English Univ. Press, London.
ist, J. G. and Edwards, J. S. 1979. Mechanisms of freezing tolerance in an Antarctic midge, *Belgica antarctica.* – Physiol. Ent. 4: 1–5.
:k, W. 1980. Survival strategies in polar terrestrial arthropods. – Biol. J. Linn. Soc. 14: 29–38.
– Young, S. R., Conradi-Larsen, E.-M. and Sømme, L. 1978. Cold tolerance of two Antarctic terrestrial arthropods. – Experientia 34: 1166–1167.
Goddard, D. G. 1979. Biological observations on the free-living mites of Signy Island in the maritime Antarctic. – Bull. Br. Antarct. Surv. No. 49: 181–205.
Sokal, R. R. and Rohlf, F. J. 1969. Biometry. – Freeman, San Francisco.
Sømme, L. 1964. Effects of glycerol on cold-hardiness in insects. – Can. J. Zool. 42: 87–101.
– 1976. Cold-hardiness of winter active Collembola. – Norw. J. Ent. 23: 149–150.
– 1978a. Cold-hardiness of *Cryptopygus antarcticus* (Collembola) from Bouvetøya. – Oikos 31: 94–97.
– 1978b. Notes on the cold-hardiness of prostigmate mits from Vestfjella, Dronning Maud Land. – Norw. J. Ent. 25: 51–55.
– 1981. Supercooling in two Antarctic terrestrial arthropods from Bouvetøya. – Norsk Polarinst. Skr. 175: 29–35.
– and Block, W. 1982. Cold hardiness of Collembola at Signy Island, maritime Antarctic. – Oikos 38: 168–176.
– and Conradi-Larsen, E. M. 1977. Anaerobiosis in overwintering collembolans and oribatid mites from windswept mountain ridges. – Oikos 29: 127–132.
Sweeley, C. C., Bentley, R. Makita, M. and Wells, W. W. 1963. Gas-liquid chromatography of trimethylsilyl derivatives of sugars and related substances. – J. Amer. chem. Soc. 85: 2497–2507.
Tilbrook, P. J. 1973. Terrestrial arthropod ecology at Signy Island, South Orkney Islands. – Ph.D. thesis, Univ. of London.
Young, S. R. and Block, W. 1980. Experimental studies on the cold tolerance of *Alaskozetes antarcticus.* – J. Insect Physiol. 26: 189–200.

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Cold hardiness of Collembola at Signy Island, maritime Antarctic

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The cold hardiness of two Antarctic species of Collembola, *Cryptopygus antarc*
Willem and *Parisotoma octooculata* (Willem), was studied in field fresh, starved
low temperature acclimated specimens at Signy Island, in the South Orkney Isla
Supercooling points of both species clearly fell in a high group (HG) and a low g
(LG) with a division at ca. –15°C. Field fresh specimens mainly had HG supercoo
points, while starvation at 5° and 15°C greatly increased the number of LG anir
Further evidence of the relation between supercooling and feeding status
obtained in *C. antarcticus*. Specimens fed moss turf homogenate almost enti
returned to HG supercooling points, indicating the presence of efficient nucleato
this substrate. In specimens fed purified green algae a high proportion of LG su
cooling points was retained, which suggests a lack of nucleators in this kind of fo
Increased ability of LG specimens to supercool was demonstrated in *C. antarc*
following acclimation at –5°C, and in *P. octooculata* at 0°C. In *C. antarcticu*
increase in concentrations of cryoprotective substances took place at –5°C concu
with the lowering of the mean supercooling point. The main substances of the
ticomponent cryoprotectant system of this species were trehalose, mannitol
glycerol.
Chill-coma temperatures of specimens collected in the field differed in *C. antarc*
and *P. octooculata* with mean values of –8.3° and –4.8°C, respectively. *P. octooc*
was less resistant to anaerobic conditions than *C. antarcticus*. All specimens o
former species were killed within 8 d in nitrogen at 0°C, while ca. 30% of *C.*
arcticus specimens survived after 28 d.

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Холодовое оцепенение двух Антарктических видов коллембол *Cryptopygus*
arcticus Willem и *Parisotoma octooculata* (Willem) исследовали на живо
ных, только что собранных в природных местообитаниях, у голодных и ак
лимированных к низким температурам животных на о-ве Сайни, Южно-Оркне
кие о-ва. Точки переохлаждения у обоих видов заметно снижаются у груп
высокими температурами (HG) и с низкими температурами (LG) с разницей
–15°C. Животные, взятые из природных биотопов, большей частью имеют
ки переохлаждения группы HG, причем, голодание при 5 и 15°C существе
повышает количество животных в группе LG. Получены новые доказательс
взаимосвязи между переохлаждением и пищевым статусом у *C. antarcticu*
Особи, которых кормили гомогенатом моховой дернины, почти полностью
нулись к точкам переохлаждения группы HG, что свидетельствует о нали
активных кристаллогенных веществ в этом субстрате. У особей, которых
мили очищенными культурами зеленых водорослей, сохраняется высокий п
цент животных с температурой переохлаждения группы LG, что говорит о
сутствии кристаллогенных веществ в этой пище. Повышенная способность
вотных из группы LG к переохлаждению показана на примере *C. antarcti*
акклимированных к –5°C и у *P. octooculata* при 0°C. У *C. antarcticus*
–5°C повышение концентрации криозащитных соединений наблюдалось нара
понижением средней точки переохлаждения. Основные агенты многокомпон
ной криозащитной системы этого вида – трегалоза, маннитол, глицерол.
Температуры холодовой комы у особей, собранных в полевых условиях, р
чаются у представителей *C. antarcticus* и *P. octooculata*, со средними
чениями –8,3° и –4,8° соответственно. *P. octooculata* менее выносливы
аэробных условиях, чем *C. antarcticus*. Все особи первого вида погиба
течение 8 дней в атмосфере азота при 0°C, а у *C. antarcticus* почти
особей оставались живыми через 28 дней.

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ntroduction

he climate becomes more severe, both at high al-
les and in polar regions, there is a tendency for
embola to play an increasingly dominant role in the
ct fauna. About twenty species of this order are
wn from the maritime and continental Antarctic
ssitt 1967), which correspond to 85% of all
living insects in these zones. Because of their ability
urvive under conditions which most other insects
ot tolerate, the mechanisms of adaptation to low
peratures in Collembola are of particular interest.
om a review of available literature (Sømme 1981a)
pears that no freezing tolerant species of alpine,
ic and Antarctic Collembola are known. All species
ir investigated depend on supercooling to survive
temperatures. As with other insects (Salt 1966,
), the ability to supercool in Collembola is prob-
affected by their feeding status. In *Tetracanthella greni* Linnaniemi from Norwegian mountains in-
ed supercooling ability in preparation for low
r temperatures is a two-step process (Sømme and
adi-Larsen 1977a) consisting of the elimination of
ontent and the accumulation of glycerol in the body
. A relation between supercooling and the con-
ation of glycerol and other cryoprotective sub-
es have been demonstrated for a number of other
ts (e.g. Salt 1961, Sømme 1964, Ring 1977, Han-
978).

ta on the cold-tolerance of Antarctic species of
mbola, however, are scarce. Early studies were
rned with lethal temperatures, and did not
ine the mechanism of survival. Thus, Pryor (1962)
that the lethal cold temperatures of adult *Isotoma adi* Carpenter were between –50° and –60°C, and
al specimens survived –16°C for one month. Ac-
g to Janetschek (1967), specimens of *Gomephalus hodgsoni* Carpenter survived tempera-
from –20° to –28°C, and for the same species
nons (1971) found lower lethal temperatures
en –11° and –23°C. In the latter study, super-
g at –11°C was demonstrated, since contact with
sulted in rapid freezing and death.

liminary studies on *Cryptopygus antarcticus* Wil-
om Signy Island (Block et al. 1978) and from
tøya (Sømme 1978, 1981b) showed that starved
ens of this species may have mean supercooling
in the range of –25° to –27°C. In the case of fed
ls, individual supercooling points ranged from –3°
°C reflecting the possible presence of effective ice
tors in the gut content (Block et al. 1978). Mean
ooling points were slightly lowered by acclima-
t –10°C (Sømme 1981b). No glycerol or other
otective substances were detected on paper
atograms during these studies.

ddition to supercooling, other factors are impor-
the overwintering success of Collembola and
nsects. Activity at sub-zero temperatures may be of particular importance to soil arthropods seeking appropriate microhabitats when cold weather occurs. Mean chill-coma temperatures in the range –4° to –9°C have been recorded in various species of Collembola, including *C. antarcticus* from Bouvetøya (Sømme 1976, 1978, 1979). Furthermore, species living in exposed habitats are frequently enclosed by ice and may experience an oxygen deficiency when the ground freezes. Survival during prolonged periods of anoxia has been demonstrated in alpine species of Collembola from Norway (Sømme and Conradi-Larsen 1977b) and Austria (Sømme 1979).

During the Antarctic summer, Collembola and other terrestrial arthropods are exposed to highly variable field temperatures. At Signy Island, temperatures around or below 0°C may be encountered for extended periods even in January and February, which are the warmest months of the year (Walton 1977). During periods of sunshine the temperature in the microhabitats of the Collembola used for the present study may exceed 20°C. In warm weather, the animals are active and presumably feeding.

Since fed specimens of *C. antarcticus* are killed by freezing at relatively high sub-zero temperatures (Block et al. 1978), an increase in the ability to supercool must occur during the autumn. The purpose of the present investigation was to study in detail how this increase in cold tolerance is accomplished. Since the study was carried out during the austral summer, an experimental approach was adopted. By acclimation at constant low temperatures in the laboratory, the animals were exposed to temperature conditions similar to those of the late summer and autumn in the field. Because of the importance of chill-coma and anoxia for winter survival, experiments on these factors were included. Two isotomid species were investigated: *C. antarcticus* and *Parisotoma octooculata* (Willem). A parallel study was conducted on four species of Acari from the same localities (Block and Sømme 1982).

2. Methods

2.1. Field collection and culture

The animals used in the present study were collected during January–March 1980 at Signy Island (60°43'S, 45°38'W) in the South Orkney Islands. Experimental work was performed at the British Antarctic Survey's station on Signy Island. Alcohol extracts of field-collected Collembola and specimens from acclimation experiments were transported to the Univ. of Oslo for chemical analysis.

Due to the lack of organic soils, terrestrial arthropods are easily sampled from Antarctic habitats. Collembola were collected for the present study by shaking specimens from plant material into a dish, or by picking them directly from turned stones by suction with a microaspirator. No heat extraction was applied.

2.2. Temperature acclimation, starvation and feeding

For temperature acclimation experiments the Collembola were sorted into single species groups, and 15–100 individuals were placed with or without food in 15-ml glass vials, the tops of which were covered by nylon mesh gauze to prevent escape. The vials were placed in 250-ml glass jars with screw lids, in which a saturated atmosphere was maintained from moist filter paper at the bottom. The jars were stored in controlled (±1°C) temperature cabinets at –5°, 0° and 5°C, and specimens were removed at different time intervals for measurements of supercooling points and extraction for chemical analysis.

Two kinds of experimental conditions were applied to test the effect of starvation on supercooling ability. In some experiments, 50–100 Collembola were stored in each glass vial. To avoid desiccation the vials were partly filled with distilled water on which the Collembola floated. No harmful effects of this treatment were observed. However, during bulk storage of this kind some specimens may have been feeding on excrement, or on exuviae shed by some of the animals during the experimental period. To reduce the risk of reconsumption of potential nucleators during starvation, new experiments were designed, in which the Collembola were stored in separate vials. In each vial a drop of water was provided in which the excrement pellets sank. The temperature during starvation was 5° or 15°C (±1°C), and animals were removed after various time intervals.

To test the effect of feeding on supercooling in starved animals, specimens of *C. antarcticus* were presented with two kinds of food in the laboratory. In the first experiment, moss turf (*Polytrichum – Chorisodontium*) was homogenized in water and filtered through a Millipore filter (Burn pers. comm.). The filter was cut into small squares and given to the Collembola in glass vials, ten specimens in each. Following storage at 5°C for 3 d, the supercooling points of the animals were measured. In the second experiment, the Collembola were fed on green algae (a mixture of *Stichococcus* and *Monodus* spp.) isolated from shoots of the moss turf species. The algae were cultured in Bold's basal medium (Burn pers. comm.), and the suspension was filtered through a Millipore filter which was cut into similar sized pieces and presented to the Collembola in the same way as the moss turf homogenate. Glass vials with pieces of clean moist Millipore filter served as controls in both experiments.

2.3. Supercooling points

Supercooling points, in the sense of Salt (1966), were measured with copper-constantan thermocouples connected to a single-point, battery-operated Grant temperature recorder (for details see Block and Sømme 1982). Collembolans were attached to the thermocouple by a thin layer of petroleum jelly (Sømme and Conradi-Larsen 1977a). The supercooling points o or six specimens could be measured simultaneous attaching them to the same thermocouple. To slo rate of cooling, the thermocouple was placed inside or two glass tubes, closed by rubber stoppers, thr which the thermocouple wire was run. The tubes lowered into a thermos flask containing a cooling ture made from $CaCl_26H_2O$ and coarse, granular s The rate of cooling was manually controlled by th tent to which the tubes were lowered into the co mixture, attempting to maintain a decrease of 1° t min^{-1}. Supercooling points were read from the rec chart as the point of origin of the small, but signifi temperature rise that accompanied the emission tent heat from the insects during spontaneous free A detailed description of these methods is give Block and Sømme (1982).

2.4. Cryoprotective substances

Extracts for chemical analysis of sugars and po were prepared by homogenizing samples of the Co bola in 70% ethanol. Each sample consisted of a number of specimens with a total fresh weight of mg. Three or four parallel samples were taken for field collection and experimental treatment. Pri analysis each sample was centrifuged, the precip washed and recentrifuged, and the supernatants bined and evaporated.

A trimethylsilyl reagent with pyridine was us prepare derivates of sugars and polyol compoun the sample extracts according to Laine and Sw (1971). Identification was made on a Varian com gas chromatograph – mass spectrometer (MAT, men), using a SE-40 (LKB) column, connect on-line and off-line computer systems (Jellum 1976). The gas chromatography peaks were ma against comprehensive library files of known spectra. Final verification of the structures was do comparison of mass spectral data and retention with those obtained from authentic compounds. titative analyses were carried out by gas chro graphy, using a Carlo Erba Fractovap Model 21 glycerol and a Hewlett-packard Model 5880 A f other compounds.

2.5. Chill-coma temperatures

Chill-coma temperatures were determined fo fresh specimens of *C. antarcticus* and *P. octoocul* well as for specimens of *C. antarcticus* acclima –5°C for 14 d. The collembolans, up to five at were observed during gradual cooling in a p chamber on a microscope stage (Sømme 1976 chill-coma temperature was defined as the temp at which walking activities ceased, although movements of legs and antennae could still be ob Further details are given by Block and Sømme (

Anoxia

est survival under anaerobic conditions, 25–50 col-
olans of the same species were placed in 5-mm-
eter glass tubes, which were flushed with nitrogen
and sealed at both ends by heating (Sømme and
radi-Larsen 1977b). After storage at 0°C for var-
time intervals the tubes were broken, and the per-
age survival calculated (for details see Block and
me 1982).

esults

Supercooling in C. antarcticus

. *Feeding status*

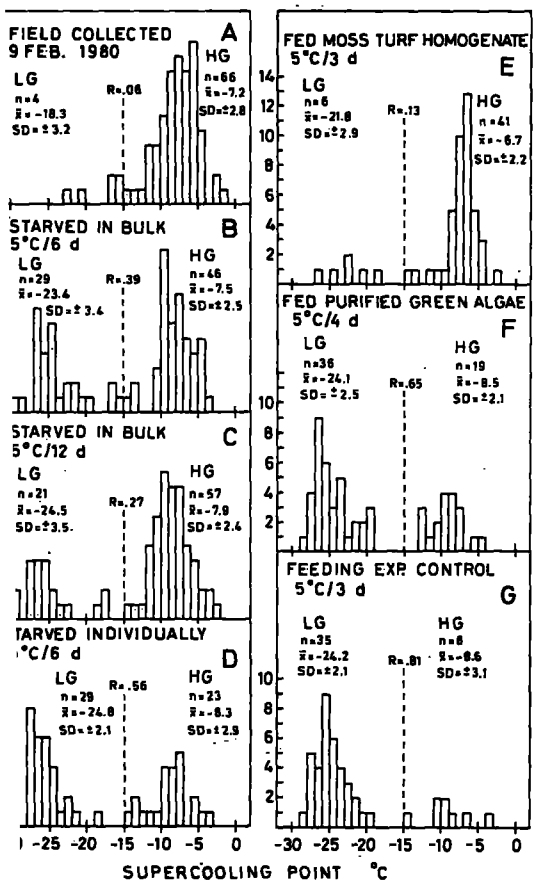
t specimens of *C. antarcticus* collected from the field had supercooling points in the range of –5° to –10°C (Figs 1A, 2). In all samples, however, a small proportion of the animals had much lower supercooling points. This bimodal distribution of supercooling points was seen most clearly in samples collected on 15 Jan and 28 Feb 1980. Since a division appeared at ca. –15°C, values above this temperature were treated as high group (HG) supercooling points and values below this temperature as low group (LG) supercooling points. Mean values of the LG supercooling points were in the range –18° to –23°C (Fig. 2).

To test if the bimodal distribution of the supercooling points reflects differences in feeding status, specimens of *C. antarcticus* collected on 9 Feb (Fig. 1A) were starved in vials individually and in groups. While the LG/(LG + HG) ratio for field fresh specimens was only 0.06, more than one third of those starved in bulk at 5°C for 6 d had LG supercooling points (Fig. 1B). Although a similar tendency was found after 12 d of starvation at 5°C (Fig. 1C), no increase in the proportion of LG specimens occurred. During this experiment a large number of animals shed their cuticle, and it was thought that both exuviae and excrement were eaten under these conditions. With a large number of specimens in each tube there was a high probability for such feeding to take place. A much larger LG/(LG + HG) ratio was obtained when specimens, starved in bulk at 5°C for 12 d, were transferred individually to vials and starved for a further 6 d at the same temperature (Fig. 1D). In this case, more than half the specimens had supercooling points in the LG.

These experiments show that the ratio of LG/(LG + HG) supercooling points is greatly influenced by feeding status. To determine if the reverse change would occur, starved animals were fed on two types of food. As in the previous experiment, the Collembola were at first starved at 5°C for 12 d in bulk and then individually for 6 d. After this treatment the animals appeared to be very hungry, because feeding was observed immediately. Indirectly, evidence of feeding was observed from the disappearance of the substrate, and the production of numerous pellets of the same colour as the substrate.

From Fig. 1E it is clear that most specimens fed on filtered moss turf homogenate returned to HG supercooling points. In those fed on purified green algal cultures (Fig. 1F), however, the LG/(LG + HG) ratio was almost as large as in the control group (Fig. 1G). These results demonstrate the presence of efficient nucleators in the moss turf homogenate, causing a reduced ability to supercool in specimens fed on this substrate. The green algae, on the other hand, appeared to be free from nucleators, suggesting that some kinds of food may be consumed without a reduction in supercooling ability.

As a control, some specimens were kept on filter paper for the same time period as those fed on the food substrates. In these Collembola (Fig. 1G), the LG/(LG + HG) ratio was higher than in specimens from the



Supercooling point distribution histograms for *Cryp-antarcticus*. A. Field collected specimens. B, C. Speci-arved in bulk at 5°C. D. Specimens starved individually 5 d, following starvation in bulk at 5°C/12 d. E, F. Fed rf homogenate and purified green algae, respectively, g starvation as in D. G. Feeding experiment control. w group supercooling points, HG = high group super-points, R = LG/(LG + HG) ratio. n = number of ns; mean (±SD) is presented for each LG and HG.

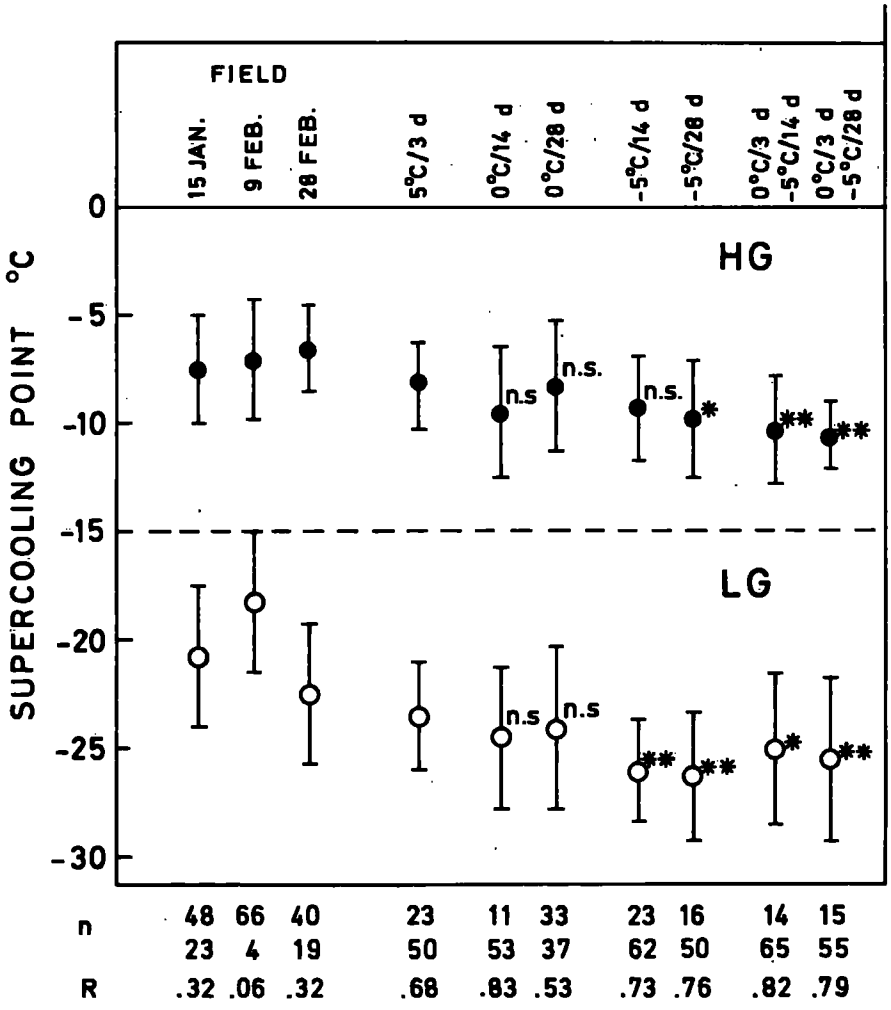


Fig. 2. High group (HG) and low group (LG) m (±SD) supercooling po of *Cryptopygus antarcti* collected in the field a acclimated at 5°, 0° an –5°C for various time intervals. n = number specimens in HG and = LG/(LG + HG) rat Comparisons by t-test mean supercooling poi 5°C/3 d specimens with and –5°C acclimated specimens are shown. difference not significa = significant at 5% lev = significant at 1% lev

starvation experiment, indicating that the gut contents of additional specimens were voided in the control group.

3.1.2. Temperature acclimation

Since starvation at 5°C resulted in a higher proportion of LG animals (Fig. 1B–D), all specimens for temperature acclimation experiments were kept initially for 3 d at this temperature. Following this treatment, about two thirds of the Collembola had supercooling points below –15°C, with a mean value of –23.5°C. The results of acclimation for varying time periods at 0° and –5°C are presented in Fig. 2.

Only a slight increase in the supercooling ability was found after acclimation at 0°C. Specimens stored at this temperature for 14 and 28 d had mean LG supercooling points of –24.6° and –24.1°C, respectively. These values are not significantly different from the mean values for specimens kept at 5°C for 3 d.

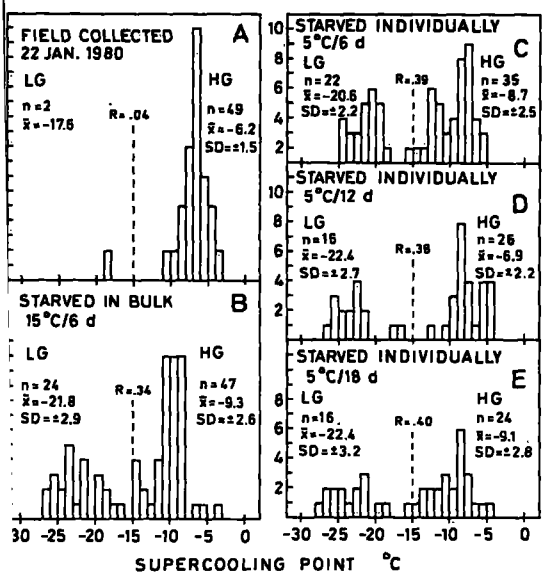
At –5°C, acclimation was more effective, resulting in LG mean supercooling points of ca. –26°C after 14 and 28 d, which values are significantly lower than tho specimens stored at 5°C for 3 d. Similar result slightly higher LG mean supercooling points obtained in a second series of experiments, for the animals were kept initially for 3 d at 0°C acclimation at –5°C for 14 and 28 d.

Specimens kept at 5°C for 3 d had a HG mean cooling point of –8.0°C. Compared with this val climation at –5°C also had an effect on HG a (Fig. 2). While 14 or 28 d at 0°C did not alter the supercooling points, 28 d at –5°C resulted in a cant lowering. Lowest HG mean supercooling were found in specimens kept at 0°C for 3 d p acclimation at –5°C. In these animals, the HG values after 14 and 28 D at –5°C were –10. –10.6°C, respectively.

3.2. Supercooling in P. octooculata

3.2.1. Feeding status

In field fresh specimens of *P. octooculata*, super



3. Supercooling point distribution histograms for *ioma octooculata*. A. Field collected specimens. B. nens starved in bulk at 15°C. C, D, E. Specimens starved dually for 6, 12 and 18 d, respectively, at 5°C. For further nation, see Fig. 1.

; were almost exclusively above –10°C (Figs 3A, ower supercooling points, however, appeared g starvation. In one group of animals, stored in t 15°C, increased ability to supercool was found in ird of them after 6 d without access to food (Fig. Other specimens were kept individually in vials at nd after 6 d more than one third had low super- g points (Fig. 3C). As in *C. antarcticus*, the divi- etween HG and LG animals appeared to be at ca. . Further starvation at 5°C for both 12 and 18 d 3D, E) did not increase the proportion of speci- with low supercooling points. The reason for this fully understood, but it may have been due to eeding on excrement. Several specimens shed uticle during the experiment, but differences in ooling points between moulted and non-moulted ens were not observed.

Temperature acclimation

oculata appeared to be a fragile species, which ficult to maintain in the laboratory. At –5°C al- ll specimens died within a few days. Acclimation however, resulted in a lowering of both HG and ercooling points (Fig. 4). Thus, compared with esh animals collected on 29 Jan 1980, a signifi- crease in HG supercooling points took place. ens with LG supercooling points appeared after 0°C, although the LG/(LG + HG) ratio was higher ratio was found in specimens starved for 5°C prior to acclimation at 0°C, but their mean LG supercooling points did not differ from those of starved animals at 5° and 15°C (Fig. 3). Lower LG supercooling points, with a mean of –26.0°C were found in those acclimated for 15 d at 0°C, indicating that this species is also able to lower its supercooling point below the level obtained when the gut is evacuated.

3.3. Sugar and polyol content

An irregular pattern of sugar and polyols was found in samples of *C. antarcticus* subjected to different kinds of acclimation (Tab. 1). Glucose, fructose and trehalose

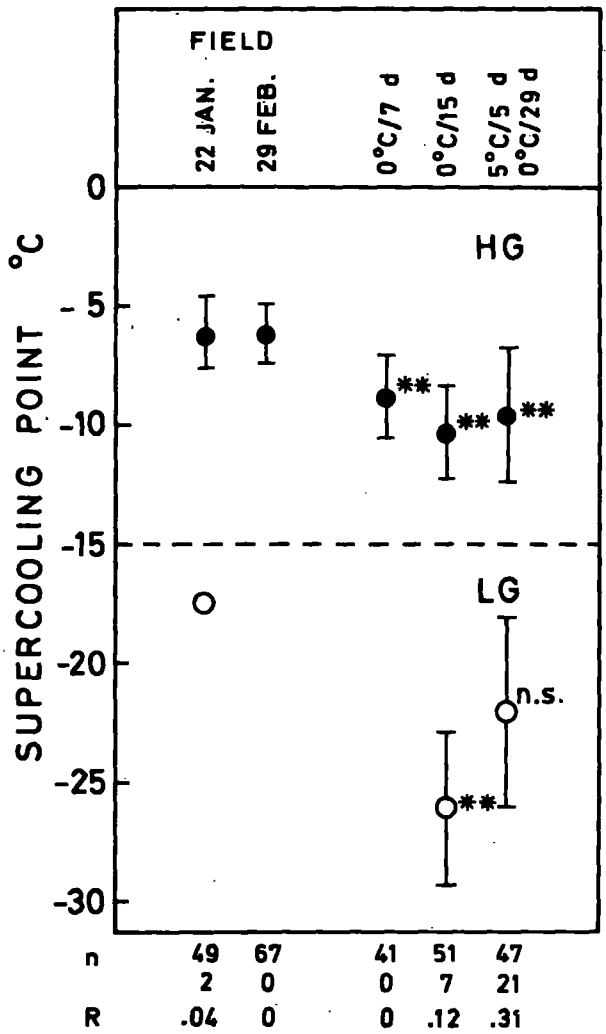


Fig. 4. High group (HG) and low group (LG) mean (±SD) supercooling points of *Parisotoma octooculata* collected in the field and acclimated at 0°C for various time intervals. n = number of specimens in HG and LG, R = LG/(LG + HG) ratio. Comparison by t-test of HG field specimens from 22 January with 0°C acclimated specimens are shown. LG specimens acclimated at 0°C are compared with LG specimens starved at 15°C (see Fig. 3). n.s. = difference not significant, ** = significant at 1% level.

were present in all samples. Of polyols, glycerol was found in all samples, mannitol in most of them, while low concentrations of sorbitol appeared in only a few samples.

Lowest concentrations of most of the substances were found in specimens collected in the field on 31 Jan 1980 and acclimated for 3 d at 5°C in the laboratory. Compared with these samples there was a general tendency for an increase in fructose and trehalose content in specimens acclimated at 0° and –5°C. Smaller variations were observed in the concentration of glucose. Sorbitol and mannitol were not present in specimens acclimated at 5°C, but mannitol appeared in collembolans kept for 14 d at 0°C, and increased in concentration with storage time at –5°C, and in specimens acclimated at 0° and –5°C. Glycerol was found in the 5°C specimens, but the highest concentration was in specimens kept for 28 d at –5°C, with or without prior acclimation for 3 d at 0°C.

The concentrations of sugars and polyols in field fresh specimens collected on 28 Feb 1980 were similar to those of 5°C specimens, with the exception of higher fructose and glycerol contents. The high value for glycerol may have been caused by a previous period of sub-zero temperatures in the field. It is not understood, however, why this was not accompanied by higher concentrations of trehalose and mannitol, which would have been expected from the acclimation experiments.

In spite of the variability among samples, there was a clear tendency for most substances to increase in concentration at –5°C. Highest levels of fructose, trehalose, mannitol and glycerol were found in specimens kept for 28 d at this temperature. Such increases suggest a bined, cryoprotective effect of these substances.

In *P. octooculata*, the concentrations of sugars polyols were too low to be of any cryoprotective portance (Tab. 2). Since those kept at –5°C i laboratory died, only samples from specimens mated at 0°C were analysed. Glycerol was prese traces only, and sorbitol in very small amounts. concentrations of glucose, fructose and treh showed considerable variation. While specimens mated for 7 or 14 d at 0°C had high trehalose co only small amounts were found after 28 d. Field specimens collected on 29 Feb 1980 contained trac trehalose only, while glucose and fructose contents higher than in the animals acclimated at 0°C.

3.4. Chill-coma temperatures

Chill-coma temperatures of *C. antarcticus* an *octooculata* are presented in Tab. 3. For both sp field fresh specimens were used, in addition to s mens of *C. antarcticus* acclimated at –5°C for There was a significant difference between the coma temperatures of the two species, with a me –4.8°C for *P. octooculata* and –8.3°C for *C. antarc* Acclimation at –5°C apparently had no effect on coma temperatures of *C. antarcticus*.

The reaction to decreasing temperatures above coma was similar in both species. From 0° to –3°C were quite active, walking normally and relatively Specimens of *P. octooculata* were observed to ju

Tab. 1. Concentrations of sugars and polyols in samples of *Cryptopygus antarcticus* acclimated at 5°, 0° and –5°C and fo animals at Signy Island. n = number of samples.

Temperature acclimation	n	Mean (±SD) concentrations (μg mg^{-1} fresh weight)					
		Glucose	Fructose	Trehalose	Sorbitol	Mannitol	Glyce
5°C/3 d	3	2.3±0.8	2.8±2.6	traces	–	–	11.1±
0°C/14 d	4	3.5±1.9	7.4±1.6	6.1±3.4	0.2±0.2	11.3±7.6	3.5±
0°C/28 d	4	1.2±0.4	0.4±0.2	0.2±0.1	–	–	14.0±
–5°C/14 d	6	3.2±1.6	4.9±1.5	4.7±3.0	–	0.9±0.8	7.5±
–5°C/28 d	3	1.5±0.2	4.9±0.5	6.6±0.6	0.2±0.1	13.7±1.0	28.8±
0°C/3 d and –5°C/14 d	4	2.6±0.7	4.8±1.3	1.9±0.9	–	4.0±4.9	7.9±
0°C/3 d and –5°C/28 d	4	3.2±0.7	6.1±1.1	8.7±2.3	traces	7.8±4.3	71.0±
Field 28 Feb 1980	4	3.8±1.1	6.1±1.0	traces	–	–	42.9±

Tab. 2. Concentrations of sugars and polyols in samples of *Parisotoma octooculata* acclimated at 0°C and for field animals Island. n = number of samples.

Temperature acclimation	n	Mean (±SD) concentrations (μg mg^{-1} fresh weight)				
		Glucose	Fructose	Trehalose	Sorbitol	G
0°C/7 d	2	3.4	2.9	7.3	0.1	
0°C/14 d	3	2.9±1.0	1.6±1.0	13.1±1.0	0.7±0.5	
0°C/28 d	4	2.5±0.6	0.9±0.5	1.1±1.2	0.2±0.1	0
Field 28 Feb 1980	4	7.5±3.2	9.9±7.2	traces	0.2±0.1	

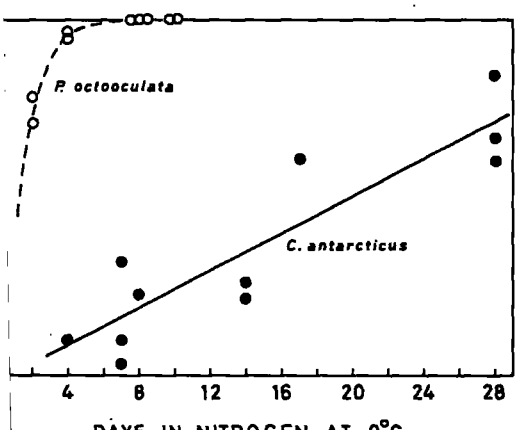
3. Chill-coma temperatures of field collected *C. antarcticus* and *P. octooculata*, and of *C. antarcticus* acclimated at –5°C for veeks. n = number of animals.

es	Treatment	n	Chill-coma temperature (°C) Mean	Range
opygus antarcticus	Field	18	–8.3	–6.0 to –10.0
	–5°C/14 d	19	–8.2	–7.5 to –9.5
ɔtoma octooculata	Field	12	–4.8	–4.0 to –5.5

experimental chamber. Below –3°C both species ed at decreasingly slower speeds, until they stopped letely in chill-coma. All *P. octooculata* and some *ntarcticus* reached their supercooling points at eratures slightly below chill-coma, and were ved to freeze with a sudden jerk of their body. mens of *C. antarcticus* climbed the vertical walls of bservation chamber at temperatures down to –6°C. e specimens that fell on their backs were able to round to an upright position even at –7° to –8°C. wing chill-coma, specimens of *C. antarcticus* were ble to make slow movements of legs and antennae ' to –10°C, and *P. octooculata* at –6° to –7°C. m these experiments it is concluded that both s are able to perform a variety of activities even at ero temperatures. Although the animals were cooled by several degrees, movements of body and dages did not result in instantaneous freezing.

noxia

ortality of *C. antarcticus* and *P. octooculata* kept creasing time intervals in nitrogen at 0°C is illus- in Fig. 5. High mortalities were recorded in *P. ulata* after 2 d, and no specimens survived 8 or



Mortality of *Cryptopygus antarcticus* and *Parisotoma ata* stored in nitrogen at 0°C for increasing time inter- ch point represents a separate sample consisting of ecimens.

10 d of anoxia. Better survival was found in *C. antarcticus*, where mortality after 7 or 8 d was low, and a high proportion of the specimens survived 28 d of anoxia.

4. Discussion

From the present study, it appears that the cold hardiness of *C. antarcticus* and *P. octooculata* is based on a two-step process. In the first place, residues of food have to be eliminated from the gut, as demonstrated in starvation and feeding experiments. Secondly, the ability to supercool may be further increased by temperature acclimation, probably due to the accumulation of cryoprotective substances, as demonstrated in *C. antarcticus*.

A relation between gut content and low supercooling ability has also been established in *Tetracanthella wahlgreni* from mountain ridges in Norway (Sømme and Conradi-Larsen 1977a). The effect of gut content on supercooling is thought to be due to the presence of highly efficient nucleators in the food (Salt 1966, 1968).

The increases observed in the LG/(LG + HG) ratios during the present study show that gut evacuation in itself has an effect on supercooling in *C. antarcticus* and *P. octooculata*. Feeding moss turf homogenate to starved specimens of *C. antarcticus*, on the other hand, greatly decreased the LG/(LG + HG) ratio. The homogenate was prepared from coarse moss turf, in which ice nucleators are very likely to be present. It is of particular interest that the proportion of LG supercooling points did not decrease by feeding purified green algae to specimens of *C. antarcticus*. During the process of cultivation the algae apparently have been separated from potential nucleators, yielding a type of food that may be consumed without disturbing the supercooling ability of the collembolans. From an ecological point of view, a nucleator free diet, if available in nature, would confer a distinct advantage on the animal. During the spring most species of terrestrial arthropods are exposed to warm days, during which feeding takes place, alternating with cold nights, during which freezing may occur due to gut nucleators. Diel temperature fluctuations like these are particularly pronounced in the Arctic and the Antarctic and at high

altitudes on temperate and tropical mountains. Thus, the conflict between maintenance of the individual's supercooling ability in order to survive and the need to feed during such periods is always present in freezing susceptible species.

A relation between supercooling and the concentrations of cryoprotective substances, in particular, glycerol, has been demonstrated in a number of freezing susceptible insect species from different orders. As shown by Ring (1977) in the birch engraver *Scolytes ratzeburgi* Jans, a multicomponent cryoprotective system has been evolved in some species. The presence of cryoprotective substances in Collembola has been demonstrated only in *T. wahlgreni* (Sømme 1981a). In this species, the optimum temperature for glycerol accumulation was ca. –5°C. The results of the present study show that glycerol may also be the main cryoprotective substance in *C. antarcticus*. In addition, mannitol and trehalose, and possibly fructose, may accumulate at low temperatures, forming a multicomponent cryoprotective system with glycerol. The accumulation of these substances was most pronounced in specimens stored at –5°C (Tab. 1), while a decrease in the concentration of fructose, trehalose and mannitol occurred at 0°C.

Similar systems were not detected in *P. octooculata*, although field animals had relatively high levels of glucose and fructose. As in *C. antarcticus*, the concentration of trehalose decreased during 14 to 28 d storage at 0°C. Although higher concentrations of cryoprotective substances were expected at –5°C, acclimation experiments at this temperature were not accomplished due to the high mortality of the animals. Further experiments are required for a better understanding of the cryoprotective systems of both *P. octooculata* and *C. antarcticus*.

Acknowledgements – We thank the British Antarctic Survey for the provision of transport, living and research facilities during the 1979–80 Antarctic field season. Travel to and from the Antarctic for L. Sømme was financed by a travel grant from the Norwegian Research Council for Science and the Humanities. We are grateful to K. Richard for assistance at Signy Island, and to Mrs U. Gehrken, who undertook analyses of polyols and sugars at the Inst. of Clinical Biochemistry, Rikshospitalet, Univ. of Oslo.

References

Block, W. and Sømme, L. 1982. Cold hardiness of terr
mites at Signy Island, maritime Antarctic. – Oiko
157–167.
– , Young, S., Conradi-Larsen, E.-M. and Sømme, L.
Cold tolerance of two Antarctic terrestrial arthrop
Experientia 34: 1166–1167.
Fitzsimons, J. M. 1971. Temperature and three species o
arctic arthropods. – Pacific Ins. Monogr. 25: 127–1
Gressitt, J. L. 1967. Entomology of Antarctica, Introduct
Antarct. Res. Ser. 10: 1–33.
Hansen, T. 1978. On seasonal changes in the glycerol c
in pupae of two different populations of *Apatele ps*
Eesti NSV Teaduste Akad., Biol. 27: 301–305.
Janetschek, H. 1967. Arthropod ecology of South Vi
Land. – Antarct. Res. Ser. 10: 205–293.
Jellum, E., Storseth, P., Alexander, J., Helland, P., Stok
and Teig, E. 1976. Application of glass capillary-c
gas chromatography-mass spectrometry to the stud
human diseases. – J. Chromatogr. 126: 487–493.
Laine, R. A. and Sweeley, C. C. 1971. Analysis of trim
silyl O-methyloximes of carbohydrates by combine
liquid chromatography-mass spectrometry. –
Biochem. 43: 533–538.
Pryor, M. E. 1962. Some environmental features of H
station, Antarctica, with special reference to so
thropods. – Pacific Ins. 4: 681–728.
Ring, R. A. 1977. Cold-hardiness of the bark beetle *Sc*
ratzeburgi Jans. (Col., Scolytidae). – Norw. J. En
125–136.
Salt, R. W. 1961. Principles of insect cold-hardiness. –
Rev. Ent. 6: 55–74.
– 1966. Factors influencing nucleation in supercool
sects. – Can. J. Zool. 44: 117–133.
– 1968. Location and quantitative aspects of ice nuclea
insects. – Can. J. Zool. 46: 329–333.
Sømme, L. 1964. Effects of glycerol on cold-hardiness
sects. – Can. J. Zool. 42: 87–101.
– 1976. Cold hardiness of winter active Collembola. –
J. Ent. 25: 51–55.
– 1978. Cold hardiness of *Cryptopygus antarcticus* (C
bola) from Bouvetøya. – Oikos 31: 94–97.
– 1979. Overwintering ecology of alpine Collembo
oribatid mites from the Austrian Alps. – Ecol. E
175–180.
– 1981a. Cold tolerance of alpine, Arctic and Antarct
lembola and mites. – Cryobiology. 18: 212–220.
– 1981b. Supercooling in two Antarctic terrestrial
pods from Bouvetøya. – Norsk Polarinst. Skr. 175: 2
– and Conradi-Larsen, E.-M. 1977a. Cold hardiness
lembolans and oribatid mites from windswept m
ridges. – Oikos 29: 118–126.
– and Conradi-Larsen, E.-M. 1977b. Anaerobiosis i
wintering collembolans and oribatid mites from wi
mountain ridges. – Oikos 29: 127–132.
Walton, D. W. H. 1977. Radiation and soil tempe
1972–74: Signy Island terrestrial reference sites
Antarct. Survey Data 1: 1–12.

THE SIGNY ISLAND TERRESTRIAL REFERENCE SITES: XIV. POPULATION STUDIES ON THE COLLEMBOLA

By WILLIAM BLOCK

ABSTRACT. Field data for Collembola extracted from a series of 25 monthly samples of a moss turf and a moss carpet at Signy Island have been analysed to provide information on species composition, population density and biomass, size-class structure and field distribution. Three species were found: *Friesea grisea* (Schäffer), *Parisotoma octooculata* (Willem) and *Cryptopygus antarcticus* Willem, with the latter species being numerically dominant throughout the study at both sites. Population densities for all Collembola averaged 49 928 (moss turf) and 9 913 (moss carpet) individuals m^{-2}, of which *C. antarcticus* comprised 99% and almost 100%, respectively. Mean biomass equivalents were 688 and 154 mg live weight m^{-2} (250 and 56 mg dry weight m^{-2}). Size-class analyses for *C. antarcticus* showed an almost stable distribution in the moss turf, whereas summer growth was evident in the moss-carpet population. A similar degree of aggregation was observed for *C. antarcticus* at the two sites. Between 78% and 88% of the Collembola were located in the zone from the moss surface down to 6 cm depth in the turf, whilst 96–99% occurred in the same zone of the moss carpet. These findings are discussed in relation to the micro-climate and structure of the two habitats, and compared with data available for other Antarctic sites, the Arctic and temperate studies.

EVIOUS research on the Collembola of the Antarctic region has been concerned with onomy and systematics (e.g. Wise, 1967, 1971), distributional ecology (e.g. Janetschek, 57*a*; Tilbrook, 1967*a*, *b*), field biology (e.g. Strong, 1967; Janetschek, 1970; Tilbrook, 1970) l physiology (e.g. Marsh, 1970; Block and Tilbrook, 1975, 1978; Block 1979). Detailed estigations of the population dynamics of single species are few: on *Isotoma klovstadi* rpenter at Hallett Station, North Victoria Land (Pryor, 1962), on *Gomphiocephalus hodgsoni* rpenter at Cape Crozier (Ross Island) and Mount England, South Victoria Land (Janetschek, 57*b*), on *G. hodgsoni* at Cape Bird, Ross Island (Peterson, 1971), and on *Cryptopygus arcticus* Willem at Signy Island, South Orkney Islands (Tilbrook, 1977). The present paper vides information on the dynamics of the populations of two species of Collembola in two ophyte communities at Signy Island, maritime Antarctic. One of these, *C. antarcticus*, is both largest and the most abundant arthropod in these communities. This paper is a further tribution to the Signy Island terrestrial reference sites (SIRS) ecosystem programme, which is ed at an analysis of the structure and function of such systems in the maritime Antarctic. The ly sites have been described (Tilbrook, 1973*a*), and data are available on seasonal changes in population numbers of protozoans (Smith, 1973), tardigrades and rotifers (Jennings, 1979), ıatodes (Caldwell, 1981*a*, *b*; Maslen, 1981) and the mites or Acari (Goddard, 1979). Davis 31) has made an initial synthesis of the results and the information available, which suggests the Collembola play a relatively minor role in the turnover of material and energy in such ımunities. This is in contrast to their relatively high population density and biomass.

he aims of the present work were:

1. To determine the species composition and population structure of the Collembola at the two sites.
2. To study seasonal variations in their numbers.
3. To examine the distribution of the animals in the peat profile.
4. To obtain information on their life cycles.

METHODS

ly sites and sampling

RS 1 and 2, situated on Gourlay Peninsula in the south-east of Signy Island, are a *trichum–Chorisodontium* moss turf (site 1) and a *Calliergon–Calliergidium–Drepanocladus* ı carpet (site 2). The sites, each containing 100 m^2 of sample strata, have been studied for

over 10 years (Tilbrook, 1973*a*), and Goddard (1979) has reported on the methods for mic arthropod sampling.

Twenty-four vegetation and peat cores, collected at random within the 1 m wide sample str of each site, comprised a sample. Samples were collected from both sites at approximately week intervals between 20 December 1971 and 7 December 1973 (25 occasions in all). Ea core was 6 cm in depth from the moss surface and 0.002 m^2 in surface area. It was horizontally into two 3-cm-deep sections, and the arthropod fauna extracted separately fr each section. In addition, on at least two occasions in 1973, the peat of each site was sampled the underlying bedrock, the cores being similarly subdivided into 3-cm-deep sections. T maximum depths of peat found from these samples were 24 cm (SIRS 1) and 18 cm (SIRS 2).

Sampling was undertaken using a hand corer in summer and using a corer with tungs carbide cutting teeth driven by an electric drill powered from a portable generator, when moss was frozen in winter. Up to 1 m of snow and ice was present on both sites at times dur winter (Block, 1980*a*), and this was removed before sampling.

Faunal extraction and analysis

Micro-arthropods (Acari and Collembola) were recovered from individual 3-cm core secti in a high-gradient canister extractor (Macfadyen, 1961). The sections, contained in core ri from the field, had their cut surfaces sealed with parafilm and were thawed at 2°–5°C for 2 before extraction. The extraction regime, using increasing temperature and desiccation gradie over 6 d, has been described by Goddard (1979). The fauna was extracted into a 50% solutio picric acid in the canisters, the extracts were filtered through 30-μm-mesh Nybolt gauze transferred to 70% ethanol and 5% glycerol solution for analysis. Arthropods were identified sorted under ×25 to ×50 magnification using a grid. The Collembola, separated into spec were individually measured in terms of body length for assignment to size class (Tilbrook Block, 1972; Block and Tilbrook, 1975) and to derive their live and dry weights.

In the United Kingdom, data for derivation of the relationship of individual live weight to weight were obtained using a LM 500 micro-balance at 5°C from specimens transported from Signy Island.

Environmental monitoring

The following parameters were monitored during the field study: hourly moss and temperatures recorded at the moss surface (0 cm), at −1.5, −4.5, −7.5 and −10.5 cm below surface, and at 1.8 m in the air above the surface, together with incident solar radiation. T data were recorded by a battery-driven Grant Model D recorder, which was housed in a field near SIRS 1 and 2. Details of the instrument and the thermistor probes have been give Walton (1977). Throughout the winter, frequent measurements of snow depth were made a positions on each site using permanent snow poles.

RESULTS

Species composition

Only three species of Collembola were found during the 2-year study: *Cryptop antarcticus* Willem, *Friesea grisea* (Schäffer) and *Parisotoma octooculata* (Willem). The referred to by their generic names throughout this paper. These species represent *c.* 75% o total collembolan fauna of Signy Island (Tilbrook, 1973*b*). *Parisotoma* was recorded only i moss turf (SIRS 1) and only during summer. *Cryptopygus* was present in all the sam collected from both sites in each month of the year, whereas *Friesea* was more common i moss turf than the moss carpet and was found only in six samples from the moss carpet d the summer of 1972.

pulation density

The mean numbers of *Cryptopygus* estimated from monthly samples of the moss turf (SIRS 1) ıged from a minimum of 19 585 (September 1973) to a maximum of 98 520 (February 1972) lividuals m^{-2} (Fig. 1a), whereas in the moss carpet the population density was more variable, ıging from a minimum of 40 (July 1973) to a maximum of 64 690 (December 1971) lividuals m^{-2} (Fig. 1b). In the moss turf, smaller populations of *Cryptopygus* were found ring winter in August 1972 and September 1973 with relatively higher numbers throughout summer (December–March) of both years. In the moss carpet, lower population densities ıurred in June and September 1972, and in July 1973. Similarly, higher numbers of *ptopygus* were recorded in the summers of both years. Thus, a pattern suggestive of seasonal ınges in overall population numbers can be discerned (Fig. 1a and b), which is probably ıted to the life cycle of this species under maritime Antarctic conditions.

Cryptopygus was more abundant in the relatively drier moss turf than in the carpet nmunity, its mean annual population being five times (1972) and 11 times (1973) larger in the ner site (Table I). On an annual basis also, there were major differences in population density ween years on both sites (Table I). Populations of *Cryptopygus* were just over half the size RS 1) and just over one-quarter of the size (SIRS 2) in 1973 of those recorded in the previous r. Throughout the 2-year study, there was a decline in population numbers of *Cryptopygus* ı time, which can be expressed as:

$$y = 78.37 - 2.21x \ (r^2 = 0.69; P < 0.001) \text{ for SIRS 1,}$$
$$y = 33.63 - 10.18x \ (r^2 = 0.38; P < 0.001) \text{ for SIRS 2,}$$

re $n = 25$ in both cases, y is the population density (number $\times 10^3$ m^{-2}) and x is the time nths). Recent observations suggest that the population densities are much lower (personal ımunication from R. G. Booth).

riesea occurred in both communities but in much lower population densities than *ptopygus* (Fig. 2). The maximum population noted was 2 335 (December 1971) and the imum 20 (September 1973) individuals m^{-2} in the moss turf, whilst, in the moss carpet, ıbers ranged from 20 to 585 individuals m^{-2} during January–May 1972. Annual mean ılation densities for *Friesea* (Table I) show that it was almost five times more abundant at S 1 than at SIRS 2 in 1972, but it was not recorded at all on SIRS 2 in 1973. Again, as with *ptopygus*, a reduction (by 50%) in mean annual population density occurred between the two y years in the moss turf. The overall decline in population with time at SIRS 1 calculated for tudy period may be expressed as:

$$y = 0.992 - 0.037x.$$

ı population decline occurred in both *Cryptopygus* and *Friesea*, it may be that a common ır affected the populations of both species.

ıe numbers of *Parisotoma* in the moss turf were very small. A total of 18 specimens was d, mostly during the summer months; it was not recorded in the samples from the moss et. Clearly, bryophyte-dominated communities do not afford suitable habitats for this es, and it is found in more open situations such as fellfields on Signy Island (W. Block, blished).

terms of the entire Collembola community of the two sites, total numbers varied from 3 093) 957 individuals m^{-2} during the study period (Table I) with mean values around 49 928 s turf) and 9 913 (moss carpet) individuals m^{-2}. In all cases, fewer Collembola were found : moss carpet than in the turf.

lation biomass

ing published live-weight data for the five size classes of *Cryptopygus* (Block and Tilbrook,), estimates of the population biomass for this species were calculated. Monthly population

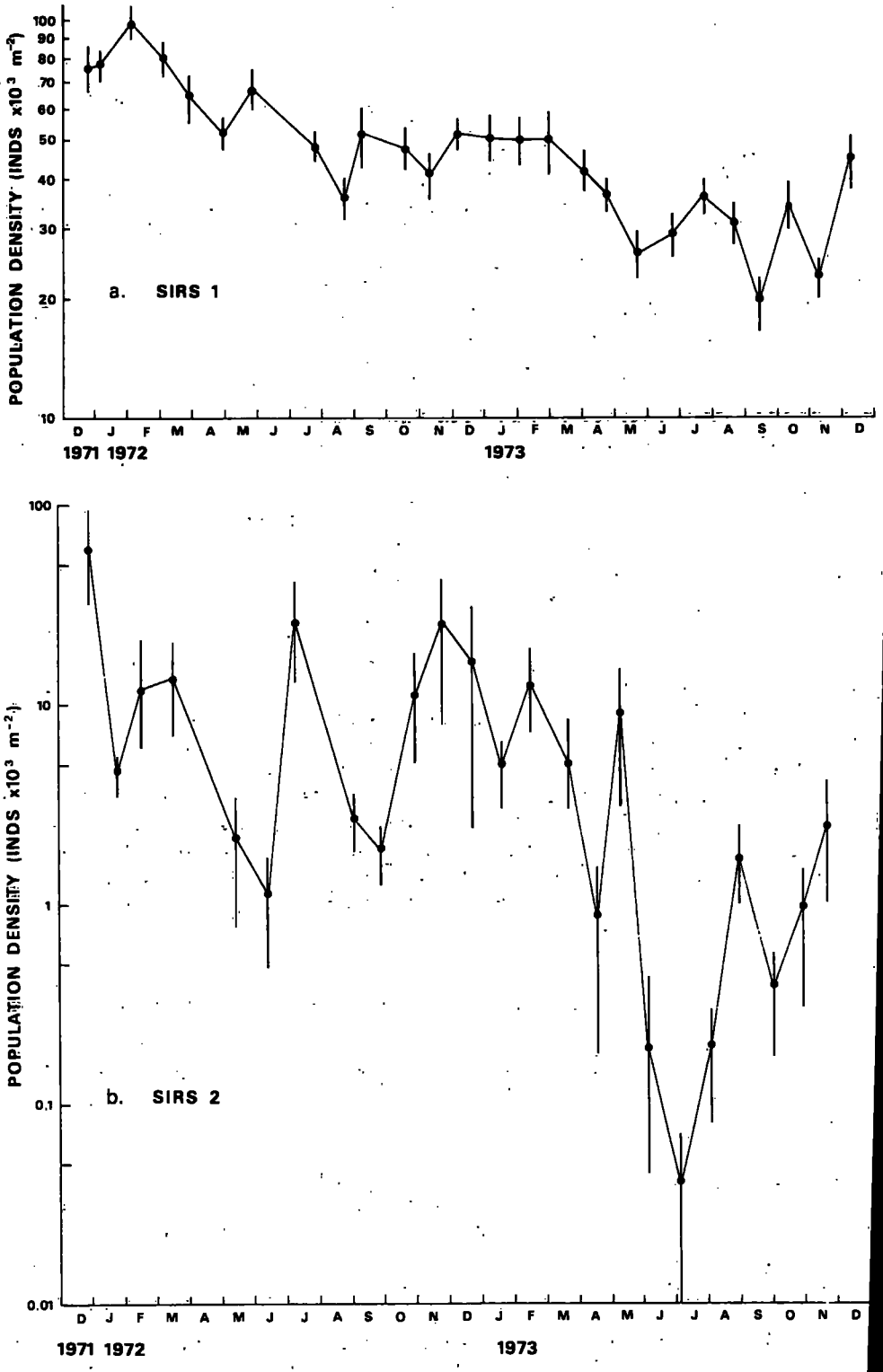
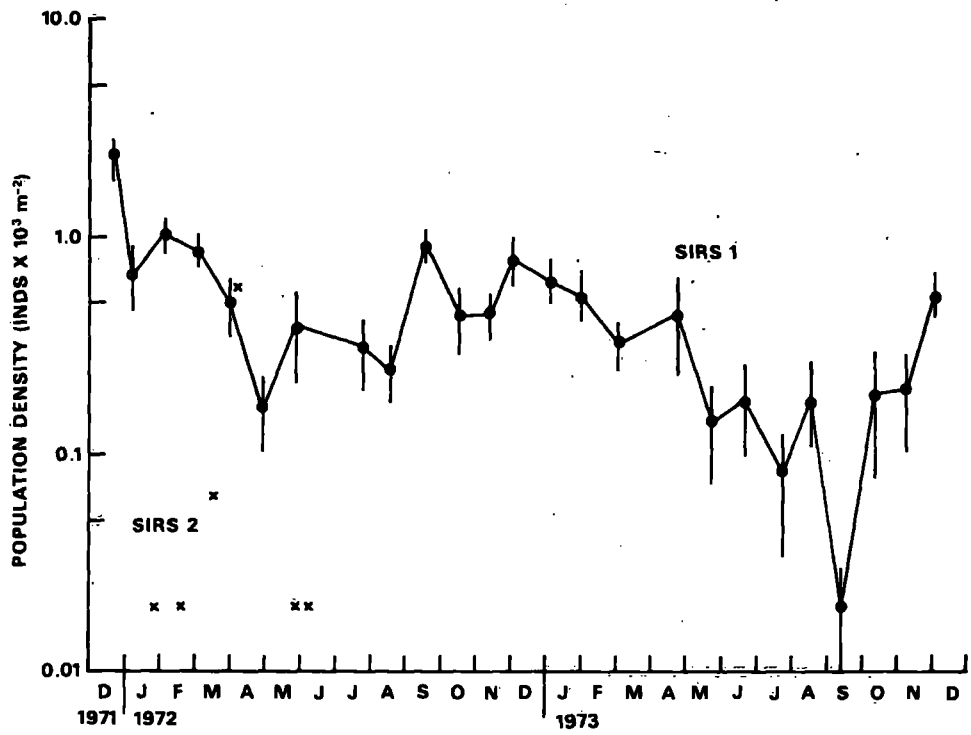


Fig. 1. Seasonal changes in population density of *Cryptopygus antarcticus* in a moss turf (SIRS 1) (Fig. 1a) moss carpet (SIRS 2) (Fig. 1b) during 1972–73 at Signy Island. Values are mean ± SE and $n = 24$ f sample.

ABLE I. MEAN ANNUAL POPULATION DENSITIES OF COLLEMBOLA IN MOSS-TURF (SIRS 1) AND MOSS-CARPET (SIRS 2) COMMUNITIES AT SIGNY ISLAND DURING 1972–73. VALUES ARE NUMBER OF INDIVIDUALS m^{-2}

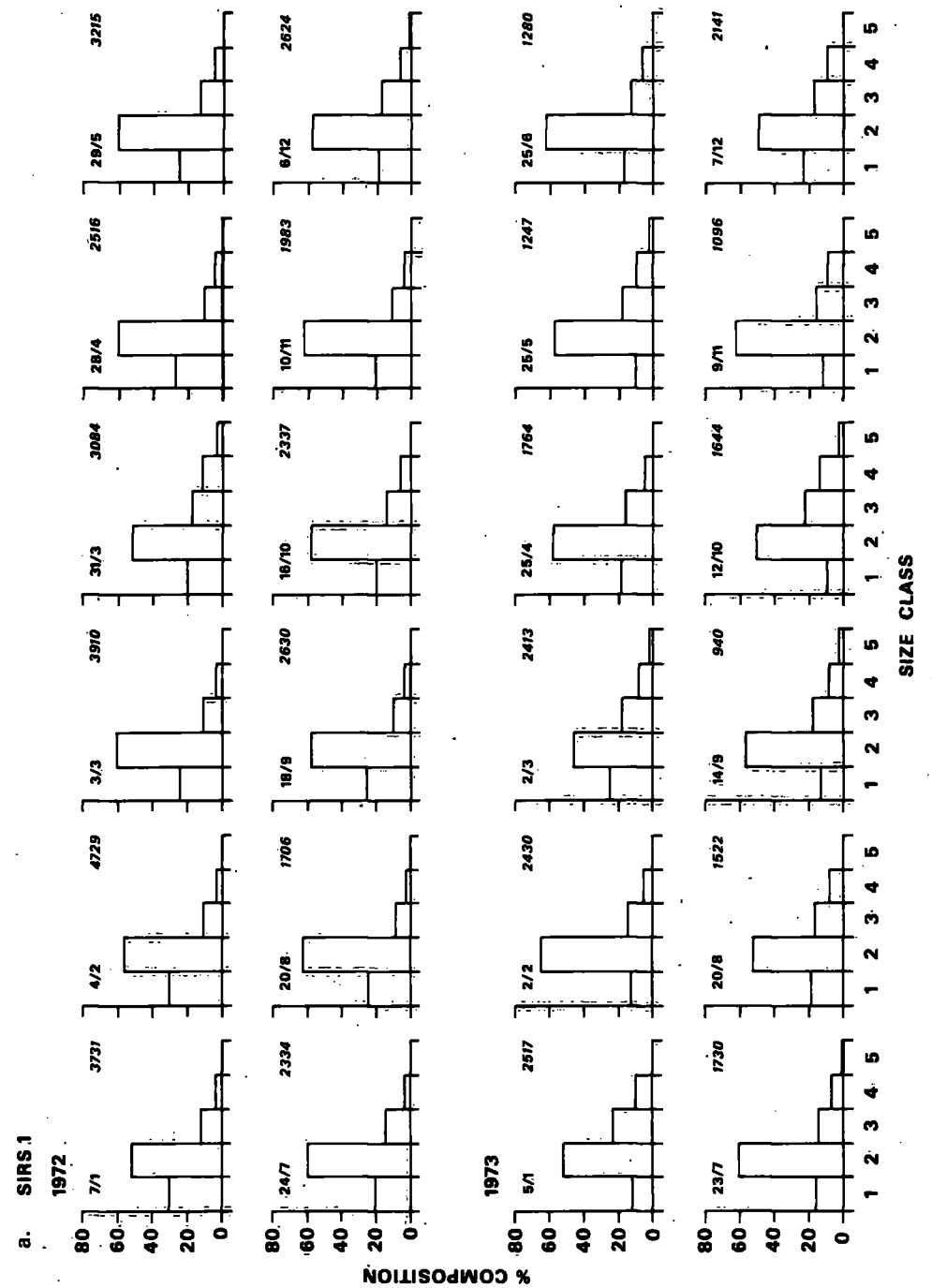
Year	*n*	*Cryptopygus antarcticus*		*Friesea grisea*		*Total Collembola*	
		SIRS 1	SIRS 2	SIRS 1	SIRS 2	SIRS 1	SIRS 2
1972	12	60 398	12 161	567	122 (*n*=6)*	60 965	12 283
1973	12	36 190	3 093	297	—	36 487	3 093
Study period	25	49 420	9 908	508	5	49 928	9 913

n Number of monthly samples.
— Only a few individuals recorded.
* January–June 1972.



2. Seasonal changes in population density of *Friesea grisea* in a moss turf (SIRS 1) and a moss carpet (SIRS 2) during 1972–73 at Signy Island. Values are mean ± SE and $n = 24$ for each sample.

nass varied from 363 to 1 125 (SIRS 1) and from 0.6 to 863 (SIRS 2) mg live weight m^{-2}, >30% of the total being contributed by size classes 2 and 4 (SIRS 1) and by size class 3 S 2). The lowest biomass was calculated for the winter months for both sites, and the highest e was obtained during summer. On the basis of mean annual estimates of biomass (Table II), otal population estimate for *Cryptopygus* declined between the two study years at both sites, 2% in the moss turf and by 79% in the moss carpet. Mean biomasses over the 25-month y were 688 and 154 mg live weight m^{-2} for SIRS 1 and 2, respectively. In terms of the ribution made by the size classes to total *Cryptopygus* biomass, size class 2 dominated in the s turf by comprising *c.* 42%. In the moss carpet, size class 4 contributed >30% of the total ıass over the study period. The smallest fractions of total biomass in this species were ıed from size classes 1 and 5, the smallest and largest individuals in the populations.


a. SIRS 1
1972
1973
7/1
4/2
3/3
28/4
31/3
25/5
25/4
12/10
9/11
7/12
24/7
20/8
18/9
10/11
16/10
6/12
2/2
2/3
14/9
9/1
23/7
20/8
% COMPOSITION
SIZE CLASS

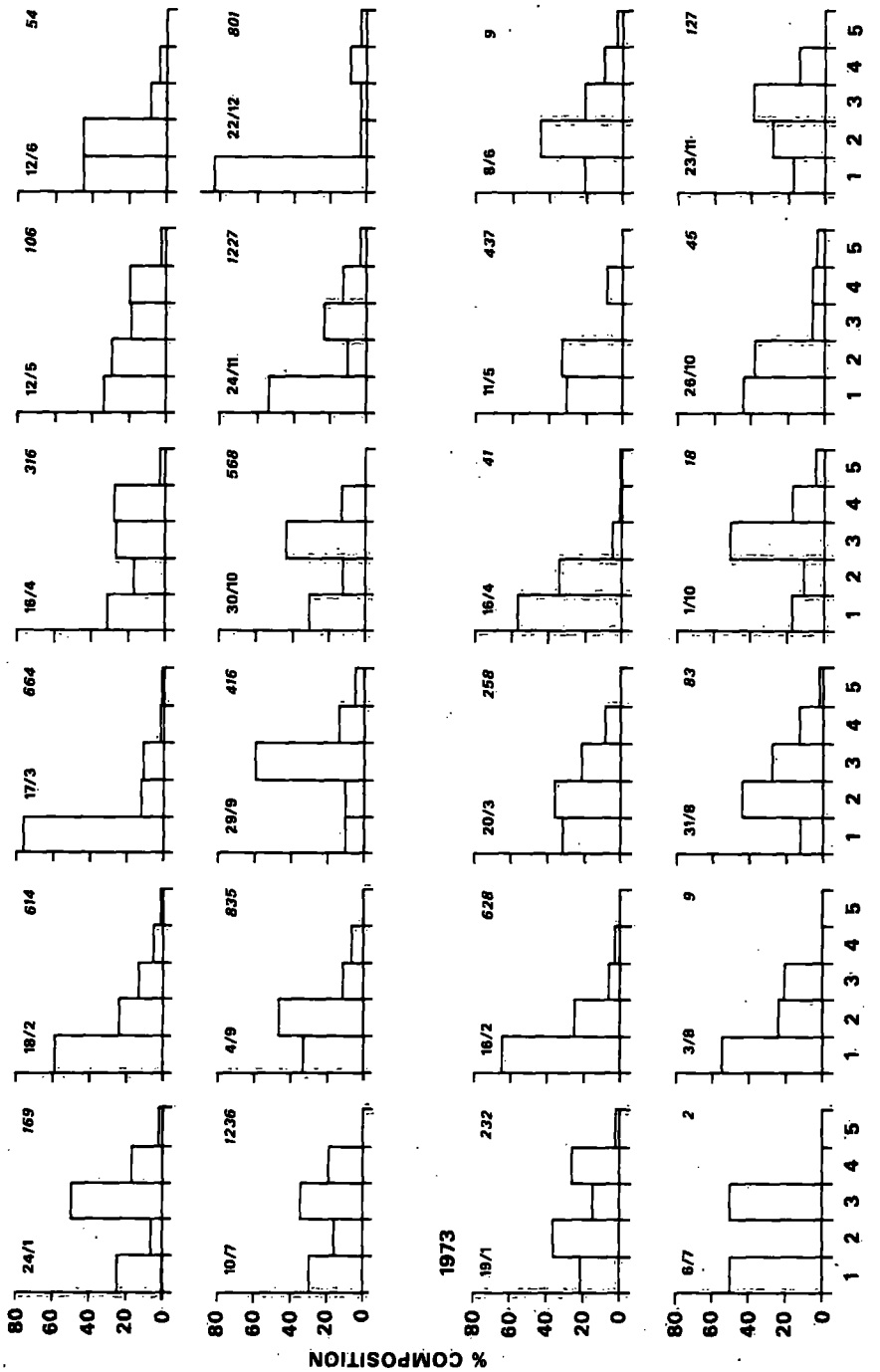


Fig. 3. Percentage composition by size class of monthly samples of the populations of *Cryptopygus antarcticus* in a moss turf (SIRS 1) (Fig. 3a) and a moss carpet (SIRS 2) (Fig. 3b) at Signy Island during 1972–73. The total number of *C. antarcticus* in each monthly sample is also shown, and $n = 24$ cores per sample.

TABLE II. BIOMASS ESTIMATES (mg LIVE WEIGHT m^{-2}) FOR POPULATIONS OF *Cryptopygus antarcticus* IN MOSS-T (SIRS 1) AND MOSS-CARPET (SIRS 2) COMMUNITIES AT SIGNY ISLAND DURING 1972–73. THE CONTRIBUTIONS EACH OF THE FIVE SIZE CLASSES ARE ALSO SHOWN TOGETHER WITH MEAN INDIVIDUAL LIVE WEIGHTS

Site	*Year (n)*	*Mean biomass per size class* 1	2	3	4	5	*Mean total biomass* *Live weight*	*Dry weigh*
	Mean live weight individual^{-1}	3.0	10.2	25.7	52.5	92.8		
SIRS 1								
	1972 (12)	45.0	365.0	195.5	141.0	27.4	773.9	281.5
	%	5.8	47.2	25.3	18.2	3.5		
	1973 (12)	17.8	205.3	164.8	167.8	48.4	604.1	219.7
	%	2.9	34.0	27.3	27.8	8.0		
	Study period (25)	32.9	287.9	178.3	151.6	36.9	687.6	250.1
	%	4.8	41.8	25.9	22.0	5.4		
SIRS 2								
	1972 (12)	16.8	21.0	73.5	75.5	18.1	204.9	74.5
	%	8.2	10.2	35.9	36.8	8.8		
	1973 (12)	3.9	10.5	10.2	16.1	3.9	44.6	16.2
	%	8.7	23.5	22.8	36.0	8.7		
	Study period (25)	13.0	22.2	60.6	47.9	10.7	154.4	56.1
	%	8.5	14.4	39.3	31.2	6.9		

n Number of monthly samples.

Using a mean water content for individual *Cryptopygus* of 63.6% (n = 61), dry-we equivalents of the mean annual biomass estimates were calculated to be in the range 219– (SIRS 1) and 16–74 (SIRS 2) mg dry weight m^{-2}.

Live-weight data are not available for *Friesea* but, on the basis of general body size length, average individuals correspond to size class 2 of *Cryptopygus*. Hence, a live weigh 10.2 µg individual^{-1} has been used for the computation of its mean population biomass. species contributes between 1.2 and 5.8 mg live weight m^{-2}. Thus mean annual biomasses fo Collembola are estimated to be 607–780 (moss turf) and 45–206 (moss carpet) mg live we m^{-2}.

Size-class structure

It was hoped that, by assignment of individual *Cryptopygus* to five size classes based on b length (Tilbrook and Block, 1972), changes would be seen which could provide informatio growth and life history. The numbers of *Cryptopygus* in each size class were used to calculat proportion of each class in each monthly sample, and the results are given in Fig. 3 for both s

The striking feature of the *Cryptopygus* population of the moss turf over the two study y was its apparently stable size-class structure. Size class 2 (body length 750–1 060 µm) form 57% of the samples throughout the study. Size classes 1 and 3 composed 20 and respectively, with the larger individuals being <10% of the population. There were no obv seasonal changes in the size-class structure of the *Cryptopygus* population in the moss turf 3a). In contrast, the composition of the population in the moss carpet changed between s years, and there was evidence of seasonal shifts in the size-class structure. Size class 1 (length 440–750 µm) comprised, on average, *c.* 39% of the samples during the 2-year pe whilst size classes 2 and 3 formed *c.* 23% each of the population. Larger individuals were (size class 4) and 2% (size class 5) in terms of mean values. The size-class compositi *Cryptopygus* in the moss carpet (Fig. 3b) suggests that growth occurred principally in sur (e.g. February to May 1972; December 1972 to January 1973; February to June 1973) posssibly at times during winter (e.g. September to October 1972; August to October, 1 However, caution is required when interpreting such changes based on low mean numbe core, i.e ⩽2 which represents a total of ⩽48 individuals per monthly sample, and the possi of differential mortality should not be overlooked.

Fig. 4a and b shows the seasonal fluctuations in mean numbers per core for each size class of *yptopygus* at both sites. As reflected from the overall population-density levels, the moss-rpet community experienced much greater fluctuations than that of the moss turf over the 2 ars. Juveniles, especially size class 1, increased in numbers during November–December 1972 SIRS 2, which was followed by an upsurge in size class 2 individuals, but only in April 1973.) such pattern was discerned for SIRS 1.

rizontal distribution

The range of variances about the mean populations of *Cryptopygus* was much greater for the ss carpet than for the turf. The degree of aggregation of this species at the two sites was mpared by plotting monthly mean ($\bar{x}$) numbers core^{-1} against variance (s^2) on a double log le. The fitted regressions:

$\log s^2 = 11.61 + 0.42 \log \bar{x}$ ($n = 25$, $r^2 = 0.78$) for SIRS 1,
$\log s^2 = 1.97 + 0.47 \log \bar{x}$ ($n = 19$, $r^2 = 0.95$) for SIRS 2,

icated no significant difference in slope. Taylor's power law ($S^2 = a\bar{x}^b$) (Taylor, 1961), when plied to these data, yielded indices of aggregation of 2.82 and 3.12 for SIRS 1 and 2, pectively. It is concluded that the degree of aggregation of *Cryptopygus* is similar in both strates. A reciprocal square-root transformation of the population data was indicated (p = .41 and −0.56 for SIRS 1 and 2, respectively), and this allowed independence of the variance m the mean.

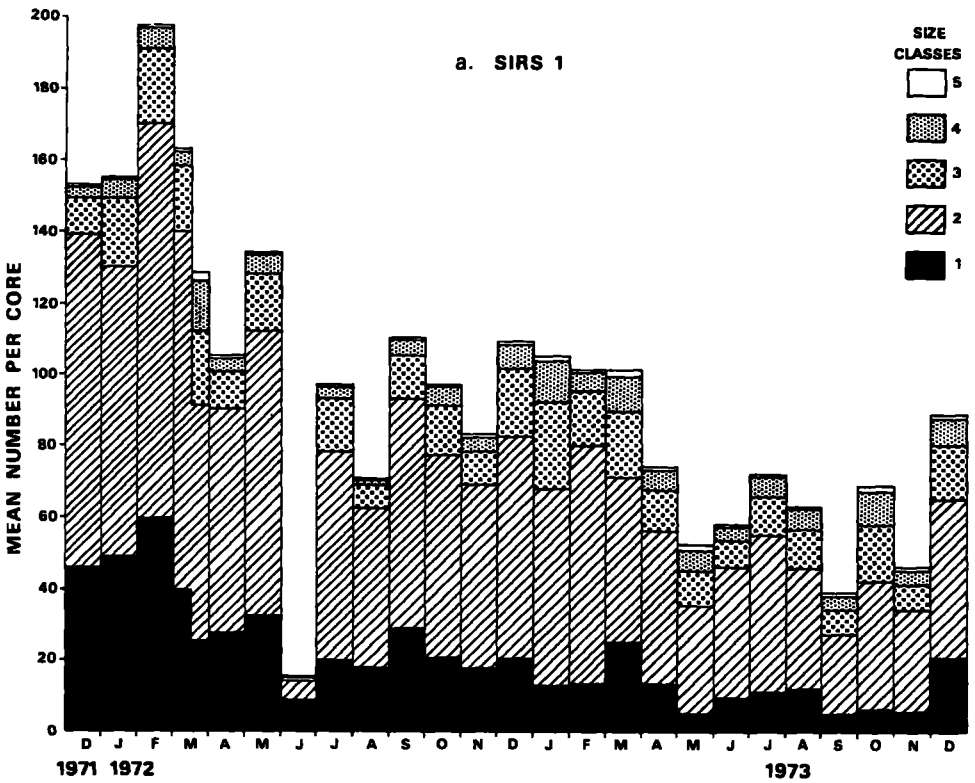


Fig. 4a.

. Population structure of *Cryptopygus antarcticus* on the basis of the mean numbers of each size class per core for a moss turf (SIRS 1) (Fig. 4a) and a moss carpet (SIRS 2) (Fig. 4b) at Signy Island during 1972–73.

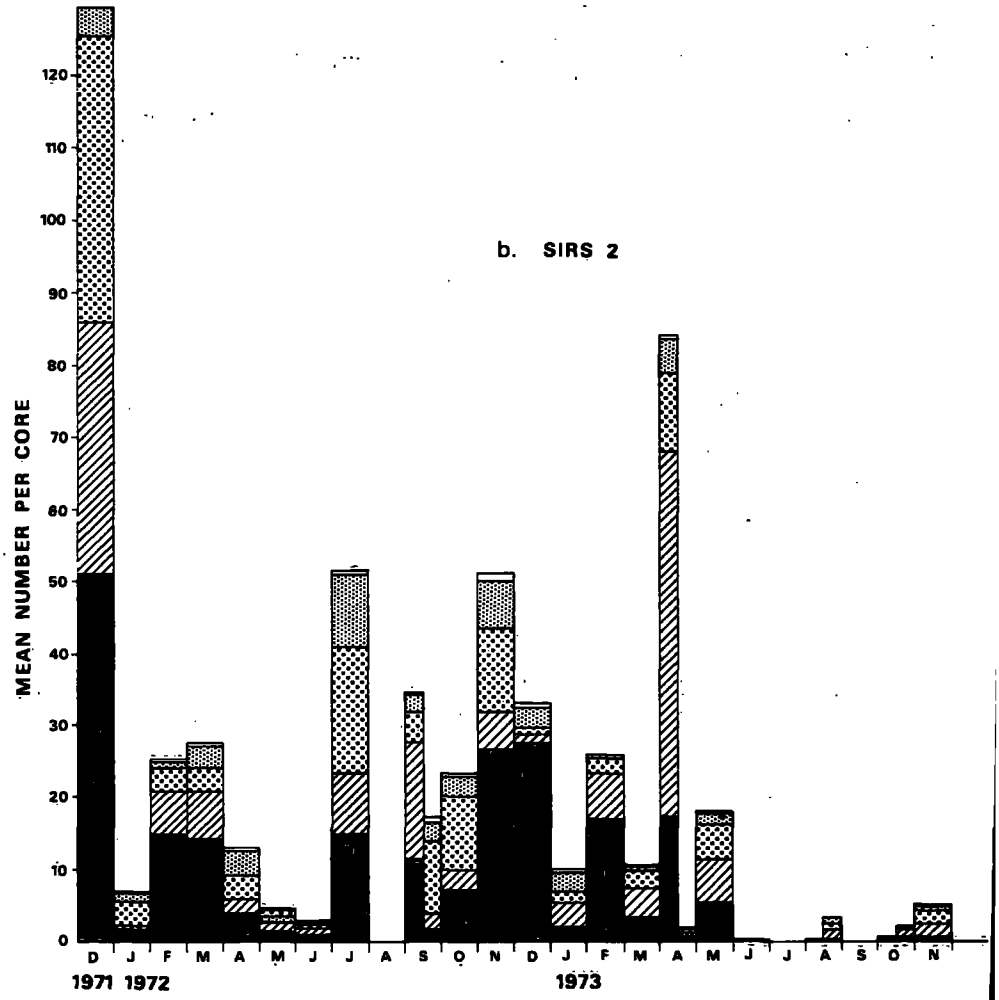
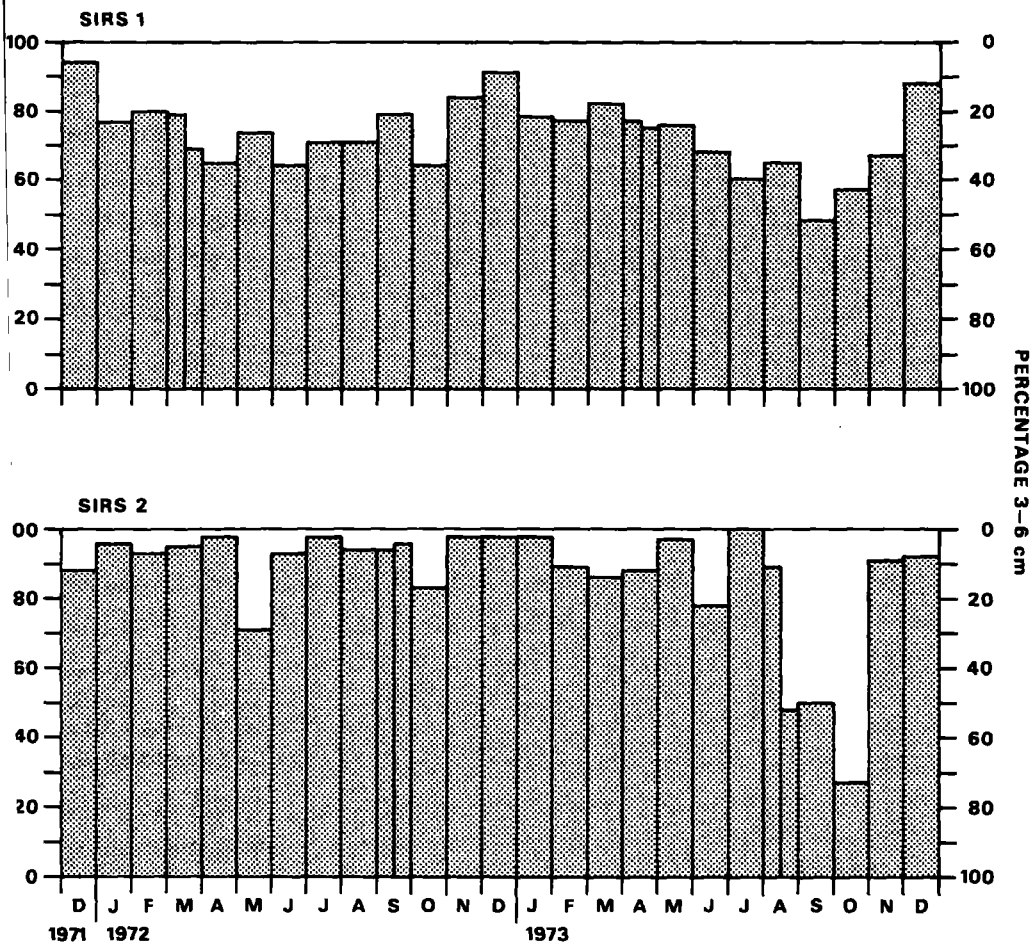


Fig. 4b.

Vertical distribution

From the monthly samples, it was possible to examine the distribution of *Cryptopygus* wi the two layers, 0–3 and 3–6 cm from the surface of the moss peat profile. Proportions of total numbers for this species in each layer for each monthly sample were calculated (Fig. 5 general, a greater proportion of the *Cryptopygus* population occurred in the upper 3 cm o sample cores from the moss carpet (mean of 86%), compared to the moss turf (mean of over the study period). This was probably a reflection of the waterlogged nature of the pe SIRS 2 for much of the thawed period of the year, compared to the free-draining natu SIRS 1.

There were indications of seasonal changes in the vertical distribution of *Cryptopygus* i moss turf (Fig. 5), with a general increase in the proportion of fauna in the upper (0–3 cm) during summer (maximum 94%), and a decrease in the proportion therein during w



5. Proportion of *Cryptopygus antarcticus* occurring in two vertical zones (0–3, 3–6 cm) of a moss-turf (SIRS 1) and a moss-carpet (SIRS 2) community at Signy Island during 1972–73.

imum 48%). There were changes in the percentages of the collembolan in the moss-carpet rs, but these were less well defined and not obviously related to season. During the late er and early autumn of 1973 only 27–50% of the Collembola occurred in the upper 3 cm, pared to >70% for the rest of the study. This may have been caused by the accumulation of ss melt water above a frozen horizon in the peat profile at this time but, due to the low bers involved, firm conclusions cannot be advanced. As indicated for the population-density ıates, extraction efficiency will also affect the vertical distribution of the fauna.

ı five occasions, deeper cores to the underlying bedrock were collected from SIRS 1 and 2 in : to examine the distribution of Collembola in the peat profile. Three such samples to greater 24 cm in depth were taken from the moss turf and two samples to 18 cm depth were cored the moss carpet in 1973. The numbers of Collembola observed per 3-cm vertical section of cores are shown in Fig. 6 together with their water contents.

risotoma was not found in these deeper samples at either site. In the moss turf both *topygus* and *Friesea* were found, although the latter occurred only in small numbers. *topygus* was found down to a depth of 21 cm (9 February 1973) and *Friesea* to one of 18

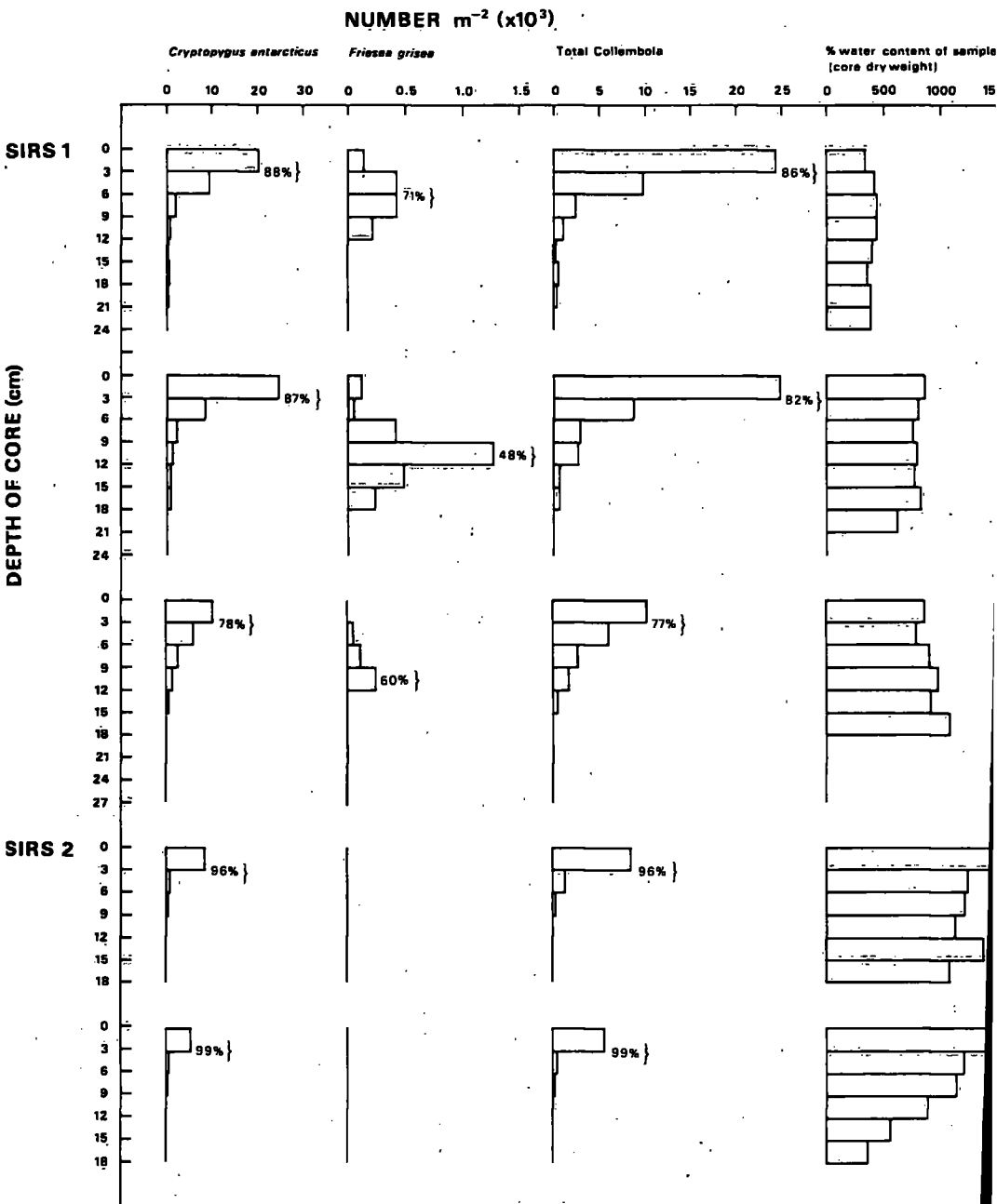


Fig. 6. Vertical distribution of two species of springtails and total Collembola in deep samples from a moss-turf (
1) and a moss-carpet (SIRS 2) community at Signy Island during 1973. The percentage water content
dry-weight basis of each 3-cm section of the profile is also shown together with the proportion of Collemb
selected sections of the profile.

1 (1 June 1973). The majority of the *Cryptopygus* population occurred in the 0–6 cm zone nge from 78% to 88% of the total population), whilst *Friesea* was abundant in the 3–9 cm ne (71% on 9 February 1973) and at 9–12 cm on the other two sampling occasions (range m 48% to 60% of the total population). There was, therefore, a distinct contrast in the vertical tribution of *Cryptopygus* and *Friesea* in the moss turf. As *Cryptopygus* was numerically minant at SIRS 1, the distribution pattern for total Collembola (Fig. 6) was almost identical to t for this species. The water content in the moss-peat profile varied only slightly within the nples but there was a general increase in moisture of the 1973 samples from SIRS 1.

Friesea was absent from the moss carpet and *Cryptopygus* was almost entirely restricted to top 6 cm of the profile (range of 96% to 99% of the total population) (Fig. 6). The water ntents of the SIRS 2 samples were higher than those of the moss-turf samples which were lected at similar seasons, and the data suggest a decline in moisture content from the moss face to a depth of 18 cm at certain times of the year.

:ro-climate

Data of soil and air temperatures together with incoming solar radiation levels for the two sites 1972–73 and analyses therefrom have been presented by a variety of workers (e.g. Walton, 77, 1982; Goddard, 1979; Jennings, 1979; Block, 1980*a*, *b*). Therefore, only information tinent to the Collembola study will be summarized here. Generally, the moss-carpet peratures are less extreme than those of the moss turf, probably due to the larger volume of er contained in the former and other factors such as aspect, snow depth, etc. Data from the temperature sensors in the two profiles indicate seasonal maxima and minima around +25° −20°C at the moss surface (SIRS 1) over the 2 years, and slightly less for SIRS 2 (Block, 0*b*). The thermal variations, especially at the ground surface, were much greater during mer (e.g. 0° to +30°C) than in winter (−13° to −16°C) for 5 d periods. In both sites, the ver layers of the profile were buffered from the extremes of temperature characteristic of the er layers (Goddard, 1979; Walton, 1982). For soil invertebrates, the duration of exposure particular temperature is especially important in relation to their activity and survival at sub- temperatures. Also, the thermal zone −5° to +5°C is critical to their locomotion, feeding, under field conditions (Block, 1981). Calculations based on hourly data from the moss ace, show that the temperature was within this zone for 57% and 64% of 1972 and 1973, ectively, for SIRS 1 (Walton 1982). The corresponding proportions of time for SIRS 2 67% and 61%, respectively. The surface layers of the two sites were generally warmer in 3 than in 1972, with a 7–9% increase in the time that the temperatures remained in the 0° to C band.

he depth of snow in winter differed both between sites and years (Block, 1980*a*). There was oximately twice the depth of snow on both sites in 1973, and on average, the moss carpet a larger accumulation of snow than the moss turf (range of maximal depths of 27–38 cm for S 1, and 48–72 cm for SIRS 2). The increased potential insulation combined with a longer od of snow-lie may have been responsible in part for the observed temperature differences.

coming solar radiation was maximal in the period from late September to March, when l conditions allowed, with values approaching 0.66 J m^{-2} s^{-1} (Walton, 1977; Goddard,). However, soil temperatures may be relatively unaffected during times of high radiation to surface snow but, when the moss substrate is exposed after melt, it warms rapidly lings, 1979).

Discussion

e species diversity of Collembola in the two communities examined at Signy Island is low in parison with some other polar sites and most temperate soil communities. Four species are l at Signy Island, of which three occurred in samples from the SIRS, with *Cryptopygus*

being dominant. Similar numbers of Collembola species were found by Pryor (1962), Wise a Shoup (1967) near Hallett Station (three species), and by Janetschek (1967*a*) in South Victo Land (six species). However, in some localities only a single species of Collembola was recor (Janetschek, 1967*b*; Peterson, 1971). In the Arctic, six species have been found on Bathu Island (Danks and Byers, 1972), eight species from Ellef Ringnes Island (McAlpine, 19 whilst 30 species occurred at Devon Island (Addison, 1977). A range of between 23 and species of Collembola has been listed from tundra sites by Ryan (1981). In a temperate be wood in Denmark, a total of 60 species has been recorded by Petersen (1980). Clearly, terrest habitats in polar regions are colonized by relatively few species of Collembola, which gener achieve high population numbers.

Collembola population numbers estimated for the SIRS exhibit large fluctuations, b between sites and the two study years (Figs 1 and 2). A similar decline in numbers of Acari observed over the same time period for the SIRS (Goddard, 1979), which suggests a comm influence on both groups. It is not known, however, whether these changes are part of a gen trend or an unusual catastrophe. The extraction efficiency probably varies seasonally due physical changes in the sample cores and the physiological state of the fauna, but it is unlikel influence population levels in such a drastic regular manner.

Little data on the population densities of Antarctic Collembola are available. *Gomphiocephalus hodgsoni*, Wise and Spain (1967) estimated maximum numbers of individuals m^{-2} (Lake Penny) and 540 individuals m^{-2} (Flatiron), both in South Victoria La In a more detailed study, Peterson (1971) recorded a summer population range from *c.* 1 00 3 400 individuals m^{-2} of the same species at Cape Bird, Ross Island, during 1967–68. Non these populations in chalikosystem habitats (Janetschek, 1970) achieve levels of *c.* 10–50 individuals m^{-2} (Table II), as was found in the two bryosystem habitats in the marit Antarctic. Comparable Collembola densities have been observed in Arctic sites, where the p cover is more diverse and often more complete. A sedge–moss community in the Taimyr, US supported 4 000 Collembola m^{-2} (Matveyeva, 1972), whilst habitats on Devon Island ran from sedge–moss to a polar plateau desert had populations of 7 800 to 29 900 individuals (Addison, 1977). Lichen tundra in Spitsbergen contained 20 800–38 300 individuals (Bengston and others, 1974), and several tundra habitats at Point Barrow, Alaska, populations of 61 100–171 900 Collembola m^{-2} (MacLean, 1980). The latter estimates higher than those of 19 000–67 000 Collembola m^{-2} obtained for a temperate wood (Petersen, 1980), and those of Hale (1966) for a range of British moorland sites (20 930–52 Collembola m^{-2}).

The only biomass information available for Antarctic Collembola are those of Tilbrook (1 and the present study for *Cryptopygus* at Signy Island. These suggest an annual mean of *c.* mg live weight (250 mg dry weight) m^{-2} for the moss turf, and *c.* 154 mg live weight (56 mg weight) m^{-2} for the moss carpet. By comparison, similar biomasses have been calculated fo total Collembola of a temperate beech wood (76–160 mg dry weight m^{-2}) (Petersen, 1980).

Life cycles of Antarctic Collembola, including age structure and growth, have been stu (e.g. Janetschek, 1967*b*; Peterson, 1971) but few conclusions have emerged. The data *Cryptopygus* show an almost constant size structure in the moss turf and evidence of growth maturation at certain periods in the moss carpet. The differences in size-class structure of the populations at Signy Island are difficult to explain. The approximate constant proporti young individuals (*c.* one-fifth of each monthly sample) in the SIRS 1 mosses suggest that hatch is possible in any season when conditions are suitable. The proportion of such Collembola in the SIRS 2 mosses is much more variable, but nevertheless this size predominates through the year, which supports the idea that eggs may hatch whe environmental conditions allow. Using data for laboratory growth rates of this species, (1981) proposed that at a body length of between 1 040 and 1 134 μm (approximating t lower portion of size class 3), individuals either increase or decrease in size at subsequent m

hich may be influenced by nutritional and/or excretory factors. If such a situation prevails in e field, the failure of the population at SIRS 1 to show significant seasonal shifts in size stribution may be explicable. It could be hypothesized that *Cryptopygus* is not limited in this ay in the moss carpet (Fig. 4). Addison (1977) analysed weight data for *Hypogastrura tullbergi* häffer and obtained evidence of growth from field samples at Devon Island, but she concluded at individuals could remain in the population for at least 3 years after reaching sexual maturity th a total life span of *c.* 5 years. For *Cryptopygus* under maritime Antarctic conditions, a life cle extending over 3–7 years has been postulated (Burn, 1981).

The Collembola only penetrated slightly to depths >6 cm in the SIRS profiles, and did so less an the Acari over the same period (Goddard, 1979). Whilst between 78% and 88% of the llembola were found in the upper 6 cm of the SIRS 1 profile, some of the mites extended per but 94% of all the Acari were located in the 0–12 cm zone. Differences in the arthropod netration of the moss peat in the carpet and turf may be accounted for by the seasonally aerobic conditions which may prevail below 3–9 cm in the carpet (Wynn-Williams, 1980; vis, 1981). Many species of Collembola are unable to survive in periodically flooded habitats uhnelt, 1976), a phenomenon which occurs annually at the moss-carpet site on Signy Island.

Little can be concluded about the horizontal distribution of the Collembola in moss substrates, l a similar degree of aggregation was found in *Cryptopygus* for both sites. Evidence is umulating on the association between species density and vegetation cover and, from the core a, the distribution of *Cryptopygus* in the moss turf and carpet is very clumped. Significantly her numbers of *Cryptopygus* occur in core samples of moss turf containing *Polytrichum* ne, and *Chorisodontium* and surface lichens together, than in dead mosses and bare peat rsonal communications from M. B. Usher and R. G. Booth). Analyses of gut contents of *ptopygus* suggest that this species feeds extensively in the field on unicellular green algae rsonal communication from A. J. Burn), which grow epiphytically on the live shoots of these mosses. Until more is known about the factors which influence arthropod micro-distribution rganic substrates, and the main features of their life cycle, it is difficult to draw any further clusions. A current research project is examining the micro-arthropod distribution in moss in more detail. The information on the Signy Island Collembola contrasts with that of the lembola of a beach-ridge site at Devon Island studied by Addison (1977), which were not ciated with particular plant species, and which contributed to the unspecialized nature of this ip in the Arctic.

is evident that micro-climatic conditions which prevail within the habitats of both these phyte-dominated communities are important influences on the population density, size ibution and life cycles of the Collembola. Of the limited collembolan fauna of the maritime rctic (eight species; Wallwork, 1973), *C. antarcticus* is the only species to have colonized habitats to any extent. Present research is aimed at a clarification of the biology, and cially the feeding relations, of this species, and the role of environmental factors such as erature and moisture in its seasonally changing cold hardiness. These adaptations must be ined in detail before conclusions can be drawn concerning the processes of arthropod nization and survival in Antarctic terrestrial ecosystems.

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REFERENCES

ADDISON, J. A. 1977. Population dynamics and biology of Collembola on Truelove Lowland. (*In* BLISS, L. C., *Truelove Lowland, Devon Island, Canada: a High Arctic ecosystem.* Calgary, The University of Alb Press, 363–82.)

BENGSTON, S. A., FJELLBERG, A. *and* T. SOLHØY. 1974. Abundance of tundra arthopods in Spitzber *Entomologica Scandinavica*, **5**, 137–42.

BLOCK, W. 1979. Oxygen consumption of the Antarctic springtail *Parisotoma octooculata* (Willem) (Isotomid *Revue d'Écologie et Biologie du Sol*, **16**, 227–33.

——. 1980*a*. Aspects of the ecology of Antarctic soil fauna. (*In* DINDAL, D. L., ed. *Soil biology as related to land practices.* Washington, D.C., Environmental Protection Agency, 741–57.)

——. 1980*b*. Survival strategies in polar terrestrial arthropods. *Biological Journal of the Linnean Society*, **14**, 29–

——. 1981. Terrestrial arthropods and low temperature. *Cryobiology*, **18**, 436–44.

——. *and* P. J. TILBROOK. 1975. Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. *Oi* **26**, 15–25.

——. *and* ——. 1978. Oxygen uptake by *Cryptopygus antarcticus* (Collembola) at South Georgia. *Oikos*, **30**, 61–

BURN, A. J. 1981. Feeding and growth in the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos*, **36**, 59–64.

CALDWELL, J. R. 1981*a*. Biomass and respiration of nematode populations in two moss communities at Signy Isl maritime Antarctic. *Oikos*, **37**, 160–66.

——. 1981*b*. The Signy Island terrestrial reference sites. XIII. Population dynamics of the nematode faci 33–46.

DANKS, H. V. *and* J. R. BYERS. 1972. Insects and arachnids of Bathurst Island, Canadian Arctic Archipel *Canadian Entomologist*, **104**, 81–88.

DAVIS, R. C. 1981. Structure and function of two Antarctic terrestrial moss communities. *Ecological Monogra* **51**, 125–43.

GODDARD, D. G. 1979. The Signy Island terrestrial reference sites: XI. Population studies on the Acari. *Br Antarctic Survey Bulletin*, No. 48, 71–92.

HALE, W. G. 1966. A population study of moorland Collembola. *Pedobiologia*, **6**, 65–99.

JANETSCHEK, H. 1967*a*. Arthropod ecology of South Victoria Land. (*In* GRESSITT, J. L., *ed. Entomolog Antarctica.* Washington, D.C., American Geophysical Union, 205–93.) [Antarctic Research Ser Vol. 10.]

——. 1967*b*. Growth and maturity of the springtail, *Gomphiocephalus hodgsoni* Carpenter, from South Vic Land and Ross Island. (*In* GRESSITT, J. L., *ed. Entomology of Antarctica.* Washington, D.C., Amer Geophysical Union, 295–305.) [Antarctic Research Series, Vol. 10.]

——. 1970. Environments and ecology of terrestrial arthropods in the High Antarctic. (*In* HOLDGATE, M. W. *Antarctic ecology.* London and New York, Academic Press, 871–85.)

JENNINGS, P. G. 1979. The Signy Island terrestrial reference sites: X. Population dynamics of Tardigrada Rotifera. *British Antarctic Survey Bulletin*, No. 47, 89–105.

KUHNELT, W. 1976. *Soil biology.* London, Faber and Faber.

MCALPINE, J. F. 1965. Insects and related terrestrial invertebrates of Ellef Ringnes Island. *Arctic*, **18**, 73–103.

MACFADYEN, A. 1961. Improved funnel-type extractors for soil arthropods. *Journal of Animal Ecology*, **30**, 171–

MACLEAN, S. F. 1980. The detritus-based trophic system. (*In* BROWN, J., MILLER, P. C., TIESZEN, L. L., *and* BUNNEL, *ed. An Arctic ecosystem: the coastal tundra at Barrow, Alaska.* Pennsylvania, Dow Hutchinson and Ross, 411–57.)

MARSH, J. B. 1970. *Radioisotopic determination of the ingestion rates of three species of Antarctic arthro Crytopygus antarcticus Willem (Collembola: Isotomidae), Belgica antarctica Jacobs (Di Chironomidae) and Alaskozetes antarcticus (Michael) (Cryptostigmata: Podacaridae).* M.Sc. t University of California at Davis, 72 pp. [Unpublished.]

MASLEN, N. R. 1981. The Signy Island terrestrial reference sites: XII. Population ecology of nematodes additions to the fauna. *British Antarctic Survey Bulletin*, No. 53, 57–75.

MATVEYEVA, N. W. 1972. The Tareya word model. (*In* WIELGOLASKI, F. E. *and* T. ROSSWALL, *ed. Proceedings IV International Meeting on the Biological Productivity of Tundra.* Stockholm, Tundra Biome St Committee, 156–62.)

PETERSEN, H. 1980. Population dynamics and metabolic characterization of Collembola species in a beech ecosystem. (*In* DINDAL, D. L., *ed. Soil biology as related to land use practices.* Washington, Environmental Protection Agency, 806–33.)

PETERSON, A. J. 1971. Population studies on the Antarctic collembolan *Gomphiocephalus hodgsoni* Car *Pacific Insects Monograph*, **25**, 75–98.

PRYOR, M. E. 1962. Some environmental features of Hallett Station, Antarctica, with special reference arthropods. *Pacific Insects*, **4**, 681–728.

RYAN, J. 1981. Invertebrate faunas at I.B.P. tundra sites. (*In* BLISS, L. C., HEAL, O. W. *and* J. J. MOORE, *ed. ecosystems: a comparative analysis.* Cambridge, Cambridge University Press, 517–39.)

SMITH, H. G. 1973. The Signy Island terrestrial reference sites: III. Population ecology of *Corythion* (Rhizopoda : Testacida) in site 1. *British Antarctic Survey Bulletin*, Nos. 33 and 34, 123–35.

STRONG, J. 1967. Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. (*In* GRESSITT, J. *Entomology of Antarctica.* Washington, D.C., American Geophysical Union, 357–71.) [Antarctic Re Series, Vol. 10.]

TAYLOR, L. R. 1961. Aggregation, variance and the mean. *Nature, London*, **189**, 732–35.

BROOK, P. J. 1967*a*. The terrestrial invertebrate fauna of the maritime Antarctic. (*In* SMITH, J. E., *organizer*. A discussion on the terrestrial Antarctic ecosystem. *Philosophical Transactions of the Royal Society*, Ser. B, **252**, 261–78.)

—. 1967*b*. Arthropod ecology in the maritime Antarctic. (*In* GRESSITT, J. L., *ed. Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 331–56.) [Antarctic Research Series, Vol. 10.]

—. 1970. The biology of *Cryptopygus antarcticus*. (*In* HOLDGATE, M. W., *ed. Antarctic ecology*. London and New York, Academic Press, 908–18.)

—. 1973*a*. The Signy Island terrestrial reference sites: I. An Introduction. *British Antarctic Survey Bulletin*, Nos. 33 and 34, 65–76.

—. 1973*b*. *Terrestrial arthropod ecology at Signy Island, South Orkney Islands*. Ph.D. thesis, University of London, 254 pp. [Unpublished.]

—. 1977. Energy flow through a population of the collembolan *Cryptopygus antarcticus*. (*In* LLANO, G. A., *ed. Adaptations within Antarctic ecosystems*. Houston, Texas, Gulf Publishing Company, 935–46.)

—. *and* W. BLOCK. 1972. Oxygen uptake in an Antarctic collembole *Cryptopygus antarcticus*. *Oikos*, **23**, 313–17.

ALLWORK, J. A. 1973. Zoogeography of some terrestrial micro-Arthropoda in Antarctica. *Biological Reviews*, **48**, 233–59.

ALTON, D. W. H. 1977. Radiation and soil temperatures 1972–74: Signy Island terrestrial reference site. *British Antarctic Survey Data*, No. 1, 51 pp.

—. 1982. The Signy Island terrestrial reference sites: XV. Micro-climate monitoring, 1972–74. *British Antarctic Survey Bulletin*, No. 55, 111–26.

BE, K. A. J. 1967. Collembola (springtails). (*In* GRESSITT, J. L., *ed. Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 123–48.) [Antarctic Research Series, Vol. 10.]

—. 1971. The Collembola of Antarctica. *Pacific Insects Monograph*, **25**, 57–74.

—. *and* J. SHOUP. 1967. Distribution of Collembola at Cape Hallett. (*In* GRESSITT, J. L., *ed. Entomology of Antarctica*. Washington, D.C., American Geophysical Union, 325–30.) [Antarctic Research Series, Vol. 10.]

—. *and* A. V. SPAIN. 1967. Entomological investigations in Antarctica, 1963–64 season. *Pacific Insects*, **9**, 271–93.

NN-WILLIAMS, D. D. 1980. Seasonal fluctuations in microbial activity in Antarctic moss peat. *Biological Journal of the Linnean Society*, **14**, 11–28.

COLLOQUE SUR LES ECOSYSTÈMES SUBANTARCTIQUES.
1981, Paimpont, C.N.F.R.A., n° 51.

RESPIRATION STUDIES ON SOME SOUTH GEORGIAN COLEOPTERA

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Résumé

1. Le taux de consommation d'oxygène des larves et adultes d'*Hydromedion sparsutum* MÜLLER (Perimylopidae), d'adultes de *Merizodus soledadinus* (GUÉRIN-MÉNEVILLE) (Carabidae) ont été mesurés à l'aide d'un respiromètre ilson dans une gamme de températures allant de 5 à 20 °C.

2. Les poids frais individuels moyens s'échelonnaient de 10,9 à 25,4 mg chez les larves et de 7,3 à 22,9 mg ez les adultes.

3. Les taux respiratoires moyens se sont situés entre 1,96 et 4,06 µl 0_2 ind^{-1} h^{-1} chez les larves et entre 51 et 7,70 µl 0_2 ind^{-1} h^{-1} chez les adultes, avec des taux métaboliques correspondants compris entre 103,21 207,69 µl 0_2g^{-1} h^{-1} chez les larves et entre 94,17 et 422,74 µl 0_2 g^{-1} h^{-1} chez les adultes.

4. Le poids frais n'a pas eu d'incidence notable sur la consommation d'oxygène chez ces espèces.

5. L'influence de la température sur le taux métabolique de ces trois espèces a été semblable mais diffère s autres arthropodes vivant dans les zones subantarctiques et dans les régions maritimes de l'Antarctique. loi d'Arrhenius plaide en faveur de l'hypothèse selon laquelle les poïkilothermes adaptés au froid ont des ergies d'activité et des valeurs du Q_{10} plus basses que les organismes vivant sous climats tempérés.

Abstract

1. Oxygen uptake rates of individual larvae and adults of *Hydromedion sparsutum* MÜLLER, *Perimylops tarcticus* MÜLLER (Perimylopidae) and of adult *Merizodus soledadinus* (GUÉRIN-MÉNEVILLE) (Carabidae) were asured by Gilson respirometry over the temperature range 5° to 20 °C.

2. Mean individual live weights ranged from 10.9 to 25.4 (larvae) and 7.3 to 22.9 (adults) mg.

3. The ranges of mean respiration rates were 1.96 to 4.06 (larvae) and 1.51 to 7.70 (adults), µl 0_2 ind^{-1} h^{-1} h corresponding metabolic rates of 103.21 to 207.69 (larvae) and 94.17 to 422.74 (adults) µl 0_2 g^{-1} h^{-1}.

4. Live weight had no appreciable effect on oxygen uptake in these species.

5. The effect of temperature on metabolic rate of the three species was similar, but differed from other -Antarctic and maritime Antarctic arthropods. Arrhenius plots support the hypothesis that cold adapted poikilotherms e lower activation energies and Q_{10} values than forms lving in temperate habitas.

INTRODUCTION

Some 40 species of Coleoptera have been recorded for the sub-Antarctic (BLOCK in press), of which only t species have been identified from the island of South Georgia (GRESSITT, 1970). These include one

freshwater form (Dytiscidae), a carabid and two species each of the Family Lathridiidae, Staphylinidae a Perimylopidae. Over 50 % of the beetle fauna of other sub-Antarctic islands belong to the Family Curculionid (e.g. DAVIES 1973; BURGER, 1978), and coleopterous insects may occupy an important ecological nic as herbivores in such ecosystems where arthropod species diversity is low compared to temperate situatio SMITH & WALTON (1975) noted that Coleoptera grazed shoot apices, moss sporophytes, leaves of *Acae magellanica* Vahl (Lam.) and various grasses. High densities of beetles (up to 455 adults and 620 larvae m− have been found in moist, sheltered micro-sites in *Festuca contracta* Kirk grassland (SMITH & STEPHENSO 1975). These were mainly Perimylopidae which feed on plant material.

The present studies were confined to three species from South Georgia: *Hydromedion sparsutu* MÜLLER, and *Perimylops antarcticus* MÜLLER (Perimylopidae) (WATT, 1970) together with *Merizod soledadinus* (GUÉRIN-MÉNEVILLE) (Carabidae) (DARLINGTON, 1970). They are referred to by their generic nam throughout this paper. The Perimylopidae were earlier included in the Tenebrionidae, and the family is kno from Patagonia, the Fuegian region, the Falkland Islands and South Georgia (WATT, 1967). The single speci of *Perimylops* (*P. antarcticus*) is confined to South Georgia, whilst *H. sparsutum*, although only recorded fro that island has four congeneric species which are found in the vicinity of the Straits of Magellan especial on Tierra del Fuego. Larvae and adults of both species were described by BRINCK (1945) together with a sing pupa of *Hydromedion*. There are six larval instars (WATT, 1970) in both perimylopids. *Perimylops* is found fro sea level up to 810 m, whilst *Hydromedion* occurs mostly below 240 m. Adults of *Perimylops* are found main in the summer (November-April), larvae in all months and the pupa is unknown. Adults of *Hydromedion* ha been observed in every month except June and August at South Georgia, whilst larvae occur throughout t year with first instars and pupae in summer. Both perimylopids live under stones, corpses of birds, etc. a in tussocks of *Poa flabellata* (Lam.) Hook. f. with *Hydromedion* being the commoner of the two species South Georgia. Little is known of their biology, but larval guts contain grass leaf fragments and inorgan debris, and they feed on tussock litter in culture. *Hydromedion* is more common than *Perimylops* at Sou Georgia, and its remains have been collected from peat aged at *c.* 6,000 years in a profile at Jason Island, Sou Georgia (COOPE, 1963).

The distribution and biology of the carabid *M. soledadinus* at South Georgia is largely unknown, a a few data on adult respiratory levels are given here for comparison with the other two species.

The relatively abundant perimylopid beetles were selected for investigation as they are suitable subje for physiology and for energy studies due to their relatively large size, long larval life and ease of cultu This paper presents results of respiration measurements undertaken on cultured individuals from collectio made during two austral summers from the area around King Edward Cove, Cumberland East Bay, Sou Georgia. The aims of the work were: (a) to determine the relationship of oxygen uptake to live weight a to temperature representative of the field range, (b) to compare sub-Antarctic data with those of terrestr arthropods from climatically more severe habitats, and (c) to contribute to the discussion on cold adaptati of such invertebrates.

MATERIALS AND METHODS

Field collections were made during April 1972 and March 1974 from a variety of habitats ranging fr tussock grass, litter and humus under *Acaena* spp., several mosses and underneath rocks, stones and wo laid on the ground surface. Adults and larvae were collected by hand and aspirator, placed in polythe containers with moss and tussock grass litter and leaves and provided with a moist plaster of paris substra Such collections were maintained at outside ambient air temperatures at the British Antarctic Surve research station at King Edward Point for up to four weeks before being transferred to the RRS Bransfi for transport at + 4 °C to the U.K. The insects were provided with chopped tussock leaf bases for fo throughout the transport and for subsequent culture at Leicester University, U.K.

The two perimylopid species were separated in the laboratory using WATT (1970), the adults on features of the prothorax, elytra and procoxal cavities and the larvae by their ventral thoracic sclerotisati and head widths.

Respiratory determinations were made at 5°, 10° and 20 °C for larvae, males and females of *Hydromedion* d *Perimylops*, and with a few measurements at 5°, 10° and 15 °C for adult *Merizodus*. All the beetles re acclimated for at least five days with food at a new temperatures before oxygen uptake rates were termined. Individual live and dry weights were measured using a microbalance (EMB 1) accurate to 5 μg, and the insects dried at 40 °C to constant weight. Oxygen consumption of individual insects is measured within three months of field collection, using a 20 channel Gilson respirometer with a nperature control of ± 0.1 °C. Chambers of 1.5 to 5.0 ml volume were utilized with two controls per run, d 5 % KOH solution on filter paper was used to absorb CO_2. Food was not provided in the respirometer ambers. Each run continued for 4-5 h with micrometer readings being made at 30 min intervals. The idings for individual chambers were subsequently corrected by the mean control change, a linear regression ed to the corrected oxygen uptake data over time and the respiration rate individual^{-1} unit time^{-1} was lculated. These results were converted to metabolic rates (oxygen uptake unit weight^{-1} h^{-1}) using the mean e weight derived from measurements made before and after respirometry.

As there were no significant differences between the two years results, the data have been pooled. ean (± S.E.) values were calculated for larvae, males and females both for the weight data and oxygen take rates at each temperature. Statistical tests for comparison of mean values and slopes of regressions re undertaken as described by BAILEY (1959).

RESULTS AND DISCUSSION

e and dry weights:

Mean live weights of the larval perimylopids are similar (c. 20 mg), whilst males and females of *Hydro-dion* were slightly heavier than *Perimylops* (Table I). The weight ranges for the two larvae were almost ntical, and mean weights for instars 3-6 of the two species are given in Table II. *Merizodus* was generally aller and lighter than either of the other two species (Fig. 1). These differences were also reflected in the an dry weight values (Table I). The sex ratios (male : female) calculated on the live weight numbers were: *dromedion* (1.55), *Perimylops* (1.89) and *Merizodus* (2.00).

ect of life weight on oxygen uptake:

TABLE I

an (± S.E.) live and dry weights of individuals of three species of Coleoptera from the King Edward Cove *area, th Georgia. n is in parentheses, n.d.: not determined, and the range (maximum and minimum values) of the data is also shown.*

Species	*Life stage*	*Live weight (mg)*	*Dry weight (mg)*
Hydromedion sparsutum	Larva	20.75 ± 0.78 (39) 10.0 – 30.7	n.d
	Male	16.15 ± 0.36 (90) 9.9 – 29.0	4.58 ± 0.13 (63) 2.6 – 7.5
	Female	22.93 ± 0.74 (58) 13.9 – 43.5	6.13 ± 0.32 (31) 3.8 – 10.5
Perimylops antarcticus	Larva	20.30 ± 1.74 (12) 10.9 – 31.6	3.06 (1)
	Male	10.79 ± 0.26 (68) 4.9 – 16.5	3.66 ± 0.10 (67) 2.1 – 6.9
	Female	15.16 ± 0.47 (36) 8.3 – 19.8	5.43 ± 0.24 (36) 2.7 – 8.1
Merizodus soledadinus	Larva	n.d.	n.d.
	Male	7.28 ± 1.34 (4) 3.8 – 10.2	n.d.
	Female	11.12 ± 0.12 (2)	n.d.

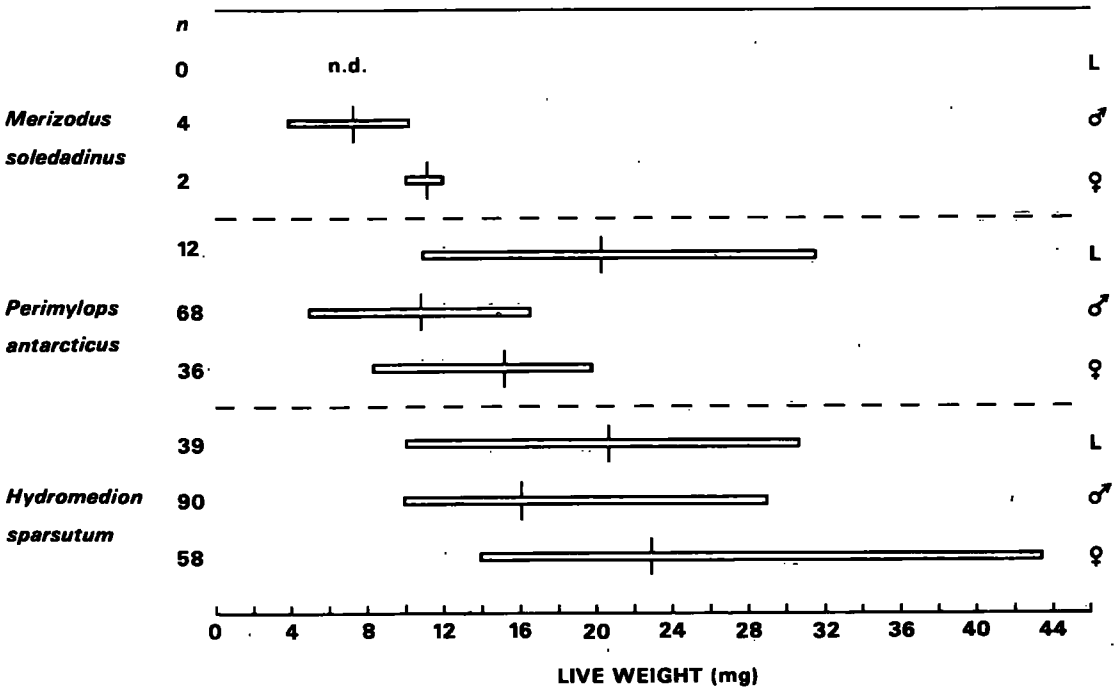


FIG. 1. — Mean live weights (and maximum and minimum values) of larvae and adults of three species of So Georgian Coleoptera. n : number of observations.

Double $\log_{10}$ plots of the data for individual respiration rate (µl O_2 ind^{-1} h^{-1}) on live weight revea no significant differences in the relationship between temperatures and between the two major species. T was also true for the regression of metabolic rate (µl O_2 g^{-1} h^{-1}) on live weight. Therefore, regression equati were calculated for each species over all temperatures using all the data, and a general equation was deri for the three species combined using mean respiration rates obtained for each species at each tempera (Table III). *Hydromedion* appeared to be the exception as its weight exponent (b) was negative, whilst the o two species were positive, but the slopes of their regression lines were not significantly different. A cle relation was observed between metabolic rate and live weight (Table III), but even then the fitted regres only accounts for 28 % of the variation (compared to 7 % for the combined respiration-weight regression).

TABLE II

Mean (± S.E.) live weights of instars 3-6 of larvae of two species of South Georgia perimylopid beetles the King Edward Cove area, South Georgia. n : number of measurements.

Species	*Larval instar*	*Mean (+ S.E.) live weight (mg)*	*n*
Hydromedion sparsutum	3	14.64 ± 1.39	25
	4	17.84 ± 0.88	23
	5	21.77 ± 0.73	18
	6	23.44 ± 1.85	21
Perimylops antarcticus	3	10.94	1
	4	16.00 ± 0.81	8
	5	19.45 ± 1.01	16
	6	25.45 ± 1.27	17

TABLE III

ear regression coefficients (a, b) relating log_{10} oxygen uptake ($\mu l\ O_2\ ind^{-1}\ g^{-1}\ h^{-1}$) to log_{10} live weight hin the temperature range 5° to 20 °C for larvae and adults of three species of South Georgian Coleoptera. n : number of data points, r^2 : coefficient of determination,
* : individual data, + : mean data.

SPECIES	TEMPERATURE °C	n	a	b	r^2
Respiration rate	($\mu l\ O_2\ ind^{-1}\ h^{-1}$) :				
Hydromedion sparsutum	5, 10, 20	167*	0.701	− 0.056	0.0013
Perimylops antarcticus	10, 20	103*	0.229	0.254	0.044
Merizodus soledadinus	5, 10, 15	6*	0.038	0.305	0.098
3 species combined		19+	0.134	0.308	0.071
Metabolic rate	($\mu l\ O_2\ g^{-1}\ h^{-1}$) :				
3 species combined		19+	3.119	− 0.680	0.281

As both the correlation coefficients (r) and the coefficients of variation (r^2) were low, it can only be cluded that live weight appears to have only a very minor influence on individual respiration rate of the e species examined, *Hydromedion* having a tendancy to decrease whilst *Perimylops* and *Merizodus* increase r respiration rate with increasing live weight of the individual.

ct of temperature on oxygen uptake :

Mean respiration and metabolic rates plotted against temperature are shown in Figs. 2 and 3 for each ies and life stage. Larval respiration in *Hydromedion* and *Perimylops* is depressed at 10 °C compared to s at 5° and 20 °C. Males and females show similar changes in respiration over the temperature range ed with both sexes of *Hydromedion* having generally higher levels especially over 10° to 20 °C. Mean en uptake was significantly ($P < 0.01$) higher in adults of *Hydromedion* than in *Perimylops* at 20 °C, and eneral respiration rates of adults for both species at $\geqslant$ 10 °C were faster than those recorded for larvae e same temperature. Although the larval picture was similar, the respiratory response to rising temperature clearly different in adults of the two perimylopids. *Hydromedion* adults showed a steady increase in individual and weight specific oxygen consumption from 5° to 20 °C, whilst *Perimylops* shows no ficant change in rates over 10° to 20 °C. The data for adult *Merizodus* are too few to derive any antial conclusions, but the levels of respiration over 5° to 15 °C were broadly similar to those of adult *nylops*. In general, the South Georgian beetles have reduced metabolic rates in contrast to temperate es of similar weight over their normal temperature ranges (data in KEISTER & BUCK, 1964).

Many workers have related arthropod metabolism (M) to temperature (T) in various ways such as a ithmic, exponential (e.g. BERTHET 1964) or the Krogh-Jorgensen function (e.g. WEBB, 1969). There reason why organisms should conform to such equations and little biological significance can be attached e constants involved. By contrast, the Arrhenius equation, $M = a.e^{-\mu/RT}$ in which T is temperature (K), a constant related to the frequency of molecular collisions, μ is the activation energy, and R is the onstant, describes the response of metabolic rate to temperature in terms of thermodynamics. It gives ue of μ that does not alter with temperature, and which generates Q_{10} values that are temperature ident, unlike the logarithmic or exponential equations. The only criticism of this approach is that nius plots yield values that are related to the enthalpy of activation rather than the more desirable nergy of activation (KEISTER & BUCK, 1964).

The present data were examined by Arrhenius plots (Fig. 4), and the regression coefficients are presented ible IV for each species separately, for the three Coleoptera combined and compared with data for

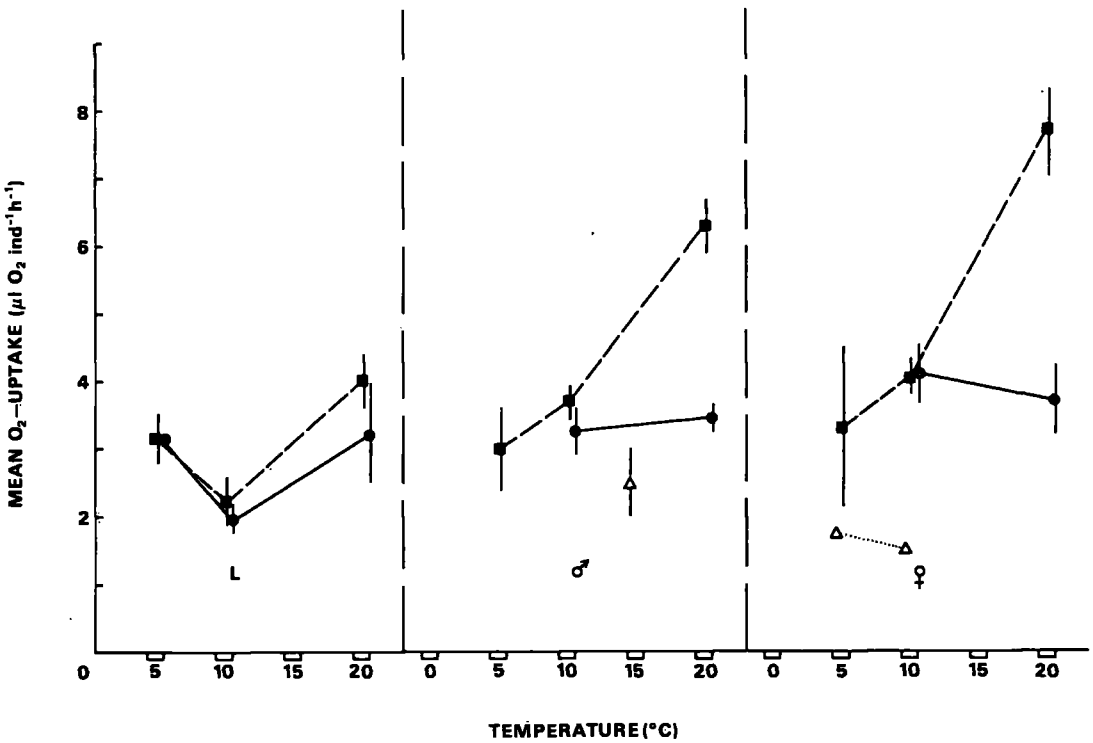


FIG. 2. — Relation of mean oxygen uptake to temperature in larvae and adults of three species of So Georgian Coleoptera.

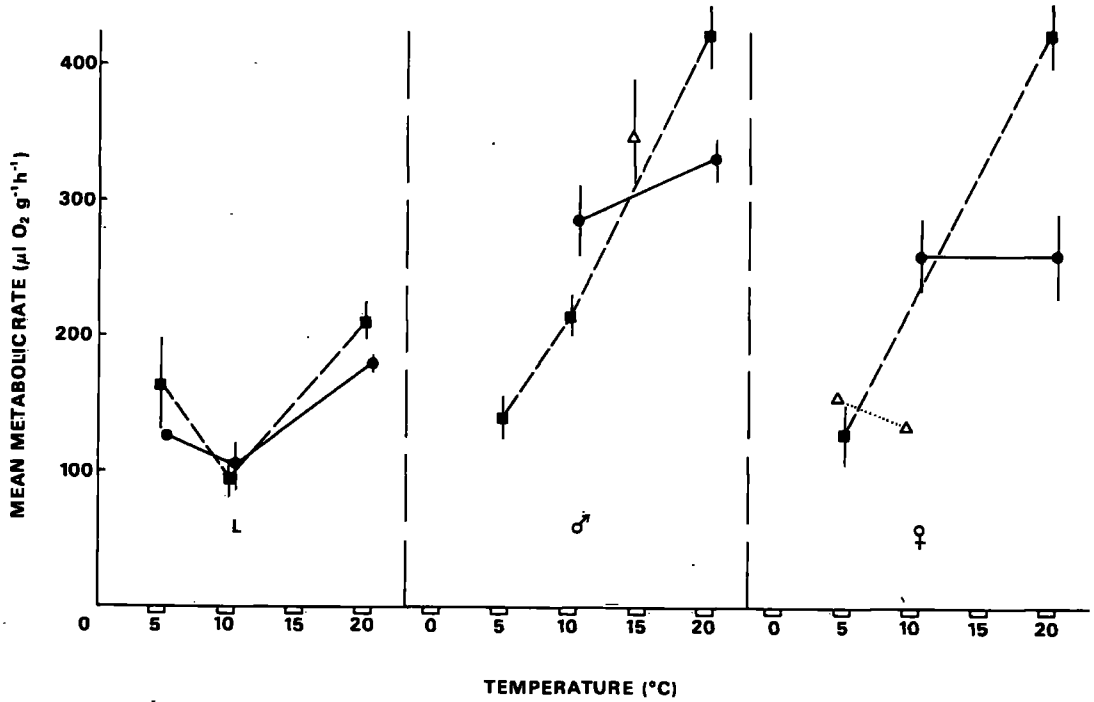
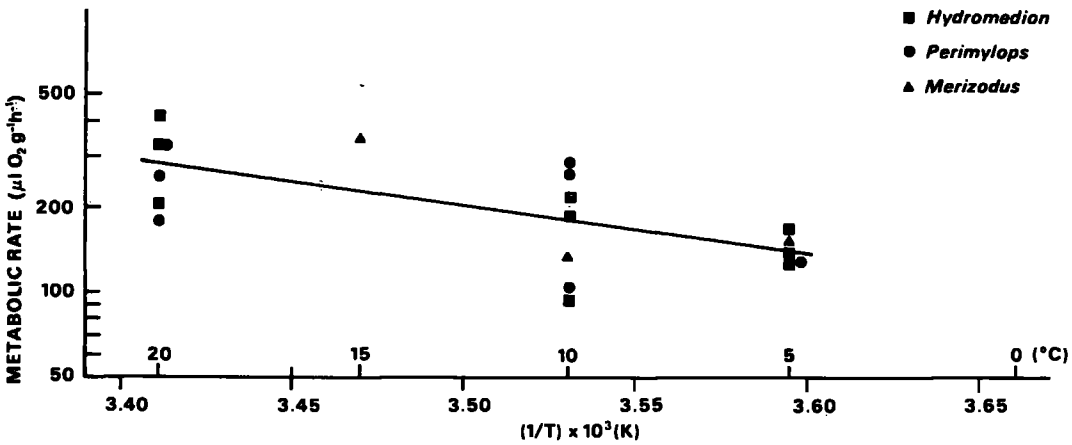


FIG. 3. — Relation of mean metabolic rate to temperature in larvae and adults of three species of S Georgian Coleoptera.



G. 4. — Arrhenius plot of metabolic rate (M) on temperature (T) for three species of South Georgian Coleoptera. The fitted regression line is shown of $\log_e M = 1.572 \times 10^8 . e^{-3.876 \times 10^3/T}$.

TABLE IV

near regression equations of $\log_e$ metabolic rate on $1/T \times 10^3$ (K) for Arrhenius plots of various Antarctic d sub-Antarctic arthropods. n: number of observations, r^2: coefficient of determination, a and b: constants in the equation $M = a.e^{b \times 10^3/T}$ where M: metabolic rate ($\mu l\ O_2\ g^{-1}\ h^{-1}$) and T: temperature (K).

SPECIES	n	a	b	r^2	REFERENCE
Hydromedion sparsutum	9	8.919×10^8	− 4.372	0.568	Present study
Perimylops antarcticus	7	5.138×10^6	− 2.901	0.248	"
Merizodus soledadinus	3	8.241×10^{11}	− 6.275	0.591	"
3 Coleoptera species combined (South Georgia)	19	1.572×10^8	− 3.876	0.433	"
Cryptopygus antarcticus (South Georgia)	3	3.367×10^{10}	− 5.209	0.999	After Block and Tilbrook (1978)
Alaskozetes antarcticus (Signy Island)	19	1.245×10^9	− 4.401	0.357	After Young (1979)
Micro-arthropods (maritime Antarctic)	32	2.606×10^{16}	− 8.920	0.507	Present study

arctic micro-arthropods (Fig. 5). The slopes of the fitted regression lines vary and, of the Coleoptera, *rizodus* has the steepest increase in metabolic rate with rising temperature. The slopes fall, however, within range calculated for the collembolan *Cryptopygus antarcticus* WILLEM at South Georgia and for the oribatid *Alaskozetes antarcticus* (MICHAEL) at Signy Island. Multiplying the coefficient b by the gas constant 8 cal $mol^{-1}K^{-1}$) provided values for activation energies (k cal mol^{-1}) (Table V). Q_{10} values were then ulated for the temperature range $T_1 - T_2$ (K) from the equation $\log_{10} Q_{10} = 2.187\ \mu/T_1 - T_2$ (PRECHT *et al.*, 3). The activation energies of the two perimylopids and *Merizodus* are low compared to some temperate ro-arthropods, and correspond to the range calculated for Antarctic Acari (Table V; YOUNG, 1979). s, whilst care must be taken when drawing conclusions from Arrhenius plots or Q_{10} values for whole

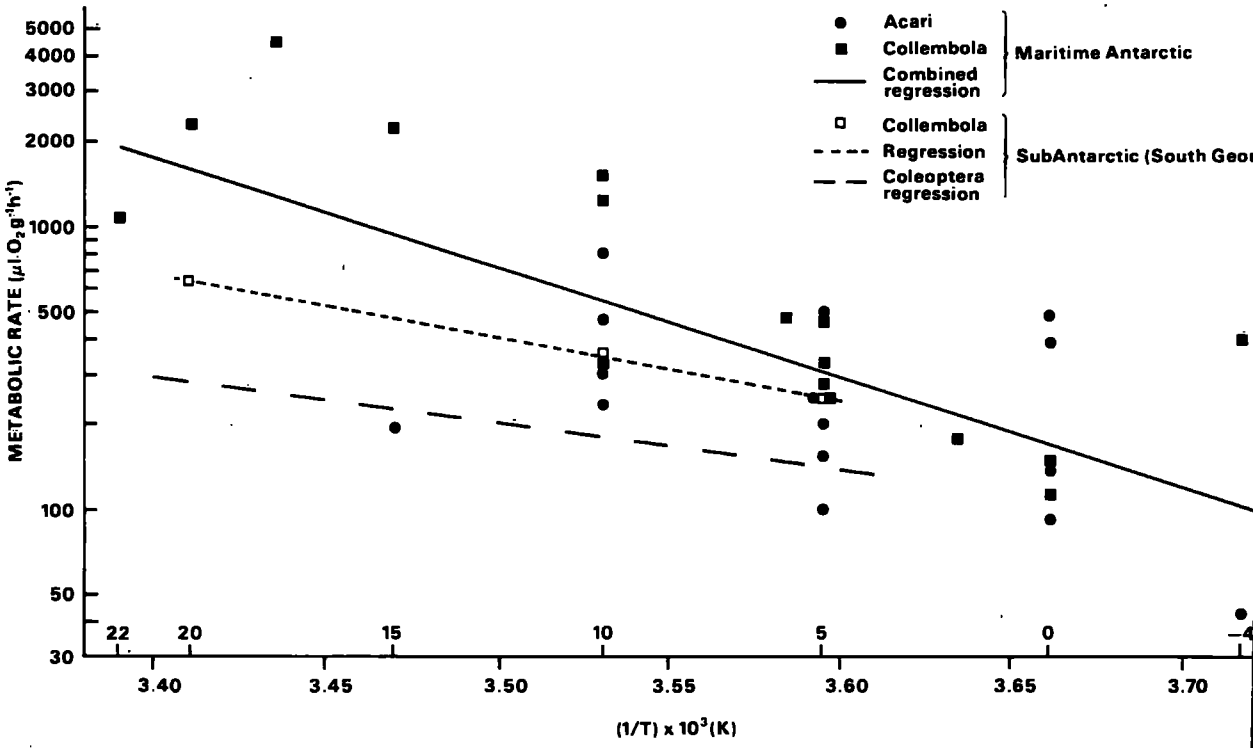


FIG. 5. — Arrhenius plot of metabolic rate (M) on temperature (T) for 11 species of micro-arthropods fro the maritime Antarctic with the fitted regression line of $\log_e M = 2.606 \times 10^{16}.e^{-8.920 \times 10^3/T}$. Regression lin for South Georgian Collembola and Coleoptera are also shown for comparison (see Table IV for equation

animal processes such as respiratory metabolism, the results presently available for individual species of bo Antarctic and sub-Antarctic arthropods support the suggestion by YOUNG (1979) that polar forms occu the lower part of the range found for activation energies. It may be that in such polar organisms, enzym have evolved that confer lower activation energies on the reactions which they mediate, thus facilitati adaptation to low temperature environments. In terms of temperature response, the calculated Q_{10}s f the South Georgian beetles and micro-arthropods (Table V) are low compared to temperate speci This gives further support to the hypothesis that poikilotherms living in cold habitats have a slower respon in terms of metabolism to rising temperature than do warm adapted forms (BLOCK & YOUNG 1978).

A considerable body of data exists on metabolic rates of Acari and Collembola in the maritime Antarct and these have been used in a comparative way in Tables IV, V and Fig. 5. Although the temperature sp (— 4 ° to 22 °C) over which these measurements have been made using a variety of micro-respirometer is greater than that for the South Georgia Coleoptera, such data enable a synthesis to be attempted (Fig. The Arrhenius plot for micro-arthropods of the maritime Antarctic shows considerable variation of me bolism with temperature, especially at sub-zero temperatures and levels > 10 °C. The slope of the over regression for this group is much steeper than those for the South Georgian Collembola and Coleopte which are broadly similar (Table IV), and this is reflected in the activation energies and Q_{10} values deriv for these groups (Table V). The relatively higher metabolic rates for the micro-arthropods from the mariti Antarctic compared to the South Georgian species, particularly at ⩾ 10 °C, may be explained on the ba of a downward shift (to sub-zero temperatures) of the metabolism — temperature curve for these anima However, differences in live weight of the species involved cannot be ruled out entirely when using metabo rates in this way. Nevertheless, adults of several similar-sized temperature coleopterans are reported to h metabolic rates in excess of 1,000 µl g^{-1} h^{-1} at 20 ° to 25 °C (KEISTER & BUCK, 1964), so the featu demonstrated for the three species of Coleoptera from sub-Antarctic South Georgia are likely to be real.

TABLE V

Activation energies and temperature coefficients (see text) over various temperature ranges calculated for some Antarctic and sub-Antarctic arthropods. Q_{10} values in parentheses are derived from mean metabolic rates. n.d. : not determined.

SPECIES	ACTIVATION ENERGY (kcal mol^{-1})	Q_{10}	TEMPERATURE RANGE (°C)
H. sparsutum	8.658	1.71 (1.71)	5 to 20
P. antarcticus	5.745	1.43 (1.14)	5 to 20
M. soledadinus	12.426	2.18 (n.d.)	5 to 15
3 Coleoptera species combined (South Georgia)	7.674	1.61	5 to 20
Cryptopygus antarcticus (South Georgia)	10.313	1.89	5 to 20
Alaskozetes antarcticus (Signy Island)	8.714	1.76	0 to 10
Micro-arthropods (maritime Antarctic)	17.662	3.07	– 4 to 22

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REFERENCES

ILEY N.T.J. (1959). — *Statistical methods in biology*. English Universities Press, London, 200 p.

RTHET P. (1964). — L'Activité des Oribates (Acari : Oribatidae) d'une Chênaie. *Mém. Inst. r. Sci. nat. Belg.*, **152**, 1-152.

OCK W. (In press). — Terrestrial microbiology, invertebrates and ecosystems. In *Ecology of the Antarctic*, ed. R. M. LAWS, Academic Press, London and New York.

OCK W. & YOUNG S.R. (1978). — Metabolic adaptations of Antarctic terrestrial micro-arthropods. *Comp. Biochem. Physiol.*, **61A**, 363-368.

INCK P. (1945). — Coleoptera. *Scientific Results of the Norwegian Antarctic Expedition*, 1927-1928. Oslo, **24**, 1-23.

RGER A.E. (1978). — Terrestrial invertebrates : a food resource for birds at Marion Island. *S. Afr. J. Antarct. Res.*, **8**, 87-99.

OPE G.R. (1963). — The occurrence of the beetle *Hydromedion sparsutum* (Mull.) in a peat profile from Jason Island, South Georgia. *Bull. Brit. Antarct. Surv.*, No **1**, 25-26.

RLINGTON P.J. (1970). — Coleoptera : Carabidae of South Georgia. *Pacif. Insects Monogr.*, **23**, 234.

/IES L. (1973). — Observations on the distribution of surface living land arthropods on the Subantarctic Ile de la Possession, Iles Crozet. *J. Nat. Hist.*, **7**, 241-253.

ESSITT J.L. (1970). — Subantarctic entomology, particularly of South Georgia and Heard Island. *Pacif. Insects Monogr.*, **23**, 1-374.

KEISTER M. & BUCK J. (1964). — Respiration : some exogenous and endogenous effects on rate of respiratio In *The Physiology of Insecta*, ed. M. ROCKSTEIN, Vol. III, pp. 617-658, Academic Press, London New York.

PRECHT H., CHRISTOPHERSON J., HENSEL H. & LARCHER W. (1973). — *Temperature and Life*. Spring Berlin.

SMITH R.I.L. & STEPHENSON C. (1975). — Preliminary growth studies on *Festuca contracta* Kirk a *Deschampsia antarctica* Desv. on South Georgia. *Bull. Brit. Antarct. Surv.*, Nos. **41** & **42**, 59-75.

SMITH R.I.L. & WALTON D.W.H. (1975). — South Georgia, Subantarctic. In *Structure and function of tund ecosystems*, eds T. ROSSWALL & O.W. HEAL, pp. 399-423, Swedish Natural Science Research Counc Stockholm. (*Ecol. Bull. Stockholm*, 20).

WATT J.C. (1967). — The families Perimylopidae and Dacoderidae (Coleoptera, Heteromera). *Proc. R. e Soc. Lond.*, B, **36** (7-8), 109-118.

WATT J.C. (1970). — Coleoptera : Perimylopidae of South Georgia. *Pacif. Insects Monogr.*, **23**, 243-253.

WEBB N.R. (1969). — Temperature and respiratory metabolism in a species of soil mite. In *Proceedin of 2nd International Congress of Acarology*, ed. G.O. EVANS, pp. 61-66, Hungarian Academy Sciences, Budapest.

YOUNG S.R. (1979). — Repiratory metabolism of *Alaskozetes antarcticus*. *J. Insect. Physiol.*, **25**, 361-369.

DISCUSSION

Question (H. G. Smith) : *Discontinuities in curves of metabolic rates or growth rates with temperature h been observed on a number of occasions. Collated data from a wide range of different studies will tend to obsc the manifestation of these small but important phenomena.*

Réponse : I agree, and this preliminary synthesis does not take account of such small, but important differenc I think variations due to live weight differences may well be important in this respect.

Question (A. J. Burn) : (i) *You have shown a decrease in metabolic rate at 5 °C for larval beetles. Is reason for this experimental technique or is it a real effect ?*

(ii) (*in reponse to discussion on the possibilities of carrying out experimental work in Europe*). *The eff of long term storage and culturing on the metabolic rates of antarctic species should be carefully controlled.*

Réponse : (i) I believe this to be a real effect, confirmed by significant differences between the mean metab rates. But I do not know why.

(ii) I agree we have examined this effect in a mite (*Alaskozetes antarcticus*) and a collembolan (*Cryptopy antarcticus*). I suggest that we should always relate our laboratory findings to those of field animals.

Question (L. Davies) : *What do you think is the biological significance of the rather large differences showed in various measures (Activation Energy, Q10's) between the « large » beetles of S. Georgia and the mi arthropods of the maritime Antarctic (S. Orkneys ?).*

Réponse : In general, I think the maritime antarctic species have a faster response to rising temperat (over their normal environmental range) than the sub-antarctic (south Georgian) coleoptera. This enables t to utilise, efficiently, small periods of higher temperature for activity, growth, reproduction, etc.

Question (G. Vannier) : *Could you get the same respiration data if you had experimented in your lab Cambridge on animals kept in culture compared with those collected straight away from the field in South Georg What do you think about ecophysiological experiments performed on antarctic arthropods reared in climate cab for a long while ?*

Réponse : Yes, all the coleopteran data presented in this paper were obtained in the laboratory u cultured specimens. The measurements were made within three months of field collection and after 5 acclimatation at each experimental temperature. I think we have to be careful when assessing laboratory ecophysiolo data to realise its limitations and uses. Such laboratory data must be viewed against the treatment of the mat and related to field conditions. It is of the utmost importance to return to the field in all cases.

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COLD HARDINESS IN INVERTEBRATE POIKILOTHERMS

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Abstract—1. A selective review is made of the information on cold hardiness in the following taxonomic groups: Protozoa. Platyhelminthes. Rhynchocoela. Rotifera. Nematoda. Mollusca. Annelida. Tardigrada. micro-Arthropoda (Collembola & Acari) and Arthropoda.

2. Most existing data are for the arthropods and, in particular, the Insecta, within which research has been concentrated on the Lepidoptera, Diptera and Coleoptera.

3. The occurrence of the freezing susceptible and freezing tolerance starategies of cold hardiness within the invertebrates cannot be explained on phylogenetic grounds at present. Considering insects to order level, nine invertebrate taxa are freezing susceptible, five are freezing tolerant, whilst eight groups have both types.

4. Factors from individual species' ecology and morphology may have largely determined the type of strategy adopted.

INTRODUCTION

rtebrate poikilotherms inhabiting polar regions alpine zones of high mountains exhibit cold liness as a form of acclimatisation to low temture conditions. Low temperature in invertebrate biology refers to temperatures in the range *ca.* to *ca.* −75°C. In general, three types of response ound in invertebrates exposed to cold: those that ıot survive exposure to cold, those that become scent and resume normal activity when rened, and those that hibernate by diapause udsley-Thompson. 1973a). The depth of cold to h an animal is subjected greatly depends on the tat, its physical structure and the conditions in, including water content, and its microclimate. ine and freshwater invertebrates, apart from tidal species, usually occupy more climatically e environments than terrestrial animals. Varis in temperature, moisture content, wind speed, in land habitats of cold regions can be very great, by increasing the potential for physiological s of poikilotherms. Cold hardiness has been obd in temperate and tropical species also.

e survival of freezing temperatures by living ıisms has been the subject of much debate: see ws by Meryman (1966), Ashwood-Smith (1970) Lozina-Lozinskii (1974). Considerable interest leveloped in low temperature preservation of a range of cells, tissues and organisms (Harris, Ashwood-Smith & Farrant, 1980), but few vs have attempted to encompass several poikim groups at once (Miller, 1978a). Much work ld hardiness in insects has been undertaken in on to overwintering survival of pest species (see ee, 1978).

ically, there are two options of strategies which been adopted by invertebrates to survive freezmperatures. Firstly, some species possess or de- the ability to supercool extensively (i.e. to maintheir body fluids in the liquid phase below the melting point). Various solutes, including polyhydric alcohols, sugars, etc., may enhance supercooling depending upon their concentration. Such animals thereby avoid intracellular freezing, as they cannot withstand the harmful effects of the conversion of water to ice in their tissues or body fluids. On freezing in the supercooled state, they invariably die, at what is termed the undercooling or supercooling point. These species are described as freezing susceptible (or frost susceptible, or freezing intolerant). Secondly, other forms can survive ice formation in their tissues, usually in the extracellular tissue fluids. Such animals frequently show poor supercooling ability, and nucleating agents may be present in their bodies to ensure freezing at relatively high sub-zero temperatures. During the freezing process solutes such as glycerol may be involved in the protection of cells from injurious ice crystals. These species are termed freezing tolerant (or frost tolerant).

This paper has the following aims: (1) to make a systematic review of the information and data available on cold hardiness in invertebrate poikilotherms: (2) to examine thereby the occurrence and the distribution of the two cold hardiness strategies over a broad taxonomic range; (3) to attempt to identify common features and mechanisms within the major faunal groups; (4) to highlight gaps in our knowledge of invertebrate cryobiology. However, this review is neither complete nor exhaustive, but it is considered timely in the progress towards the development of a common theory of poikilotherm cold tolerance.

The systematic order follows the scheme for invertebrates by Clark & Panchen (1971), except that the Collembola and Acari are considered together as a single group—the micro-Arthropoda.

PROTOZOA

Protozoan cells appear to possess a high degree of lability in relation to physical and biological factors of the environment, and an ability to adapt to chang-

ing ecological conditions. They differ in this respect from the cells of the majority of multicellular animals, which appear, on present evidence, to be significantly more conservative (Lozina-Lozinskii, 1974). The influence of low temperatures on Protozoa has been reviewed by several authors including Smith (1961) and Sukhanova (1968).

Under certain conditions, deep supercooling of Protozoa is possible (e.g., Polyanskii & Poznanskaya, 1964). Experiments conducted on *Paramecium* sp., freshwater amoebae and *Euglena gracilis* showed that during supercooling, swelling occurs which results in cell rupture and cytolysis. Breakage of the pellicle, however, does not always lead to cell death under such conditions. Ice formation in protozoan cells occurs only after the external medium has started to freeze. Increased cold hardiness through supercooling (to −2.2° to −3.8°C) occurred in individuals of *P. caudatum* maintained in 0.1 M solutions of chlorides of several salts (Ca, Li, Mg, Na, K) compared to controls (Lozina-Lozinskii, 1948), which may be significant under field conditions. Evidence has been presented for and against the survival of Protozoa after intracellular freezing in both the active and encysted states by Lozina-Lozinskii (1974). Freezing tolerance in the field occurs mainly in cysts and other resistant stages, and prior dehydration in terrestrial forms is important. Dehydrated cysts of *Colpoda cucullus* survived deep cooling experimentally in an aqueous medium at a rate of >100°C/sec down to −196°C (Taylor & Strickland, 1936).

PLATYHELMINTHES

Information is available for only a single species of turbellarian in terms of cold hardiness. In a study of tolerance to freezing and supercooling in the interstitial fauna of a sandy, tidal beach on the Island of Sylt (North Sea), Purschke (1981) found that *Notocaryoplanella glandulosa* was one of two species with the highest tolerances. Its LD_{50} occurred after 66 hr at −8°C and some individuals survived for 4 hr at −11°C in a supercooled state.

RHYNCHOCOELA (NEMERTINI)

A supercooling point of −5.0°C was measured for *Lineus corrugatus*, an Antarctic form, by Rakusa-Suszczewski & McWhinnie (1976).

ROTIFERA

It has been shown that slow cooling rates increase freezing survival in the Antarctic rotifer *Philodina* sp. (Aoki & Konno, 1961) and that, in addition, glycerol, at concentrations of 2–3% in the medium, affords the maximum protection (Koehler, 1967). Cooling rate optima were between 3° and 5°C/min and 50–60% survival could be routinely achieved. Storage of frozen rotifers in liquid nitrogen for up to 20 days did not lower their viability. Further, Koehler & Johnson (1969) found that dimethylsulphoxide (DMSO) was slightly more effective than glycerol as a cryoprotectant, and that the provision of an adequate bacterial food source after thawing increased survival. Once again, the encysted animal appears better able to survive sub-zero temperatures than the active, mo form.

NEMATODA

The ability to endure deep cooling (> −190°C) i humid condition has been discovered only in ne todes which have been prepared by desiccation (L & Hartung, 1941) and pre-cooling (De Coni 1951). In the plant parasitic nematode *Aphelencho ritzemabosi*, freezing occurred between −5°C −10°C in the active state (Asahina, 1959). In eggs larvae of two species of *Meloidogyne*, no differenc survival was observed when they were cooled 1°C/min, but the same stages in a salt solu showed differential survival after freezing. Nemat which have not lost body water rarely remain a after freezing in moist conditions. Survival of s worms is aided by protective substances such as cerol, a stepwise cooling regime (−30°, −7 −196°C) and ultra-rapid warming (Namatov, 1 and others).

The facility with which many nematodes, capabl withstanding desiccation, survive ultra-low temp tures in a dehydrated condition has been known many years. Recent studies on anhydrobiosis nematodes (Crowe & Madin, 1975) have shown drying *Aphelenchus avenae* at 97% relative hum at <3% per hr and rehydration at high relative midity increases the percentage recovery. Du rehydration from the anhydrobiotic state, this sp in unaffected by exposure to liquid nitrogen whil water content remains <21% of body weight (C & Crowe, 1979). Freezing and thawing of w causes leakage of primary amines to the surroun medium by structural disruption caused by crystals.

MOLLUSCA

Intertidal molluscs often tolerate freezing (wisher, 1959, 1966). The species investigated in the gastropods *Littorina littorea* (Kanwisher, Sømme, 1966a; Murphy, 1979), *Nassarius obs* (Murphy, 1979) and *Acmaea digitalis* (Roland & 1977), the bivalves *Mytilus edulis* (Williams, 1970 *Modiolus demissus* (Murphy 1977a,b; Murph Pierce, 1975).

The quantity of body water frozen in inte molluscs varies from 64 to 75%. Seasonal chan freezing tolerance occur although no potential protectant has been found. In some species, fr and desiccation damage is thought to be due pr ily to increased solute concentration, but the p logical mechanisms underlying freezing toleranc scarcely been studied (Murphy & Pierce, 1975). parative experiments on cold resistance of littor benthic forms and of sub-Arctic and tropical s have been undertaken by Theede (1972). R Suszczewski & McWhinnie (1976) reported supe ing points for two Antarctic molluscs between and −7.5°C. Further details are to be found in (present volume).

Only one study of a terrestrial mollusc ha undertaken (Stöver, 1973). The pulmonate *A*

ustorum survives sub-zero temperatures by super-
ling, but after rapid cooling to −10°C, tissue ice is
rated for up to 55 min. Two types of freezing were
inguished. In the first type, the supercooling
nts of active, moist snails were −1.0° to −2.5°C,
formation commenced in the protruding foot and
animal died 40–55 min after its onset. In the
ond type, supercooling points of inactive, desic-
ed snails were −3.5° to −9.0°C, ice formation
ted elsewhere than in the foot and they died
lier in the freezing process. Increased potassium
ls (2.5 times normal) in the haemolymph were
orded during frost damage, with concomitant de-
ases in sodium content. This suggests that mem-
nes, and especially the Na^+/K^+ carrier mechan-
s, are disorganised in the early stages of freezing.
sonal and altitudinal differences in freezing ability
e also detected.

t is clear that cell and tissue water contents play an
ortant role in the freezing tolerance of both inter-
l and terrestrial molluscs, although the physio-
cal mechanisms controlling these levels may be
erent.

ANNELIDA

Vestheide & von Basse (1978) distinguished
veen chilling resistance (tested using supercooled
er without ice formation) and freezing resistance
ed using frozen water) in a study of two mesop-
mel polychaetes. They found that freezing resist-
e (LD_{50}s of −4° and −7°C after 1 hr) was always
h less than chilling resistance (LD_{50}s of 8 and
r at −12°C) in both species. Differences in their
ing resistance were related to their geographical
ibution.

ive species of marine polychaete living interstit-
y on a North Sea sandy beach were examined by
schke (1981). Survival at −8°C varied from <1 hr
2 hr (LD_{50}) and correlated with their position on
sand flat and beach slope. The species *Stygocapi-
subterranea*, occurring at the uppermost position
ie intertidal zone, was the best adapted to both
ing and supercooling.

rrestrial representatives of the oligochaete family
nytraeidae often occur in high population
ities in organic soils of moorland and tundra
s. Observations on specimens from the island of
h Georgia in the sub-Antarctic suggest that they
be freezing tolerant (Block, unpublished).

TARDIGRADA

periments on the cooling of desiccated tardi-
es, rotifers and nematodes have led to the defini-
of anabiosis (suspension of life) in such primitive
ps. For the Tardigrada, studies of survival and
ration in the active and encysted states have been
by Pigon & Weglarski (1955).

MICRO-ARTHROPODA—COLLEMBOLA & ACARI

the arthropods, the springtails and mites have
extensively studied with reference to their low
erature tolerance, particularly in recent years
Block *et al.*, 1978; Young, 1979; Sømme, 1979a).
As these animals are often dominant, both in terms of numbers of species and population densities in polar tundra communities, they are of special interest in respect of low temperature adaptations. They have usually been considered together, and that tradition is followed here.

Micro-arthropods have been reported closest to both poles than most other invertebrates, and they occur in the alpine tundra of high mountains (Sømme, 1979b; Block & Zettel, 1980; Schatz & Sømme, 1981). The strategy of cold hardiness in these groups is that of freezing avoidance, and all the taxa examined to date do this by supercooling. Enhancement of this process is by various substances, including sugars and polyhydric alcohols, of which the common one is glycerol. No freezing tolerant species has been recorded. While summer animals have relatively high supercooling points (Block & Sømme, 1982; Sømme & Block, 1982), the mean supercooling point of the population is lowered in autumn and early winter by a two-stage process (Sømme, 1981). Firstly, the contents of the gut are eliminated to reduce the possibility of heterogeneous nucleation from foreign particles in the food. Secondly, supercooling is increased through the accumulation of low molecular weight compounds. The environmental conditions which trigger these physiological changes and the mechanisms involved are largely unknown. Although low temperature exposure (either during natural acclimatisation or experimental acclimation) lowers the mean supercooling point of such animals, other factors such as dehydration may influence the process through increased production of glycerol, as found in the Antarctic mite *Alaskozetes antarcticus* (Young & Block, 1980). In addition, in soil micro-habitats the possibility of inoculative freezing by contact with water/ice is increased.

Supercooling in micro-arthropods has been observed in Arctic and Antarctic species, and also in forms from Norway, the European Alps, Asia, North America and the African tropics, and is reviewed by Sømme (present volume). A very wide range of supercooling powers exist in the micro-arthropods, which probably depend upon the particular climatic and micro-climatic regimes that occur in their habitats. Heterogeneous nucleation from food present in the gut of supercooled mites and Collembola appears to play an important role in the cold hardiness and survival of sub-zero temperatures in these animals. Although glycerol, occasionally together with mannitol and other polyols in small amounts, is the predominant potential cryoprotectant in both Acari and Collembola, there is some evidence to suggest that a system based on sugars may be as important in springtails as one based on glycerol.

ARTHROPODA

Scorpionida

The first reported supercooling points for scorpions were those for *Vejovis* sp. (Arizona) at −6°C (Cloudsley-Thompson & Crawford, 1970), and for *Leirus* quinquestriatus (Sudan) at −7°C (Cloudsley-Thompson, 1973b). Adult scorpions, *Diplocentrus peloncillensis*, from the Peloncillo Mountains, New Mexico, showed no apparent supercooling point change with

season other than a significant elevation during a relatively late winter and early spring (Crawford & Riddle, 1975). Cold exposure tests showed that −7°C for 12 hr killed at least 50% of adults. Acclimation to 5°, 12° and 25°C had no significant effect on supercooling of specimens collected in April, whilst experimental desiccation caused no change in supercooling of October collected animals. Haemolymph melting points varied unaccountably and were not related to field conditions, and factors other than temperature seemed to modify individual respiration seasonally. In another species, *Paruroctonus utahensis*, neither a decrease in photoperiod nor a lowered temperature influenced supercooling. The cessation of feeding in autumn appeared to be important, together with a significant increase in the depth of supercooling (to −12°C), for the survival of naturally acclimatised scorpions, but these were not linked to changes in polyol or water contents. Differences in feeding activity of the two species which have been studied may be responsible for the observed levels of cold hardiness.

Araneida

The data available for spiders suggest that supercooling forms the basis of their cold resistance (Kirchner & Kestler, 1969; Kirchner, 1973). European species which overwinter in open, exposed habitats are more cold-resistant (supercooling points between −16° and −30°C) than cave dwelling forms (supercooling points from −3° to −7°C), but in both groups resistance may vary with age and season of the year (Kirchner, 1973). A total of 22 species were examined in this study. Both hibernating adults and young of *Araneus cornutus* were able to survive at −18°C for 2–3 days, but only during October to March, when their average supercooling point was *ca.* −23°C. This was associated with a decrease of >1°C in the haemolymph melting point and the presence of glycerol (2–3% of fresh weight). However, the concentration of glycerol was not directly correlated to individual supercooling point in this species (Kirchner & Kestler, 1969). Similarly, it was found that a crab spider, *Philodromus* sp., and a sac spider, *Clubiona* sp., both survived sub-zero winter temperatures by a depression of their supercooling points (Duman, 1979). The solutes partially responsible for this increase in supercooling were proteins, which produced a thermal hysteresis (a difference between the freezing and melting points of the haemolymph) of *ca.* 2°C, and glycerol, both being present only in winter. Thermal hysteresis was lost within two weeks at warm temperatures. Such spiders may utilize similar mechanisms to the protein and glycoprotein antifreezes found in polar marine fishes and some overwintering insects. The only eggs which have been studied were those of the linyphiid *Floronia bucculenta* from grass tussocks in West Germany, which supercooled to −31°C (Schaefer, 1976).

Pycnogonida

Collossendeis sp. from McMurdo Sound, Antarctica had a supercooling point of −3.9°C (Rakusa-Suszczewski & McWhinnie, 1976).

Crustacea

Most research has been done on the barna
Balanus balanoides. Its survival at low temperature
mainly due to a tolerance of ice formation rather th
to mechanisms that prevent freezing. Seasonal va
ations in its cold tolerance have been obser
(Sømme, 1966a), with the median lethal temperat
changing from −6°C (summer) to −17.6°C (wint
(Crisp & Ritz, 1967). Although Cook & Gabb
(1970, 1972) demonstrated increased glycerol conte
in adult winter barnacles, the maximum level (equ
vent to *ca.* 1 mM in the body tissues) was 1000-f
lower than in glycerol-forming insects and far bel
the level required to significantly lower the melt
point of the body fluids or promote their supercc
ing. At −18.6°C (median lethal temperature for
balanoides during winter) >80% of its body water
frozen, whilst at −6.6°C (summer median lethal t
perature) only 40–45% was frozen. This contrasts v
Williams' (1970) assertion that a constant propor
of the body water of intertidal molluscs is frozei
their lower lethal temperature.

Three species of Antarctic Crustacea (amphi
copepod and isopod) supercooled to between −
and −7.6°C when tested (Rakusa-Suszczewski
McWhinnie, 1976). The estuarine amphipod *C*
phium volutator showed a significant increase in
zero temperature tolerance in winter, but the free
points of whole animals did not vary seasor
(Holmstrom *et al.*, 1981). No effective cryodepres
was found by melting point studies.

Comparative studies of the lipid composition of
decapod species from warm, temperate and p
waters showed no relationship between water
perature and total lipid or pigment contents
Clarke, personal communication). Lipid class cor
sition was similar for all species, with phospholi
free sterol and triacylglycerol being present. There
a marked increase in the unsaturation of both
and individual phospholipids with lower water
perature, and it would be interesting to deter
whether this condition of unsaturation is of v
spread occurrence in polar marine invertebrates.

Myriapoda

Myriapods have been largely ignored by low
perature physiologists and only one species of
pede. *Scolopendra polymorpha*, has been studied (C
ford & Riddle, 1974; Crawford *et al.*, 1975). This
cies, which lives beneath rocks in the mountai
New Mexico, was estimated to experience tem
tures inducing 50% mortality on about one da
year. Supercooling tests suggested that adults
withstand 12 hr at −7°C (LD_{50}). Late instars coll
in winter and acclimated at 5°C recovered fr
single cooling to the supercooling point, but
than one such exposure was usually lethal. Varia
observed in supercooling points and haemol
melting points throughout the year were not r
to season. Assays of glycerol and sorbitol show
significant amounts in centipedes collected fro
field between July and January.

Insecta

The insects are the best known of all the in

tes in terms of cold tolerance, especially as much earch has been undertaken on the overwintering of t species and other insects of economic import-e. No attempt will be made to consider all the a available for each insect Order, but a selection been made of the more important information.

Reaumur (1734) is considered to be the first worker note the ability of insects to survive winter in a d, frozen state. Excellent reviews pertaining to d resistance in insects have been made, e.g. Usha-kaya (1957), Salt (1961, 1969), Asahina (1966, 9), Merivee (1978), Ring (1980) and Ring & Tesar 81). A compilation of the data on supercooling nts in freezing intolerant insects is given by nme (this volume). Undoubtedly, the elegant series more than twenty papers by R. W. Salt, which ted in 1936 and spanned 35 years, and which ered many of the fundamentals and background of subject, greatly contributed to the development of earch not only on insects but also in the field of kilotherm cold tolerance. Within the insects, both zing tolerance and freezing susceptibility are nd, sometimes in different life stages of the one cies. The underlying evolutionary causes of such a ribution of adaptations have not been elaborated, much research needs still to be done on why one ct can tolerate the formation of ice within its ues and another cannot.

Two tropical orthopterans, *Locusta migratoria* and *Schistocerca gregaria*, supercooled to between −3.5° −3.8°C and −5.4° to −7.5°C, respectively Loudsley-Thompson, 1973b). Repeated supercooling hose insects that survived the initial test indicated gnificant reduction in cold tolerance of the desert ist, as also did hydration. Preconditioning at 5°C 18 hr lowered the supercooling point significantly, pared to desert locusts kept at 22°C for 18 hr. s was not achieved by hydration, faecal elimin-n, an increase in osmolarity or by glycerol se-ion, but may have resulted from a shift in the ure or location of food already in the gut. Using a nal cycle (6 hr light:18 hr dark), the mean super-ling point was depressed significantly in the dark se (from −4.1° to −5.1°C) in the migratory locust Loudsley-Thompson, 1978). Hibernating eggs of *L. ratoria* have been observed to supercool to −30°C zina-Lozinskii, 1974).

he only study on Psocoptera is that of Glinyanaya 1) working on the eggs of four species of psocids, recorded supercooling points ranging from °C (*Caecilius flavidus*) to 37°C (*Metylophorus ilosus*).

the Hemiptera, eggs of the black willow aphid *rocomma smithia*) from near Lethbridge, Alberta, rcooled to −42°C and contained *ca.* 16% gly-l (of total weight of water plus glycerol) (Sømme,). Both mannitol and glycerol were detected by me (1969) in three aphid species from Norway, in the USSR, cold hardiness measurements have used in forecasting the winter survival of the atomid *Eurygaster integriceps* (Doronina & Mar-va, 1971). Work on a lacebug (Tingidae) of thistle e UK by Eguagie (1974) indicated that, although was much individual variation, cold hardiness ased in winter (supercooling points around °C for both sexes) in association with changes in air temperature. Gut contents and contact with a moist substrate reduced the supercooling point by *ca.* 5°C.

For Mecoptera, Sømme & Østbye (1969) recorded the lowest supercooling points of two species of *Boreus* found active on snow from September to April at Finse in Norway as *ca.* −6°C. Their chill-coma temperatures at −4° to −5°C corresponded to a depression of the haemolymph melting point of between 0.6° and 0.7°C. Thermal hysteresis antifreeze agents have been found in one species (Husby & Zachariassen, 1980) and it is thought that such species may be active when supercooled.

For freezing intolerant lepidopterans, data are available for eggs (16 species), larvae (14 species), pupae (18 species) and for the adult of one species (Sømme, present volume). Some species of Lepidoptera exhibit good survival at low and ultralow temperatures. The prepupae of the slug caterpillar, *Cnidocampa flavescens*, readily supercooled, and survived for 100 days at temperatures below −20°C in anabiosis, to develop normally (Asahina *et al.*, 1954). Also, the overwintering third instar larvae of the butterfly *Aporia crataegi* survived freezing in liquid nitrogen if they were prefrozen for at least one hour at −30°C (Asahina *et al.*, 1972). No post-thaw injury was observed and many specimens metamorphosed to adults.

Studies have been made of cold hardiness in relation to diapause in several lepidopterans. In an earlier work, it was shown that glycogen was converted to glycerol and sorbitol for protection against low temperatures in diapausing eggs of the silk moth *Bombyx mori* (Chino, 1957, 1958). Sømme (1965b) detected variations due to climate in diapause eggs of *Acrolita naevana* in eastern and western Norway, and that larvae of *Laspeyresia strobilella* were freezing tolerant in mid-winter. In larvae of the Viceroy butterfly, *Limenitis archippus*, entering diapause in response to short-daylength, the winter content was reduced from 80% to *ca.* 59% and high glycerol levels (up to 1.9 M or *ca.* 8 g%) were found after cold exposure (Frankos & Platt, 1976). A direct relationship between diapause and cold hardiness was found in larvae in *Isia isabella* (Mansingh & Smallman, 1972). During induction and the early stages of diapause, glycerol and sorbitol levels increased, glycogen, trehalose and glucose levels declined and supercooling points were depressed from −1°C to −18°C. At termination of diapause, a depletion in polyols occurred, with concomitant increases in carbohydrates and supercooling points. However, in mature larvae of the European corn borer (*Pyrausta nubialis*), Hanec & Beck (1960) considered that supercooling points were not a reliable indication of their ability to survive sub-zero temperatures. Cold-hardy winter larvae survived for up to three months at −20°C in the absence of contact with moisture. Chilling in contact with water caused freezing but fully cold-hardy larvae survived with ice in their tissues.

Few biochemical pathway studies have been made. In the silkworm *Hyalophora cecropia*, glycerol was formed from glycogen by the action of glycogen phosphorylase, which is activated by cold. Glycogenolysis in such insects was controlled by the action of environmental temperature and the haemolymph gly-

cerol level on the phosphorylase system (Ziegler & Wyatt, 1975).

Both freezing susceptible and freezing tolerant forms are found in the Diptera, with tolerance being often restricted to a single life stage within a species.

In the Antarctic chironomid midge *Belgica antarctica*, larvae are freezing tolerant, with summer supercooling points around −8°C (Block, 1982), and they elaborate several possible cryoprotectants, which may derive from their food material (Baust & Edwards, 1979). Adults live for only a few days and are freezing susceptible in that they lack sufficient cryoprotectants. Baust (1980) considers that, as the only free-living holometabolous insect of the Antarctic region, *B. antarctica* possesses relict adaptive responses to low temperatures whilst living under relatively constant winter conditions in some habitats. Moderate freezing tolerance was demonstrated in larvae of a midge, *Metioctnimus* sp., exposed to sub-zero night temperatures on *Senecio* leaves above 3500 m altitude on Mount Kenya (Sømme & Zachariassen, 1981).

In the blowfly, *Lucilia seriacata*, Ring (1972) found that its ability to supercool changed little before, during and after diapause. The egg and pharate adult had the lowest supercooling points. He concluded that the processes leading to diapause induction did not enhance its cold hardiness. In another calliphorid, the arctic *Protophormia terranovae*, cold stress induced both glycerol synthesis, to levels in excess of 10% of fresh body weight, and significant weight loss, up to 58% over 39 days. Carbohydrate, and not lipid glycerol, appeared to be the source of free glycerol which accumulated in this way.

The tephritid gall fly, *Eurosta solidagensis*, utilizes extensive supercooling or cryoprotection by solutes during its life cycle (Morrissey & Baust, 1976). All stages except the third instar larvae have supercooling points below their normal environmental temperatures, but the third instar larvae, with relatively high supercooling points, are protected by a system comprising glycerol, sorbitol and trehalose, the concentrations of which peak at different times during winter. Nucleating agents were shown to be present in their haemolymph (Sømme, 1978b). Baust *et al.* (1979) found that several overwintering strategies were utilized by separate populations of co-existing gall insects. Storey *et al.* (1981) reported that enzyme variants were not involved in metabolic regulation at low temperature in *E. solidagensis* larvae.

An extreme example of freezing avoidance has been found in Alaskan willow gall insects, which supercool to −60°C, by Miller & Werner (1980).

Among the Hymenoptera much of the work on cold hardiness has been done on sawflies (Diprionidae) with some data for bees, wasps, ants and ichneumonids. In the poplar sawfly, *Trichiocampus populi*, large amounts (5–9% of fresh weight) of trehalose and poor supercooling (to −9°C in the prepupae) were shown initially (Asahina & Tanno, 1964). Using fat body cells, Tanno (1968a) showed that intracellular freezing, and hence mortality, increased with an increased cooling rate from 0.4° to 327°C/min. However, prepupae could survive immersion in liquid nitrogen after prefreezing at −30°C with a cooling rate of *ca.* 1°C/min (Tanno, 1968b), although they had difficulty at adult emergence. In the European pine sawfly, *Neodiprion sertifer*, the eggs supercoole
−33°C (Sullivan, 1965), −41°C (Kopvillem & K
sik, 1971) and −36°C (Austarå, 1971).

Working on bees, Krunic & Salt (1971) found supercooling points of the prepupae of *Megac relativa* (indigenous to Alberta) were inversely rel to glycerol concentrations, which were double t of *M. rotundata* (an exotic species). In the latter cies, freezing temperatures were related to the p ence or absence of food in the larval digestive t and to food type and nucleator content in the a (Krunic, 1971). Some ants have been studied (Tanno, 1962; Kipyatkov, 1971). All are freezing ceptible. Maavara (1971) recorded a range of su cooling points from −7°C to −26°C for seven cies. Over-wintering queens of the bald faced hor *Vespula maculata*, are tolerant of ice in their b fluids down to −14°C, which is correlated with glycerol concentrations (Duman & Patterson, 19 Additionally, macromolecular ice nucleating ag present in the haemolymph induce extracellular formation at high temperatures (*ca.* −5°C) and th by prevent lethal intracellular ice.

In the Coleoptera, two species of Carabidae h been studied in detail, *Pterostichus brevicornis Pelophila borealis*. Alaskan *P. brevicornis* were first adult insects found to be freezing tolerant, winter beetles surviving temperatures below −3 when frozen. However, summer beetles died if fro at −7°C (Miller, 1969). Supercooling points and cerol concentrations were closely correlated (Baus Miller, 1970, 1972). *P. borealis* has been studied Norway (Østbye & Sømme, 1972; Sømme, 197 Mean supercooling points of field beetles were alw lower than their habitat temperatures through winter on the Hardangervidda, and individuals c survive freezing at temperatures above −10°C. Fr ing tolerance increased during autumn and was maximum during winter. An oxygen debt detected by the accumulation of lactate in be enclosed by ice in the field and under anaerobic ditions in the laboratory. Anaerobiosis is an imp ant component of overwintering in this species (C radi-Larsen & Sømme, 1973a,b), in some al Coleoptera (Sømme, 1974b) and in the adult cera cid *Rhagium inquisitor* (Zachariassen & Påsche, 1 The supercooling points of three carabids inhab grass tussocks in northern England were shown t their survival (Luff, 1966).

Eight species of Staphylinidae have been exam by Topp (1978), Coccinellidae by Baust & Morr (1975) and Lee (1980) and weevils of the family C lionidae by Armbrust *et al.* (1969) and Bale (198

Adult *Pytho depressus* (*Pythidae*) are freezing t ant (Zachariassen, 1977). During winter, high co trations of glycerol and nucleators occur in the molymph causing high supercooling points. Su beetles are sensitive to freezing. The temperatur which harmful, non-penetrating solutes would r an injurious level in the frozen body fluids were mated for different pre-freezing glycerol co trations, and were found to range from −7 −27°C. These fitted the observed natural super ing points perfectly, suggesting that the colli properties of glycerol are the basis of its cryop tion in such freeze-tolerant insects (Zachari

9). *Pytho americanus* is freezing tolerant in both larval and adult stages, with supercooling points he region of −4° to −8°C (Ring & Tesar, 1980). s first demonstration of the phenomenon and its lerlying mechanisms highlighted the ecological antages of such a strategy.

onsiderable cold hardiness research has been car- out on the Tenebrionidae. Low temperature imation in adult *Tribolium confusum* influences tality at 0°C (Sømme, 1968a), indicating that re- ince and capacity adaptations are based on separ- physiological mechanisms. In the darkling beetle, *racantha contracta*, macromolecular antifreeze sol- s were discovered in the haemolymph by Duman 7a,b,c). Such solutes produce a thermal hysteresis reby the haemolymph freezing point is 3°–4° w its melting point in overwintering larvae, an ct similar to that produced by protein and glyco- tein antifreezes in many cold-adapted, marine osts. The functions of this may be to hinder inocu- ve freezing in damp micro-sites, and to depress the ercooling point of freezing susceptible larvae to und −11°C. Low environmental temperature and rt photoperiod are thought to be the main con- s responsible for the antifreeze being produced ing autumn and reaching a maximum concen- ion in mid-winter. Thermal hysteresis has also n observed in larval *Tenebrio molitor*, in which low perature and short photoperiod double the hyster- from *ca.* 0.75°C (Patterson & Duman, 1978). en acclimated to low relative humidity, thermal eresis of larvae increased almost three-fold. Miller mith (1975) reported the unusual combination of polyols, sorbitol and threitol, in the adult tene- nid *Upis ceramboides*, which conferred the ability lerate prolonged freezing to at least −50°C. In species, unusually low cooling rates °–0.35°C/min) were required to produce maxi- n freezing tolerance in the adults, whose lower l temperature was *ca.* −60°C (Miller, 1978a). The itivity to very slight changes in cooling rate is ing. In the northern taiga of north America, the les may experience temperatures as low as °C, which approximates to the lower limit of cold ance for winter specimens. Supercooling points age about −6°C, without variation throughout ear in spite of major haemolymph composition freezing tolerance changes (Miller, 1978b). Sum- beetles cannot withstand temperatures below supercooling points, but with the synthesis of polyols (to concentrations between 0.25 and M) comes increased freezing tolerance. A series of rs describe the freeze tolerance strategy found in *des blanchardi* (Zachariassen & Hammel, 1976a,b; ariassen *et al.*, 1979a,b). In southern California, supercooling points were in the range −5° to C, compared to freezing susceptible beetles ercooling points from −12° to −20°C). Their low olymph osmolarity indicated that polyols were ccumulated during winter, and nucleating agents oted freezing just below 0°C. Freezing tolerant es contained *ca.* 25% unfreezable water, which have been due to osmotically highly active mac- lecules. Comparison of cold- and warm-accli- d beetles suggests that the difference in their cold nce was not due to a colligative cryoprotective mechanism, but to acclimation of nervous tissues to freezing temperatures, thus reducing injury.

For the leaf eating Chrysomelidae, only *Melasoma collaris*, from the alpine zone of the Norwegian Hardangervidda, has been investigated. Concentrations approaching 50 μg glycerol/mg fresh weight allow freezing survival to −30°C in beetles stored at −5°C (Sømme & Conradi-Larsen, 1979). Frozen beetles survived −10° to −15°C for three months, but frost resistance was rapidly lost at 21°C. Adult beetles had supercooling points of −5° to −7°C throughout the year, due to the presence of nucleating agents.

Ring (1977), in his study of the birch engraver, *Scolytus ratzeburgi*, found that overwintering larvae were freezing susceptible and non-diapausing. Supercooling points ranged from −13°C (prepupal larvae) in the spring to *ca.* −34°C in larvae in mid-winter. Glycerol, amounting to *ca* 9% fresh weight, was the most abundant cryoprotectant. Supercooling was aided by high levels of trehalose and small quantities of sorbitol. Such a multi-factorial protection may reduce possible toxic effects of large concentrations of a single solute.

Adults of 13 beetle taxa from the alpine zone of Mount Kenya were tested for cold hardiness by Sømme & Zachariassen (1981). Two curculionid species were tolerant of freezing to −7°C, possessing high supercooling points and haemolymph nucleators. The remaining taxa were all sensitive to freezing with one species supercooling to −17°C.

The reviews of the role of polyols and nucleating agents in freeze tolerant Coleoptera by Zachariassen (1979, 1980) will not be covered here.

DISCUSSION

Freezing susceptibility and tolerance

An interesting aspect of invertebrate cold hardiness concerns the distribution of the two strategies amongst the various animal groups. Several features of the overwintering mechanisms of freezing tolerant species resemble those of freezing susceptible forms. Thus members of both groups synthesize glycerol or other polyhydroxy compounds, often in response to environmental or seasonal cues. Many freezing tolerant forms also supercool to a certain degree, sometimes in proportion to their glycerol content. Such similarities have led to a certain amount of confusion in the past.

Present evidence suggests that glycerol alone is not sufficient to confer freezing tolerance, as there are several freezing susceptible species that contain equally large amounts of glycerol to those found in freezing tolerant species. Similarly, injection of glycerol into freezing susceptible arthropods does not elicit tolerance to freezing. Also, some freezing tolerant animals do not possess glycerol. However, the evidence that glycerol is implicated in freezing tolerance is considerable (Asahina, 1969).

There have been three main theories of freezing injury. The first one maintains that the rise in electrolyte concentrations which accompanies freezing is lethal to cells, and that glycerol acts colligatively by lowering the temperature at which lethal levels are reached (Lovelock, 1953). The second or "site of freezing" theory is that freezing survival in nature is due to the prevention of intracellular ice formation, which

Table 1. Occurrence of the freezing susceptible and freezing tolerant strategies in invertebrate poikilotherms

Taxon	Freezing susceptible	Freezing tolerant	Cryoprotectants	Temperature °C Lowest SCP*	Frozen	Remarks
Protozoa	+	+?	Chlorides of salts may aid supercooling	−4	−196	Dehydration prior to freezing required, especially for encysted forms.
Platyhelminthes	+			−11		Single North Sea species.
Rhynchocoela	+			−5		Single Antarctic species.
Rotifera	+	+	Glycerol, dimethylsulphoxide		−196	Single Antarctic species.
Nematoda		+	Glycerol		−190	Desiccation critical; anhydrobiosis prevalent.
Mollusca	+	+		−9	−15	Up to 75% body water may freeze in intertidal species; land forms mainly freezing susceptible(?).
Annelida	+	+				North Sea polychaetes.
Tardigrada		+				Encysted state may be anabiotic.
Micro-Arthropoda (Collembola & Acari)	+		Glycerol, glucose, mannitol, ribitol trehalose	−37		Gut contents, temperature and polyols influence supercooling; juveniles may be more cold-hardy than adults
Arthropoda						
Scorpionida	+			−12		
Araneida	+		Glycerol	−30		Thermal hysteresis caused by proteins.
Pycnogonida	+			−4		Single Antarctic species.
Crustacea		+	Glycerol (very low concentrations)		−19	>80% body water of *Balanus* spp. may be frozen in winter.
Myriapoda		+?		−7		New Mexico species recovers after one SCP passage, but not after two.
Insecta						
Orthoptera		+?		−8 −30 (eggs)		Two tropical species.
Psocoptera	+			−37		Eggs of two species.
Hemiptera	+		Glycerol, mannitol	−37 −42 (eggs)		Feeding state important for cold hardiness in aphids.
Mecoptera	+			−6		Several species may be active when supercooled; thermal hysteresis.
Lepidoptera Ova	+		Glycerol, mannitol sorbitol, glucose	−51		
Larvae	+	+?	Glycerol, sorbitol trehalose, glucose, lactate, alanine	−49	−196[1]	[1]3rd instar if prefrozen for 1 hr at −30°C; diapause important; some prepupae anabiotic.
Imago	+			−21		
Diptera	+	+	Glycerol, glycogen, sorbitol, trehalose	−8	−60	Freezing tolerance often restricted to single life stage of species; haemolymph nucleating agents reported.
Hymenoptera	+	+	Glycerol, trehalose	−42	−196[2]	[2]Prepupae after prefreezing at −30° and 10°C/min cooling rate. Haemolymph nucleating agents reported.
Coleoptera	+	+	Glycerol, sorbitol threitol, macromolecular solutes	−31	−60[3]	[3]Cooling rate may be critical, especially for adults; anaerobiosis in some species; thermal hysteresis is of 3–4°C; haemolymph nucleators reported.

onsidered to cause cell death by osmotic, mech-
al or other means (Asahina, 1969). However, fat
y cells of some insects tolerate intracellular ice
nation (Salt, 1962). The third theory, proposed by
itt (1966), is that freezing damage is caused by
tein denaturation which occurs by the formation
lisulphide bonds between molecules in close prox-
y during dehydration of cells in the freezing pro-

aust (1973) considered that the "site of freezing"
ory was untenable on present insect data. He
ught that freezing tolerance mechanisms in ani-
s were based on a multicellular system that pos-
ed glycerol in high, non-lethal concentrations, that
ld maintain activity in the presence of tissue ice,
could survive frequent freeze–thaw cycles and
could regulate cryoprotectant levels in the face of
nging environments. There seems little advantage
ttempting to separate sites of freezing and the
ous events during freezing and thawing in what
clearly dynamic processes. But there is much to be
ned in the observation of the freezing behaviour of
eous systems (Mackenzie, 1977). The phenomenon
supercooling is limited by heterogeneous nu-
tion occurring in the presence of solid impurities.
nparison of the behaviour of water droplets with
ll arthropod systems may be useful (Block &
ng, 1979). In this case, a given quantity of glycerol
essed the supercooling point more than it did the
ting point of the fluids, the effect being accen-
ed in the animal system. It is unlikely that ice
tal growth will be initiated by homogeneous nu-
tion in animals. Emphasis on the measurement of
temperature at which ice forms in a supercooled
l, the supercooling point, may not always be the
or the best approach in studying freezing suscep-
invertebrates. The supercooling point is
enced by many factors, including duration of ex-
re to low temperatures, cooling rate (if any), the
ity and quantity of nucleating agents and the laws
robability (Salt, 1961).

ne occurrence of freezing susceptible and tolerant
s in the invertebrates reviewed in this paper is
vn in Table 1. Considering the insects to the level
rder, there are nine taxonomic groups which are
rted as being only freezing susceptible, compared
ossibly five (three?) which may be only freezing
ant. In about eight taxa, both freezing susceptible
freezing tolerant species have been reported.
e appears to be no clear pattern in the distribu-
of the two strategies at this level in the inverte-
es. This raises the question as to whether freezing
ance confers any advantage over freezing suscep-
ity, especially in habitats in which both types
r. There would appear to be, on present evidence,
support for a phylogenetic component in the
tion of one mechanism rather than the other.
ever, other factors, which may be broadly classi-
under morphology and ecology could contribute
ne adoption of one strategy over the other in a
cular group or species.

lutes in the haemolymph, other than glycerol, are
ght to exert an important effect on supercooling.
arch on the Mediterranean flour moth, *Ephestia*
niella, using final instar larvae, showed the pres-
of ninhydrin positive substances due to an in-
creased alanine content of the haemolymph, together with increasing concentrations of glycerol and glucose at low temperatures (6°, 0°, −6°C) (Sømme, 1966b). This was accompanied by some inorganic phosphate increment. As glycerol levels were low, it was postulated that the haemolymph solutes were responsible for the increased supercooling. Extending the study to three species of overwintering Lepidoptera, Sømme (1967) identified increases in other solutes, especially sorbitol, trehalose, lactate and alanine which had effects similar to glycerol, with cold hardiness. When glycerol was injected into *Ephestia* larvae, it promoted supercooling and their survival at −6° and −10°C (Sømme, 1968b).

Supercooling is probably promoted by the small size of an animal, the small volume of which will have a reduced nucleator content compared to larger poikilotherms. Survival of small forms, when supercooled, will be aided also by a reduced probability of inoculative freezing, especially in micro-arthropods with sclerotised exoskeletons. In habitats where frequent freeze–thaw cycles occur, it may be ecologically advantageous for a species to supercool, at least moderately, to avoid disruption of the life cycle by a cold tolerance mechanism. Alternatively, the metabolic cost of cryoprotectant synthesis may be high in some species, and freezing tolerance could be more economical with regard to resource exploitation. Also, the level or concentration of any cryoprotectant substance should not reach toxic levels in the cells or tissues of the animal. Such factors as these will act in opposite ways and the outcome may be a compromise. The complexity facing experimental biologists in this field is considerable, and careful research on the mechanisms involved in freezing susceptibility and freezing tolerance is now required. The importance of a firm field basis for experiments cannot be over emphasised, especially with respect to the microclimatic conditions prevailing in the habitat. Only then can the subject progress beyond the correlation of a process with a possible biochemical or environmental control. This has been highlighted in a recent paper by Baust (1981). A fully predictive theory of cold hardiness for invertebrate poikilotherms must remain a future goal for low temperature biologists.

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REFERENCES

ARMBRUST J., WHITE C. E. & DEWITT J. R. (1969) Lethal limits of low temperature for the alfalfa weevil in Illinois. *J. Econ. Ent.* **62**, 464–467.

AOKI K. & KONNO H. (1961) Frost-resistance of the rotifer in Antarctic Region. *Bull. biol. Stn Asamushi* **X**, 247–250.

ASAHINA E. (1959) Frost-resistance in a nematode *Aphelenchoides ritzemabosi*. *Low Temp. Sci. Ser. B* **17**, 51–62.

ASAHINA E. (1966) Freezing and frost resistance in insects. In *Cryobiology* (Edited by MERYMAN H. T.), pp. 451–486. Academic Press, London.

ASAHINA E. (1969) Frost resistance in insects. In *Advances in Insect Physiology*, Vol. 6, (Edited by BEAMENT J. W. L., TREHERNE J. E. & WIGGLESWORTH V. B.), pp. 1–49. Academic Press, London.

ASAHINA E. & TANNO K. (1964) A large amount of trehalose in a frost resistant insect. *Nature, Lond.* **204**, 1222.

ASAHINA E., AOKI K. & SHINOZAKI J. (1954) The freezing process of frosthardy caterpillars. *Bull. ent. Res.* **45**, 329–339.

ASAHINA E., OHYAMA Y. & TAKAHASHI T. (1972) Formation of normal adults of a butterfly, *Aporia crataegi*, developed from larvae frozen to liquid nitrogen temperature. *Low Temp. Sci. Ser. B* **30**, 91–98.

ASHWOOD-SMITH M. J. (1970) Effects of low temperatures on micro-organisms, plant and cold blooded animals. In *Current Trends in Cryobiology* (Edited by SMITH A. U.), pp. 5–42. Plenum Press, New York.

ASHWOOD-SMITH M. J. & FARRANT J. (Eds.) (1980) *Low Temperature Preservation in Medicine and Biology*. Pitman Medical Ltd, Tunbridge Wells, UK.

AUSTARÅ Ø. (1971) Cold hardiness in eggs of *Neodiprion sertifer* (Geoffroy) (Hym., Diprionidae) under natural conditions. *Norsk ent. Tidsskr.* **18**, 45–48.

BALE J. S. (1980) Seasonal variation in cold hardiness of the adult beech leaf mining weevil *Rhynchaenus fagi* L. in Great Britain. *Cryo-Letters* **1**, 372–383.

BAUST J. G. (1973) Mechanisms of insect freezing survival. *Cryobiology* **10**, 197–205.

BAUST J. G. (1980) Low temperature tolerance in an Antarctic insect. A relict adaptation? *Cryo-Letters* **1**, 360–371.

BAUST J. G. (1981) Biochemical correlates to cold hardening in insects. *Cryobiology* **18**, 186–198.

BAUST J. G. & EDWARDS J. S. (1979) Mechanisms of freezing tolerance in an Antarctic midge, *Belgica antarctica*. *Physiol. Ent.* **4**, 1–5.

BAUST J. G. & MILLER L. K. (1970) Variations in glycerol content and its influence on cold hardiness in the Alaskan carabid beetle *Pterostichus brevicornis*. *J. Insect Physiol.* **16**, 979–990.

BAUST J. G. & MILLER L. K. (1972) Influence of low temperature acclimation on cold hardiness in the beetle *Pterostichus brevicornis*. *J. Insect Physiol.* **18**, 1935–1947.

BAUST J. G. & MORRISSEY R. E. (1975) Supercooling phenomenon and water content independence in the overwintering beetle *Coleomegilla maculata*. *J. Insect Physiol.* **21**, 1751–1754.

BAUST J. G., GRANDEE R., CONDON G. & MORRISSEY R. E. (1979) The diversity of overwintering strategies utilized by separate populations of gall insects. *Physiol. Zoöl.* **52**, 572–580.

BLOCK W. (1982) Supercooling points of insects and mites on the Antarctic Peninsula. *Ecol. Ent.* **7**, 1–8.

BLOCK W. & SØMME L. (1982) Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. *Oikos* **38**, 157–167.

BLOCK W. & YOUNG S. R. (1979) Measurement of supercooling in small arthropods and water droplets. *Cryo-Letters* **1**, 85–91.

BLOCK W., YOUNG S. R., CONRADI-LARSEN E.-M. & SØMME L. (1978) Cold tolerance of two Antarctic terrestrial arthropods. *Experientia* **34**, 1166–1167.

BLOCK W. & ZETTEL J. (1980) Cold hardiness of some Alpine Collembola. *Ecol. Ent.* **5**, 1–9.

CHINO H. (1957) Conversion of glycogen to sorbitol and glycerol in the diapause eggs of the *Bombyx* silkworm. *Nature, Lond.* **180**, 606–607.

CHINO H. (1958) Carbohydrate metabolism in the diapause egg of the silkworm, *Bombyx mori*. II. Conversion of glycogen into sorbitol and glycerol during diapause. *J. Insect Physiol.* **2**, 1–12.

CLARK R. B. & PANCHEN A. L. (1971) *Synopsis of Animal Classification*. 126 pp. Chapman & Hall Ltd., London.

CLOUDSLEY-THOMPSON J. L. (1973a) Terrestrial invertebrates. In *Comparative Physiology of Thermoregulation* (Edited by WHITTON G. C.). pp. 15–77. Academic Press, New York.

CLOUDSLEY-THOMPSON J. L. (1973b) Factors influencing supercooling of tropical Arthropoda, especially loc *J. nat. Hist.* **7**, 471–480.

CLOUDSLEY-THOMPSON J. L. (1978) Diurnal rhythm supercooling in locusts. *Int. J. Bioclim. Biomet.* 112–115.

CLOUDSLEY-THOMPSON J. L. & CRAWFORD C. S. (1 Lethal temperatures of some arthropods of the s western United States. *Entomologist's mon. Mag.* 26–29.

CONRADI-LARSEN E.-M. & SØMME L. (1973a) The over tering of *Pelophila borealis* Payk. II. Aerobic and a obic metabolism. *Norsk ent. Tiddsskr.* **20**, 325–332.

CONRADI-LARSEN E.-M. & SØMME L. (1973b) Anaerob in the overwintering beetle *Pelophila borealis*. *Na Lond.* **245**, 388–390.

COOK P. A. & GABBOTT P. A. (1970) Seasonal change the free glycerol level in the body parts of the a barnacle *Balanus balanoides*. *Mar. Biol.* **7**, 11–13.

COOK P. A. & GABBOTT P. A. (1972) Seasonal change the biochemical composition of the adult barn *Balanus balanoides*, and the possible relations between biochemical composition and cold-toleranc *mar. biol. Ass. U.K.* **52**, 805–825.

CRAWFORD C. S. & RIDDLE W. A. (1974) Cold hardine centipedes and scorpions in New Mexico. *Oikos* 86–92.

CRAWFORD C., S. & RIDDLE W. A. (1975) Overwinte physiology of the scorpion *Diplocentrus spitzeri*. *Ph Zoöl.* **48**, 84–92.

CRAWFORD C. S., RIDDLE W. A. & PUGACH S. (1975) O wintering physiology of the centipede *Scolopendra morpha*. *Physiol. Zoöl.* **48**, 290–294.

CRISP D. J. & RITZ D. A. (1967) Changes in tempera tolerance of *Balanus balanoides* during its life-cycle. *goländer wiss. Meeresunters.* **15**, 98–115.

CROWE J. H. & MADIN K. A. C. (1975) Anhydrobios nematodes: evaporative water loss and survival. *J. Zool.* **193**, 323–334.

DE CONINCK L. A. P. (1951) On the resistance of the living nematode *Anguillula silusiae* to low temperat *Biodynamica* **7**, 77–84.

DORONINA G. M. & MARKAROVA L. A. (1971) Cold-h ness in *Eurygaster integriceps* Put. and the forecasti its winter survival. In *Cold Hardiness in Insects Mites*. (Edited by MAAVARA V.), pp. 23–26. Acade Sciences of the Estonian SSR, Tartu (in Russian).

DUMAN J. G. (1977a) The role of macromolecular freeze in the darkling beetle, *Meracantha contract comp. Physiol.* **115**, 279–286.

DUMAN J. G. (1977b) Variations in macromolecular freeze levels in larvae of the darkling beetle, *Meracantha contracta*. *J. exp. Zool.* **201**, 85–92.

DUMAN J. G. (1977c) Environmental effects of antif levels in larvae of the darkling beetle, *Meracantha tracta*. *J. exp. Zool.* **201**, 333–337.

DUMAN J. G. (1979) Subzero temperature toleran spiders: the role of thermal-hysteresis factors. *J. Physiol.* **131**, 347–352.

DUMAN J. G. & PATTERSON J. L. (1978) The role nucleators in the frost tolerance of overwintering q of the bald faced hornet. *Comp. Biochem. Physiol.* 69–72.

EGUAGIE W. E. (1974) Cold-hardiness of *Tingis am* (Heteroptera: Tingidae). *Entomologia exp. appl* 204–214.

FRANKOS V. H. & PLATT A. P. (1976) Glycerol acc lation and water content in larvae of *Limenitis arch* their importance to winter survival. *J. Insect Physi* 623–628.

GLINYANAYA E. I. (1971) Cold-hardiness in the diap eggs in some species of Copeognatha. In *Cold Har in Insects and Mites*. (Edited by MAAVARA V.), pp.

cademy of Sciences of the Estonian SSR, Tartu (in ussian).
EC W. & BECK S. D. (1960) Cold hardiness in the uropean corn borer *Pyrausta nubilalis* (Hübn). *J. Insect hysiol.* **5**, 169–180.
RIS R. J. C. (1951) *Freezing and Drying* (Report of a mposium held in June 1951). The Institute of Biology, ondon.
MSTROM W. F., GROUT B. W. W. & MORGAN E. (1981) eliminary observations on the low temperature toler- ce of an estuarine amphipod *Corophium volutator* allas). *Cryo-Letters* **2**, 129–134.
BY J. A. & ZACHARIASSEN K. E. (1980) Antifreeze ents in the body fluid of winter active insects and iders. *Experientia* **36**, 963–964.
WISHER J. W. (1955) Freezing in intertidal animals. *iol. Bull. mar. biol. Lab., Woods Hole.* **109**, 56–63.
WISHER J. W. (1959) Histology and metabolism of ozen intertidal animals. *Biol. Bull. mar. biol. Lab., oods Hole.* **116**, 258–264.
WISHER J. W. (1966) Freezing in intertidal animals. In *yobiology* (Edited by MERYMAN H. T.), pp. 487–494. ademic Press, London.
ATKOV V. E. (1971) Photoperiodic responses and cold- rdiness in *Myrmica rubra* L. In *Cold Hardiness in sects and Mites.* (Edited by MAAVARA V.), pp. 35–38. ademy of Sciences of the Estonian SSR, Tartu (in ussian).
HNER W. (1973) Ecological aspects of cold resistance spiders (a comparative study). In *Effects of Tempera- re on Ectothermic Organisms.* (Edited by WIESER W.), . 271–279. Springer, Heidelberg.
HNER W. & KESTLER P. (1969) Untersuchungen zur ilteresistenz der Schilfradspinne *Araneus cornutus* raneidae). *J. Insect Physiol.* **15**, 41–53.
ILER J. K. (1967) Studies on the survival of the rotifer *ilodina* after freezing and thawing. *Cryobiology* **3**, 2–399.
ILER J. K. & JOHNSON L. K. (1969) Food supply as a tor in the survival of frozen and thawed rotifers. *Cryo- logy* **5**, 375–378.
ILLEM H. & KUUSIK A. (1971) On the cold-hardiness overwintering eggs of the European pine sawfly *Neo- rion sertifer* (Geoffr.) and its parasite *Achrysocharella orum* (Krausse). *Eesti NSV Tead. Akad. Toim. Biol.* 291–297.
NIC M. D. (1971) Influence of food on the cold hardi- ss of *Megachile rotundata* (F). *Can. J. Zool.* **49**, 3–865.
NIC M. D. & SALT R. W. (1971) Seasonal changes in cerol content and supercooling points of *Megachile undata* (F.) and *M. relativa* Cress. *Can. J. Zool.* **49**, 3–666.
. E. (1980) Physiological adaptations of Coccinellidae supranivean and subnivean hibernacula. *J. Insect ysiol.* **26**, 135–138.
T J. (1966) Winter hardiness in plants. In *Cryobiology* lited by Meryman H. T.), pp. 495–563. Academic ss, London.
OCK J. E. (1953) The mechanism of protective action glycerol against haemolysis by freezing and thawing. *chim. biophys. Acta* **11**, 28–36.
A-LOZINSKII L. K. (1948) The effect of salts on the d resistance of Infusoria and the causes of death ler cooling. *Zh. obshch. Biol.* **9**, 411–453.
A-LOZINSKII L. K. (1974) *Studies in Cryobiology*, pp. John Wiley & Sons, New York.
M. L. (1966) Cold-hardiness of some beetles living in ss tussocks. *Entomologica exp. Appl.* **9**, 191–199.
B. J. & HARTUNG M. C. (1941) Factors in revival of *uillula aceti* after its solidification in liquid air. *Am. J. siol.* **133**, 368–369.
ARA V. (1971) On cold-hardiness in some ant species. In *Cold Hardiness in Insects and Mites.* (Edited by MAAVARA V.), pp. 68–71. Academy of Sciences of the Estonian SSR, Tartu (in Russian).
MACKENZIE A. P. (1977) Non-equilibrium freezing behaviour of aqueous systems. *Proc. R. Soc. B* **278**, 167–189.
MANSINGH A. & SMALLMAN B. N. (1972) Variation in polyhydric alcohol in relation to diapause and cold-hardiness in the larvae of *Isia isabella*. *J. Insect. Physiol.* **18**, 1565–1571.
MERIVEE E. (1978) *Cold-hardiness in Insects*, 188 pp. Eesti NSV Teaduste Akadeemia, Tartu (in Russian).
MERYMAN H. T. (1966) Review of biological freezing. In *Cryobiology* (Edited by MERYMAN H. T.), pp. 2–106. Academic Press, London.
MILLER L. K. (1969) Freezing tolerance in an adult insect. *Science, N.Y.* **166**, 105–106.
MILLER L. K. (1978a) Freezing tolerance in relation to cooling rate in an adult insect. *Cryobiology* **15**, 345–349.
MILLER L. K. (1978b) Physical and chemical changes associated with seasonal alterations in freezing tolerance in the adult northern tenebrionid *Upis ceramboides*. *J. Insect Physiol.* **24**, 791–796.
MILLER L. K. (1978c) Physiological studies of arctic animals. *Comp. Biochem. Physiol.* **59A**, 327–334.
MILLER L. K. & SMITH J. S. (1975) Production of threitol and sorbitol by an adult insect: association with freezing tolerance. *Nature, Lond.* **258**, 519–520.
MILLER L. K. & WERNER R. (1980) Supercooling to −60°C: an extreme example of freezing avoidance in northern willow gall insects. *Cryobiology* **17**, 621–622.
MORRISSEY R. E. & BAUST J. G. (1976) The ontogeny of cold tolerance in the gall fly, *Eurosta solidagensis*. *J. Insect Physiol.* **22**, 431–437.
MURPHY D. J. (1977a) Metabolic and tissue solute changes associated with changes in the freezing tolerance of the bivalve mollusc *Modiolus demissus*. *J. exp. Biol.* **69**, 1–12.
MURPHY D. J. (1977b) A calcium-dependent mechanism responsible for increasing the freezing tolerance of the bivalve mollusc *Modiolus demissus*. *J. exp. Biol.* **69**, 13–21.
MURPHY D. J. (1979) A comparative study of the freezing tolerances of the marine snails *Littorina littorea* (L.) and *Nassarius obsoletus* (Say). *Physiol. Zoöl.* **52**, 219–230.
MURPHY D. J. & PIERCE S. K. (1975) The physiological basis for changes in the freezing tolerance of intertidal molluscs. I. Response to subfreezing temperatures and the influence of salinity and temperature acclimation. *J. exp. Zool.* **193**, 313–322.
NAMATOV T. (1969) Resistance of the nematode *Anguina tritici* and *Rhabditis* sp. to low and extremely low temperatures. *Dokl Akad. Nauk SSSR* **185**, 1382–1385 (in Russian).
O'DELL S. J. & CROWE J. H. (1979) Freezing in nematodes: the effects of variable water contents. *Cryobiology* **16**, 534–541.
ØSTBYE E. & SOMME L. (1972) The overwintering of *Pelophila borealis* Payk. I. Survival rates and cold-hardiness. *Norsk ent. Tidsskr.* **19**, 165–168.
PATTERSON J. L. & DUMAN J. G. (1978) The role of the thermal hysteresis factor in *Tenebrio molitor* larvae. *J. exp. Biol.* **74**, 37–45.
PIGON A. & WEGLARSKI B. (1955) Anabiosis in Tardigrada. Metabolism and humidity. *Bull. Acad. pol. Sci. Cl. II Sér. Sci. Biol.* **3**, 31–34.
POLYANSKII Y. I. & POZNANSKAYA T. M. (1964) Prolonged cultivation of *Paramecium caudatum*. *Acta protozool.* **27**, 271–278 (in Russian).
PURSCHKE G. (1981) Tolerance to freezing and supercooling of interstitial Turbellaria and Polychaeta from a sandy tidal beach of the Island of Sylt (North Sea). *Mar. Biol.* **63**, 257–267.
RAKUSA-SUSZCZEWSKI S. & MCWHINNIE M. A. (1976) Re-

sistance to freezing by antarctic fauna: supercooling and osmoregulation. *Comp. Biochem. Physiol.* **54A**, 291–300.
REAUMUR R. A. F. (1734) *Memoires pour Servir à l'histoire des Insectes.* **2**(170). 141–147. d'Imprimerie Royal, Paris.
RING R. A. (1972) Relationship between diapause and supercooling in the blowfly *Lucilia sericata* (*Mg.*) (*Diptera: Calliphoridae*). *Can. J. Zool.* **50**, 1601–1605.
RING R. A. (1977) Cold-hardiness of the bark beetle *Scolytus ratzeburgi* Jans (Col., Scolytidae). *Norw. J. Ent.* **24**, 125–136.
RING R. A. (1980) Insects and their cells. In *Low Temperature Preservation in Medicine and Biology.* (Edited by ASHWOOD-SMITH M. J. & FARRANT J.), Ch. 9, pp. 187–217. Pitman Medical Ltd., Tunbridge Wells, UK.
RING R. A. & TESAR D. (1980) Cold-hardiness of the arctic beetle, *Pytho americanus* Kirby Coleoptera, Pythidae (Salpingidae). *J. Insect Physiol.* **26**, 763–774.
RING R. A. & TESAR D. (1981) Adaptations to cold in Canadian Arctic insects. *Cryobiology* **18**, 199–211.
ROLAND W. & RING R. A. (1977) Cold, freezing and desiccation tolerance of the limpet *Acmaea digitalis* (Eschscholtz). *Cryobiology* **14**, 228–235.
SALT R. W. (1961) Principles of insect cold-hardiness. *A. Rev. Ent.* **6**, 55–74.
SALT R. W. (1962) Intracellular freezing in insects. *Nature, Lond.* **193**, 1207–1208.
SALT R. W. (1969) The survival of insects at low temperatures. In *Dormancy and Survival* (Edited by WOOLHOUSE H. W., pp. 331–350. Cambridge University Press, Cambridge, U.K.
SCHAEFER M. (1976) An analysis of diapause and resistance in the egg stage in *Floronia bucculenta* (Araneida: Linyphiidae). *Oecologia* **25**, 155–174.
SCHATZ H. & SØMME L. (1981) Cold-hardiness of some oribatid mites from the Alps. *Cryo-Letters* **2**, 207–216.
SMITH A. U. (1961) *Biological effects of freezing and supercooling*, 462 pp. Edward Arnold Ltd., London.
SOMME L. (1964) Effects of glycerol on cold-hardiness in insects. *Can. J. Zool.* **42**, 87–101.
SOMME L. (1965a) Changes in sorbitol content and supercooling points in overwintering eggs of the European red mite (*Paronychus ulmi* (Koch)). *Can. J. Zool.* **43**, 881–884.
SOMME L. (1965b) Further observations on glycerol and cold-hardiness in insects. *Can. J. Zool.* **43**, 765–770.
SOMME L. Seasonal changes in the freezing tolerance of some intertidal animals. *Nytt Mag. Zool.* **13**, 52–55.
SOMME L. (1966b) The effect of temperature, anoxia, or injection of various substances on haemolymph composition and supercooling in larvae of *Anagasta kuehniella* (Zell.). *J. Insect Physiol.* **12**, 1069–1083.
SOMME L. (1967) The effect of temperature and anoxia on haemolymph composition and supercooling in three overwintering insects. *J. Insect Physiol.* **13**, 805–814.
SOMME L. (1968a) Acclimation to low temperatures in *Tribolium confusum* Duval (Col., Tenebrionidae). *Norsk ent. Tidsskr.* **15**, 134–136.
SOMME L. (1968b) The effect of acclimation and glycerol injection on mortality and pupation in larvae of *Ephestia kuehniella* after exposures at low temperatures. *Entomologia exp. appl.* **11**, 143–148.
SOMME L. (1969) Mannitol and glycerol in overwintering aphid eggs. *Norsk ent. Tidsskr.* **16**, 107–111.
SOMME L. (1974a) The overwintering of *Pelophila borealis* Payk. III. Freezing tolerance. *Norsk ent. Tidsskr.* **21**, 131–134.
SOMME L. (1974b) Anaerobiosis in some alpine Coleoptera. *Norsk ent. Tidsskr.* **21**, 155–158.
SØMME L. (1978a) Cold-hardiness of *Cryptopygus antarcticus* (Collembola) from Bouvetøya. *Oikos* **31**, 94–97.
SØMME L. (1978b) Nucleating agents in the haemolymph of third instar larvae of *Eurosta solidagensis* (Fitch) (Dipt., Tephritidae) *Norw. J. Ent.* **25**, 187–188.
SØMME L. (1979a) Kuldetoleranse hos alpine og arkt collemboler. *Ent. Tidskr.* **100**, 149–151.
SØMME L. (1979b) Overwintering ecology of alpine Coll bola and oribatid mites from the Austrian Alps. *Ent.* **4**, 175–180.
SØMME L. (1981) Cold tolerance of alpine, arctic Antarctic Collembola and mites. *Cryobiology* 212–220.
SØMME L. (1982) Adaptation to low temperature in Ant tic terrestrial arthropods. C.N.F.R.A., No. 51, 219–2
SØMME L. & BLOCK W. (1982) Cold-hardiness of Col bola at Signy Island, maritime Antarctic. *Oikos* 168–176.
SØMME L. & CONRADI-LARSEN E.-M. (1979) Frost resist in alpine, adult *Melasoma collaris* (Coleoptera). *Oikos* 80–84.
SØMME L. & ØSTBYE E. (1969) Cold hardiness in s winter active insects. *Norsk ent. Tidsskr.* **16**, 45–48.
SØMME L. & ZACHARIASSEN K. E. (1981) Adaptations to temperature in high altitude insects from Mount Ke *Ecol. Ent.* **6**, 199–204.
STOREY K. B., PARK I. R. A. & STOREY J. M. (1981) zyme composition and low temperature acclimatio the overwintering gall fly larva, *Eurosta solidage Cryo-Letters* **2**, 279–284.
STÖVER H. (1973) Cold resistance and freezing in *Ari arbustorum* L. (Pulmonata). In *Effects of Temperatu Ectothermic Organisms.* (Edited by WIESER W.) 281–290. Springer, Heidelberg.
SUKHANOVA K. M. (1968) *Temperature Adaptatio Protozoa.* Leningrad (in Russian).
SULLIVAN C. R. (1965) Laboratory and field investiga on the ability of eggs of the European pine sawfly, *diprion sertifer* (Geoffroy) to withstand low winter peratures. *Can. Ent.* **97**, 978–993.
TANNO K. (1962) Frost resistance in a carpenter ant, *ponotus obscuripes.* I. The relation of glycerol to resistance. *Low Temp. Sci. Ser. B* **20**, 25–34 (in Japa English summary).
TANNO K. (1968a) Frost resistance in the poplar sa *Trichiocampus populi* Okamoto. IV. Intracellular fre in fat-cells and injury occurring upon metamorp *Low Temp. Sci. Ser. B* **26**, 71–77.
TANNO K. (1968b) Frost resistance in the poplar s *Trichiocampus populi* Okamoto. V. Freezing injury liquid nitrogen temperature. *Low Temp. Sci. Ser.* 79–83.
TAYLOR A. C. & STRICKLAND A. G. (1936) Effects of vacua and extreme temperatures on cysts of *Co cucullus. Physiol. Zoöl.* **9**, 15–26.
THEEDE H. (1972) Vergleichende ökologische-phy gische Untersuchungen zur zellulären Kälteres marinen Evertebraten. *Mar. Biol.* **15**, 160–191.
TOPP W. (1978) Untersuchungen zur Kälteresistenz b phyliniden (Col.). *Zool. Anz. Jena* **201**, 397–402.
USHATINSKAYA R. S. (1957) *Principles of Cold Resista Insects*, 314 pp. Academy of Sciences, USSR Moscow (in Russian).
WESTHEIDE W. & VON BASSE M. (1978) Chilling and ing resistance of two interstitial polychaetes f sandy tidal beach. *Oecologia* **33**, 45–54.
WILLIAMS R. J. (1970) Freezing tolerance in *Mytilus Comp. Biochem. Physiol.* **35**, 145–161.
YOUNG S. R. (1979) Aspects of the environmental ology of an Antarctic terrestrial mite. Ph.D. thesis versity of Leicester, U.K.
YOUNG S. R. & BLOCK W. (1980) Experimental stu the cold tolerance of *Alaskozetes antarcticus. J. Physiol.* **26**, 189–200.
ZACHARIASSEN K. E. (1977) Effects of glycerol in tolerant *Pytho depressus* L. (Col., Pythidae). *N Ent.* **24**, 25–29.
ZACHARIASSEN K. E. (1979) The mechanism of the c

ctive effect of glycerol in beetles tolerant to freezing. *J. sect Physiol.* **25**, 29–32.
HARIASSEN K. E. (1980) The role of polyols and nucleat-g agents in cold-hardy beetles. *J. comp. Physiol.* **140**, 27–234.
HARIASSEN K. E. & HAMMEL H. T. (1976a) Nucleating gents in the haemolymph of insects tolerant to freezing. *ature, Lond.* **262**, 285–287.
HARIASSEN K. E. & HAMMEL H. T. (1976b) Freeze-toler-ice in adult tenebrionid beetles. *Norw. J. Zool.* **24**, 9–352.
HARIASSEN K. E. & PÅSCHE A. (1976) Effect of anaero-biosis on the adult cerambycid beetle *Rhagium inquisitor* L. *J. Insect Physiol.* **22**, 1365–1368.
ZACHARIASSEN K. E., HAMMEL H. T. & SCHMIDEK W. (1979a) Osmotically inactive water in relation to toler-ance to freezing in *Eleodes blanchardi* beetles. *Comp. Bio-chem. Physiol.* **63A**, 203–206.
ZACHARIASSEN K. E., HAMMEL H. T. & SCHMIDEK W. (1979b) Studies on freezing injuries in *Eleodes blanchardi* beetles. *Comp. Biochem. Physiol.* **63A**, 199–202.
ZIEGLER R. & WYATT G. R. (1975) Phosphorylase and gly-cerol production activated by cold in diapausing silk-moth pupae. *Nature, Lond.* **254**, 622–623.

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HETEROGENEOUS ICE NUCLEATION IN SUPERCOOLED MICRO-ARTHROPODS

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SUMMARY

The probability of freezing increased exponentially with lowered temperature for seven species of Antarctic arthropods. Slopes of fitted regressions were similar for most species at two locations. Low temperature acclimation moved the regression line significantly downwards, but the slope remained unchanged. Individual arthropods behaved in a similar fashion to water droplets when supercooled at 0.5 to 1.0 deg min^{-1}, but neither stochastic nor singular models for heterogeneous nucleation appear adequate.

KEY WORDS

freezing probability, micro-arthropods, supercooling, Antarctic.

Invertebrate ectotherms are either freezing susceptible (dying at their supercooling point) or freezing tolerant (surviving the freezing process when supercooled). Supercooling (or undercooling) is the term used to describe a solution when it is cooled below its freezing point but remains in a liquid state. The supercooling point is recognised by a small but transitory rise in body temperature due to latent heat released during freezing in such invertebrates. Supercooling point data are used extensively to assess the cold hardiness of individual arthropods from both field populations in relation to environmental conditions and low temperature acclimation experiments. It is generally measured using a standard cooling rate of ca.1 deg min^{-1}, as a variation in rate of cooling does not alter the mean supercooling point significantly[1,2]. Various compounds such as polyhydric alcohols and sugars have been correlated with lowering of the supercooling point[3,4]. It is widely held that heterogeneous nucleation (formation of the ice phase being dependent on

foreign particles) occurs when such biological systems undergo supercooling. Alternatively, in homogeneous nucleation, the ice phase is initiated by the combination of water molecules to form an ice embryo which grows spontaneously[5].

This paper raises the general question of whether the supercooling point is both a valid and an adequate measure of invertebrate cold hardiness, and reports the results of analyses undertaken on data for cold adapted micro-arthropods. In this way, attempts to answer the following specific questions are made: (1) Is the increase in the probability of freezing in such animals during supercooling similar between species? and (2) Are there differences between biological systems such as terrestrial arthropods and physical systems such as water droplets?

METHODS

Data resulting from extensive supercooling point determinations in the Antarctic of field specimens of two species of springtails (Collembola), four species of mites (Acari) and one dipteran species (larval Chironomidae) were analysed. The probability of ice nucleation was calculated from the number of animals freezing per degree divided by the number unfrozen and plotted against temperature. Exponential regressions were fitted to these data plots and the slopes compared. Data resulting fron low temperature acclimation experiments in some species were similarly analysed.

Supercooling points were measured using a cooling rate of 1 deg min^{-1} and the techniques described by Block & Sømme[6]. The experimental work was undertaken in the period January - March 1980 at Signy Island in the South Orkney Islands (60°43'S, 45°36'W)[7], at Galindez Island in the Argentine Islands (65°15'S, 64°16'W) and at Rothera Point on Adelaide Island (67°34'S, 68°07'W)[8]. All these sites lie within the maritime Antarctic zone[9]. For the mites Alaskozetes antarcticus, Nanorchestes antarcticus, Stereotydeus villosus and the collembolans Cryptopygus antarcticus, Parisotoma octooculata, a range of post-embryonic life stages were used representing juveniles to adults. Exceptions were the mite Gamasellus racovitzai (deutonymphs and adults only) and the midge Belgica antarctica (larvae only). All taxa are referred to by their generic names hereafter.

RESULTS

Plots of the probability of freezing on temperature (Fig. 1) show that in some species gut contents influence nucleation events in the temperature range from 0 to $-20^{\circ}C$. This is the case for Gamasellus, Stereotydeus, Parisotoma and the larval midge (Belgica) for which all the supercooling points lie above $-20^{\circ}C$ (Table 1). The exceptions are Alaskozetes and Nanorchestes together with the collembolan Cryptopygus. In both cases, however, trends can be seen of increasing probability of freezing as temperature decreases. In order to compare species, the zones in which nucleation appears to be random were excluded. In this way, comparisons were restricted to individuals of similar feeding status and to those animals which were representative of the field situation during early winter[6,7].

The regressions derived from the field data for the seven species are given in Table 1 and the fitted lines are compared in Fig. 2. It is clear that the probability of freezing in these species increases exponentially with declining temperature under the conditions of the experiments. The intercept (a) values (Table 1) define three groups of species in terms of the lowest probability (i.e. ca 1%) of freezing, which is the temperature at which freezing events begin their exponential rise during cooling at 1 deg min^{-1}. Firstly, there are four species having relatively high intercept values, which range from -4 to $-8^{\circ}C$. Secondly, there are two taxa (Cryptopygus and Alaskozetes), which have lower intercept values of -13 to $-18^{\circ}C$. Thirdly, Nanorchestes is intermediate with a value of ca $-10^{\circ}C$. The first two groups correspond to the high and low groups of the species supercooling point distributions as observed previously[6,7]. The position of the intercept for the exponential curve varies with the species, and is probably related to the effectiveness of nucleators present in the different forms.

In seven within-species and between-sites comparisons of slopes of the fitted regression lines on the field data (Table 1), significant differences were detected in only two cases. In Stereotydeus, the slope of the regression line for the Galindez Island sample was significantly ($P<0.002$) steeper than that for the Signy Island sample. A similar result was found for Gamasellus ($P<0.05$). In both cases, the probability of freezing increased more rapidly with decreasing temperature for the Antarctic Peninsula animals compared to Signy Island specimens. For the Signy Island experiments, supercooling point data from six species which had been acclimated to low temperatures (0 and $-5^{\circ}C$ for 15 to 42 d) were

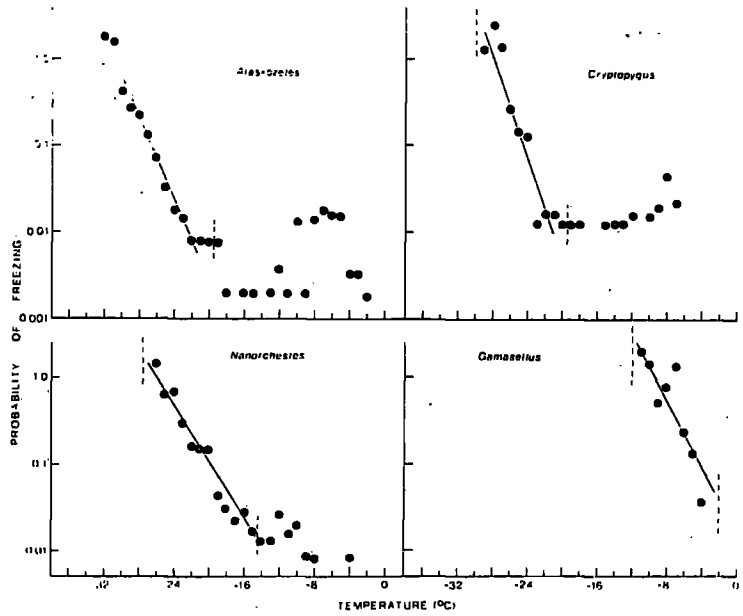

Fig. 1. The probability of freezing as a function of temperature for four Antarctic micro-arthropods: Alaskozetes (AA1), Nanorchestes (NA2), Gamasellus (GR2) and Cryptopygus (CA1). (See Table 1). The vertical dashed lines indicate the limits of the data used in fitting regressions.

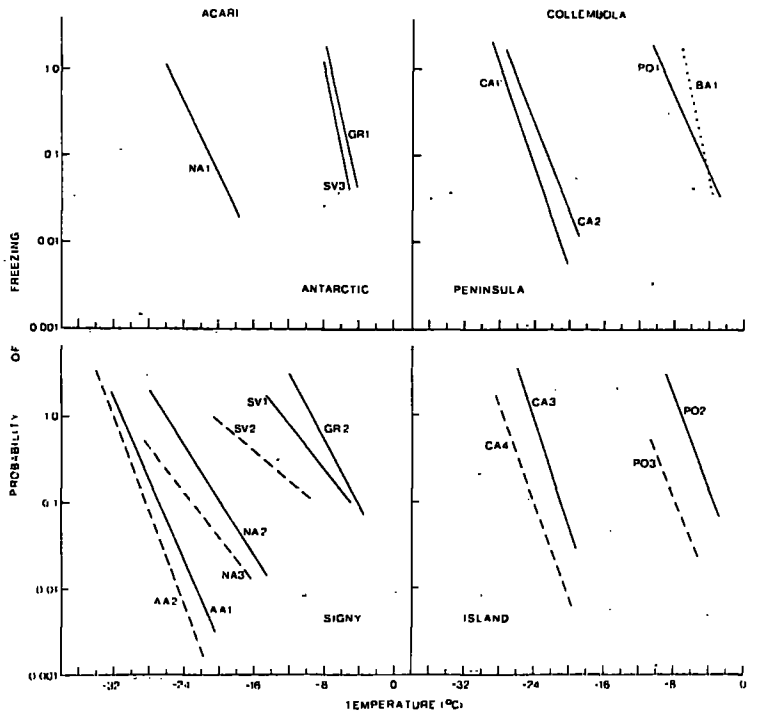

Fig. 2. Relationship of the probability of freezing to temperature during supercooling in seven species of arthropods at three Antarctic locations. (See Table 1). Solid lines: field animals; dashed lines: acclimated animals; dotted line: field larvae of Belgica (BA1).

TABLE 1. REGRESSION COEFFICIENTS FOR EXPONENTIAL CURVES OF THE PROBABILITY OF FREEZING ON DECREASING TEMPERATURE DURING SUPERCOOLING IN MICRO-ATHROPODS. SUPERCOOLING POINT (SCP) DATA ARE DERIVED FROM FIELD AND ACCLIMATED SAMPLES OF SEVEN SPECIES OF ACARI AND COLLEMBOLA AT THREE ANTARCTIC LOCATIONS. CODES ARE AS FOR FIGS 1 AND 2.

Taxon	Site	Code	Number SCPs	a	b	SE_b	r^2	n	P
Acari:									
Alaskozetes antarcticus	Signy Is Field	AA1	341	-15.734	-0.515	0.024	0.975	13	<0.01
" "	Signy Is 0°C/28d	AA2	41	-15.966	-0.510	0.113	0.742	9	<0.01
Nanorchestes antarcticus	Galindez Is Field	NA1	21	-10.891	-0.429	0.123	0.706	7	<0.05
" "	Signy Is Field	NA2	95	-9.754	-0.385	0.022	0.967	12	<0.01
" "	Signy Is 0°C/7d; -5°C/21d	NA3	68	-9.864	-0.336	0.056	0.777	12	<0.01
Stereotydeus villosus	Signy Is Field	SV1	77	-3.738	-0.300	0.090	0.613	9	<0.05
" "	Signy Is 0°C/8d; -5°C/20d	SV2	28	-3.394	-0.168	0.063	0.499	9	<0.05
" "	Galindez Is Field	SV3	30	-7.744	-0.996	0.132	0.965	4	<0.05
Gamasellus racovitzai	Galindez Is Field	GR1	12	-5.596	-0.804	0.095	0.972	4	<0.05
" "	Signy Is Field	GR2	107	-4.328	-0.497	0.085	0.850	8	<0.01
Collembola									
Cryptopygus antarcticus	Adelaide Is Field.	CA1	93	-18.175	-0.661	0.089	0.872	10	<0.01
" "	Galindez Is Field	CA2	32	-13.411	-0.508	0.112	0.773	8	<0.01
" "	Signy Is Field	CA3	26	-17.362	-0.734	0.157	0.844	6	<0.01
" "	Signy Is -5°C/28d	CA4	47	-17.121	-0.619	0.080	0.908	8	<0.01
Parisotoma ortooculata	Galindez Is Field	PO1	66	-4.587	-0.497	0.180	0.559	8	<0.05
" "	Signy Is Field	PO2	112	-4.159	-0.621	0.178	0.751	6	<0.05
" "	Signy Is 0°C/15d	PO3	45	-6.206	-0.532	0.075	0.925	6	<0.01
Diptera									
Belgica antarctica	Galindez Is Field	BA1	61	-6.104	-0.934	0.242	0.832	5	<0.05

also analysed. Although low temperature exposure resulted in a decrease in slope of the fitted regression line compared to field results (Fig. 2), in no instance was it significant. Therefore the probability of freezing for such acclimated animals was similar to that for field samples of the same species under the experimental conditions. It is concluded that, in general, the probability of freezing in a cooling regime of 1 deg min^{-1} is not altered by habitat or low temperature acclimation in such arthropods.

Comparisons of regression slopes between-species and within-sites (Signy and Galindez Islands) suggests there are two groups of species at each site (Table 1, Fig. 2). At Signy Island, the slopes of the regressions for Cryptopygus, Parisotoma and Alaskozetes are significantly steeper than those for Gamasellus, Nanorchestes and Stereotydeus. However at Galindez Island, the steepest slopes are found for Gamasellus, Belgica and Stereotydeus compared to those for Cryptopygus, Parisotoma and Nanorchestes. Thus the increase in the probability of freezing with decreasing temperature may be influenced by species characteristics to a certain extent. It is suggested that susceptibility to freezing in these terrestrial arthropods may be determined principally by species characteristics rather than by ecological or environmental factors.

DISCUSSION

According to the theory of heterogeneous nucleation, the temperature at which a supercooled water droplet nucleates will be affected by the impurity content, its size and the cooling rate[5]. Micro-arthropods may be considered to behave as water drops with a potentially high level of impurity, especially in the gut system. The effects of gut content may be largely eliminated in these species by consideration of the supercooling process below ca. -20°C[6,7]. Thus, a more direct comparison is possible between the behaviour of small arthropods and water droplets during supercooling. The observations of Vali and Stansbury[10] on freezing of distilled water droplets of 10 µl volume at a cooling rate of 0.5 deg min^{-1} provide a baseline. There is no significant difference in slope of the regression line relating probability of freezing to decreasing temperature when results from water droplets and micro-arthropods are compared. Thus it can be concluded that, for the species examined, individual Acari and Collembola behave in a similar fashion to small water drops when supercooled at 0.5 to 1.0 deg min^{-1}.

Two models have been proposed to describe the freezing of water

droplets when supercooled. The stochastic hypothesis assumes that if a collection of droplets all have the same particulate content at any one time, then the drops will have identical probabilities of freezing. Freezing would therefore be controlled by a stochastic (or statistical) process. This theory predicts that at a constant cooling rate, freezing events will occur continually with their frequency increasing as temperature declines. Alternatively, the singular model assumes that each droplet nucleates at a temperature determined by the most effective ice nucleus it contains. Thus, no freezing events should occur at a constant temperature. Both these models of heterogeneous nucleation predict that the probability of freezing per degree fall in temperature should increase exponentially with decreasing temperature, which is the case with the present results for micro-arthropods. However, in the stochastic model the probability is dependent on freezing rate, whereas in the singular model, it is independent of this variable. Clearly, neither the stochastic nor the singular model fits the available data for heterogeneous nucleation of water droplets or micro-arthropods. The nucleating temperature is determined mainly by properties of the nucleating sites (assumed by the singular model), whereas the growth of ice embryos to a critical size by random fluctuations envisaged by the stochastic model also plays a role in the process.

In respect of the time and temperature dependence of heterogeneous nucleation in micro-arthropods, both Cryptopygus and Alaskozetes exhibit[2] a trend of lower mean low group supercooling points[3] at faster rates of cooling in the range 0.125 to 1.0 deg min^{-1}. The average depression of the mean freezing temperature was 0.5 deg for an order of magnitude increase in cooling rate for both species, which is slightly less than ca. 0.65 deg for water droplets[10].

Solutes such as polyols and sugars also influence heterogeneous nucleation in invertebrate systems. Glycerol depresses the supercooling points of Alaskozetes and water droplets, which is equivalent in the former to 2.2 deg per degree of melting point depression (of isolated haemolymph)[11]. This ratio ranges from 1.3 to 3.7 for various arthropods, and confirms that the supercooling points of invertebrate systems may be depressed by more than twice the melting point at any given glycerol concentration. In addition, if thermal hysteresis proteins are present in the haemolymph, supercooling may be stabilised by blocking ice crystal growth over a wide temperature range[12]. It is difficult to conceive a mechanism whereby such solutes can exert a predictable influence on

supercooling in micro-arthropods in the presence of foreign nucleators without such stabilisation or masking of potential nucleators.

ACKNOWLEDGEMENTS

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REFERENCES

1 R.W. Salt, Can. J. Zool. 44, 655-659 (1966).

2 R.J.C. Cannon, J. Insect Physiol. (in press).

3 S.R. Young and W. Block, J. Insect Physiol. 26, 189-200 (1980).

4 J.G. Baust, Cryobiology 18, 186-198 (1981).

5 P.V. Hobbs, "Ice Physics", Clarendon Press, Oxford (1974).

6 W. Block and L. Sømme, Oikos 38, 157-167 (1982).

7 L. Sømme and W. Block, Oikos 38, 168-176 (1982).

8 W. Block, Ecol. Ent. 7, 1-8 (1982).

9 M.W. Holdgate, in "Biologie antarctique", R. Carrick, M.W. Holdgate and J. Prevost, eds. Hermann, Paris (1964), p. 181.

10 G. Vali and E.J. Stansbury, Can. J. Phys. 44, 477-502 (1966).

11 W. Block and S.R. Young, Cryo-Letters 1, 85-91 (1979).

12 K.E. Zachariassen and J.A. Husby, Nature (London) 298, 865-867 (1982

Biol (1983) 2:109–114

Polar Biology

Temperature Adaptations in Beetles from the Sub-Antarctic Island outh Georgia

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ary. Adaptations to the Sub-Antarctic climate of Georgia were studied in four species of Cole-. In larvae and adults of *Hydromedion sparsutum* *erimylops antarcticus* (Perimylopidae) collected summer, the ability to supercool was increased by mperature acclimation, and more in specimens ıigh than from low elevations. Both adults and were killed by freezing at temperatures below −5 °C. Supercooling ability of adult *Oopterus sole-s* (Carabidae) also increased slightly with acclima-hile no effect was observed in *Halmaeusa atriceps* ylinidae). Both species were freezing-intolerant. ial cryoprotectants present in the beetles were se, glycerol, myoinositol and glucose. The maxi-oncentrations of individual sugars and polyols from 4–20 μg mg^{-1} live weight, and were not ed by low temperature acclimation in the labora-he life cycles of *H. sparsutum* and *P. antarcticus* to extend for two or more years. Their adapta-lso include brachyptery and the utilisation of for food. None of the species survived anoxia for d periods.

ction

of eight species of Coleoptera have been recorded e Sub-Antarctic island of South Georgia (Gressitt vhere they experience a climate resembling that of conditions. According to Smith and Walton ınnual mean temperature is 1.8 °C, and the range n monthly air temperatures varies from 5.3 °C ry) to −1.5 °C (August). At King Edward Point, land East Bay, where continuous meteorological tions have been made over 68 years, winter tem-s below −19 °C have not been recorded. The of winter is long, generally with a permanent ver from May to October. Insects and mites seek-r in plants and litter underneath the snow are tected from low winter temperatures in their microhabitats. Their main problem may be to survive near zero temperatures which occur for four to five months in winter, and to continue their development during the short, cold summers.

The purpose of the present investigation was to examine the cold hardiness of representative beetles from South Georgia, as well as to study other aspects of their adaptation to the particular Sub-Antarctic climatic conditions of the island. Four species of beetles were chosen, of which two species (a carabid and a staphylinid) live in sheltered lowland habitats close to the seashore. The other two species (both perimylopids) may be exposed to low temperatures in the valleys and in particular on mountain slopes at higher elevations.

The studies were undertaken at the Grytviken station of the British Antarctic Survey during the austral summer months of January, February and early March 1982.

Materials and Methods

Field Collection

Of the four species, the carabid *Oopterus soledadinus* (Guérin 1830) was found mainly under rocks and debris, and in tussock grass litter around Grytviken and King Edward Point. According to Darlington (1970) this beetle has been found from sea level to 150 m a.s.l. The staphylinid *Halmaeusa atriceps* (Waterhouse 1875) inhabits the seashore as well as moss, tussock grass, albatross nests and penguin rookeries away from the shore (Steel 1970), and was collected by us from tussock grass litter close to the beach at Grytviken and Maiviken. *Hydromedion sparsutum* (Müller 1884) and *Perimylops antarcticus* Müller 1884, which belong to the family Perimylopidae, were collected from lowland localities, under rocks and vegetation along streams in Bore Valley and the valleys surrounding Gull Lake. They were also collected from highland localities in sparse mosses *(Bartramia, Brachythecium* and *Tortula* spp.) on mountain sides below Narwhal Peak and Mount Hodges at elevations of about 350–400 m a.s.l. According to Watt (1970) most specimens of *H. sparsutum* have been collected previously below 150 m, but some at 240 m a.s.l., while *P. antarcticus* has been found from sea level to about 800 m a.s.l. on South Georgia.

Larvae of *O. soledadinus* and *H. atriceps* were not found in sufficient numbers, and experimental work was done on adults only. In *H. sparsutum* and *P. antarcticus* studies were made on both adults and

larvae in the last three of their six instars, without distinguishing between instars IV – VI.

Acclimation and Starvation

For studies on cold hardiness, winter conditions were simulated by depriving the beetles of food and storing them in temperature cabinets at 0 ± 0.5 °C and 2 ± 0.5 °C in a saturated atmosphere. The effect of starvation was also studied in beetles stored in a cold room at 9 ± 2 °C. The cabinets and cold room were without light.

Supercooling

Supercooling points were measured either by a single-point battery operated Grant recorder, or by a Linseis L 2061 six-channel continuous recorder. Individual beetles were placed in contact with copper-constantan thermocouples (40 – 36 swg), which were then fixed in position inside glass or polythene tubes. To control the rate of cooling the thermocouple was placed inside one or two polythene vials, closed by rubber stoppers, through which the thermocouple wire was run. The vials were lowered into a thermos flask one-third filled with ethyl alcohol that previously had been cooled to ca. −25 °C in a freezer, and in which the temperature was lowered further by the addition of CO_2-ice made in a Jencons Snowpack apparatus connected to a CO_2-flask. The rate of cooling was controlled manually by the extent to which the vials were lowered into the cold alcohol, and a cooling rate of 1 to 2 °C min^{-1} was achieved. Supercooling points were read from the recorder charts as the point of origin of the temperature rise that accompanied the emission of latent heat from the insect during spontaneous freezing.

Freezing-Tolerance

The degree of freezing-tolerance of the beetles was determined by a method modified from Zachariassen (1979). Following their spontaneous freezing at the supercooling point, and the accompanying rise in temperature, the beetles were slowly cooled for a second time. When the desired temperature was reached at or below the supercooling point, the beetles were removed, and left at room temperature (ca. 20 °C) to recover. After 15 – 30 min their condition was assessed by their ability to move. Those showing normal activity, or only slightly unco-ordinated movements were considered as survivors. Beetles with strongly unco-ordinated movements, as well as specimens unable to walk, were considered as moribund, and placed in the same category as motionless ones. The test was repeated with surviving beetles at slightly lower temperatures, until they were found to be dead or moribund.

During handling, some specimens, in particular adult beetles, tended to regurgitate liquid gut content, which probably caused ice formation to start around the mouth and to spread inside the beetle when cooled. For this reason supercooling was greatly inhibited and since it was considered an artefact, specimens with supercooling points above −2 °C were not included in the mean and range of supercooling points. Beetles frozen at temperatures above −2 °C, however, were also cooled to lower temperatures as desired, and the results included in the data on survival and mortality during freezing.

Cryoprotective Substances

Individual adults and/or larvae of three species of Coleoptera were macerated in 70% ethanol for each sample and treatment. For *H. atriceps* three specimens were utilised per sample as the adult live weight was only ca. 1 mg. Table 1 provides the live weight ranges for individual adults and larvae obtained for each of the four species using a microbalance (Beckman LM 500), and these are representative of the sample weights used for chromatography.

The ethanol extracts were stored below 0 °C during transport from South Georgia to the BAS laboratories in Cambridge, UK. Analyses of the extracts for polyhydric alcohols and sugars using GLC techniques were undertaken after derivatives had been prepared with a trimethylsilyl reagent with pyridine (Sigma Sil-A) (Sweeley et al. 1963). A Pye-Unicam GCD instrument with a Chrompack CP^{tm}-Sil 5 non-polar capillary column was used with helium as the carrier gas. Confirmation of sample peaks was obtained by co-injection of standards. Integration of curve areas and corrections were undertaken using a Hewlett-Packard Integrator 3380A. A total of five to six determinations wa for each treatment and sample, and mean concentrations of the fied substances were derived in μg mg^{-1} live weight (lw) of ins

Table 1. Individual live weight ranges for four species of Georgian Coleoptera. Larval weights include IV – VI instars

Species	Life stage	Live wt ran
Hydromedion sparsutum	adult	11.7 – 44.6
	larva	8.7 – 33.9
Perimylops antarcticus	adult	6.2 – 18.9
	larva	4.8 – 18.9
Oopterus soledadinus	adult	5.4 – 11.2
Halmaeusa atriceps	adult	0.8 – 1.0

Anoxia

Anaerobic conditions were produced in 6 mm diameter glas (Conradi-Larsen and Sømme 1973; Block and Sømme 1982), were flushed and filled with nitrogen and sealed by melting bo after the introduction of three to six beetles. A few preli experiments were performed on adults of three species of bee *sparsutum*, *P. antarcticus* and *O. soledadinus*. The tubes were for various times at 0 °C, after which the beetles were remov normal atmosphere and placed on moist filter paper in a Pet Their recovery within 24 h at room temperature was recorded percentage mortality calculated.

Larval Instars

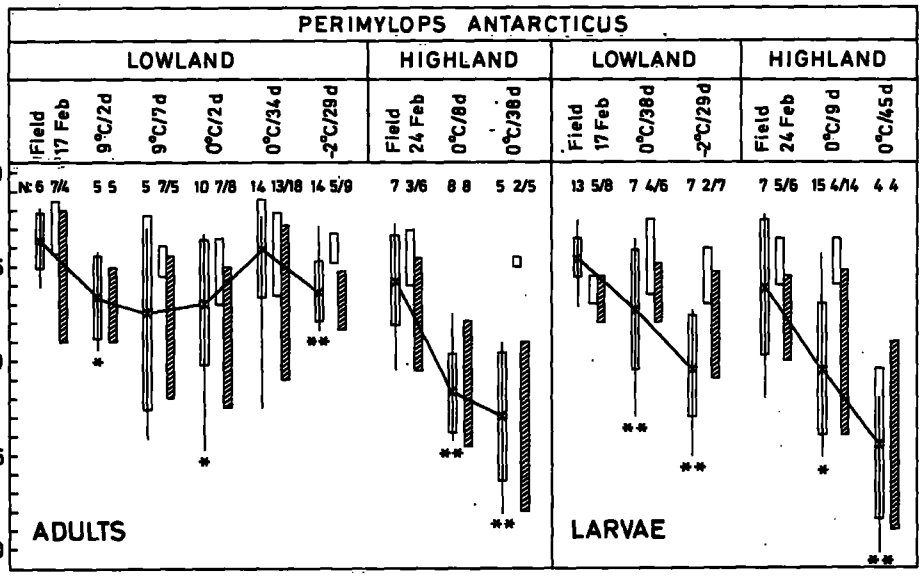
Head capsule widths were measured to the nearest 0.025 m × 40 magnification on ca. 200 larvae of *H. sparsutum* and 25 l *P. antarcticus* to determine the instar composition.

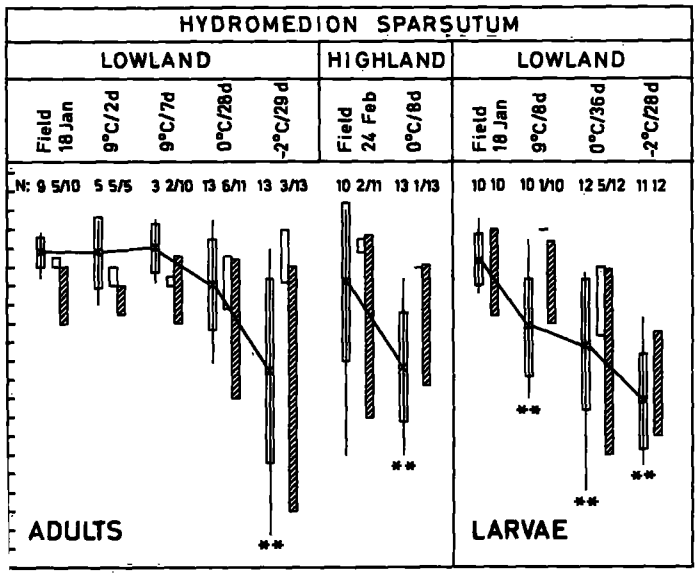
Results

Cold-Hardiness

The results of experiments on supercooling and fr tolerance in *P. antarcticus* and *H. sparsutum* are p ed in Figs. 1 and 2. Field collected adults of both from lowland habitats showed very poor ability to cool. Mean supercooling points were −3.6 and − for *P. antarcticus* and *H. sparsutum* respective specimens were killed by freezing at temperatures −5 °C, and some specimens of *P. antarcticus* died to −3 °C. Supercooling points of field-collected l larvae of both species were slightly lower, but differ significantly from those of the adults. La *H. sparsutum* were killed by freezing at tempe below −3 °C, while a few specimens of *P. ant* survived to −7 °C.

Starvation at 9 °C for up to one week had n on adult *H. sparsutum* from lowland localities, b ed to improve the supercooling capacity of *P. ticus*. In *H. sparsutum* the mean supercooling pc lowered to −5.9 °C during acclimation at 0 °C, −10.5 °C in beetles acclimated at −2 °C for 2 Low temperature acclimation also increased the a supercool in adult *P. antarcticus*, with the exce specimens acclimated for 34 days at 0 °C. The re this deviation is not known. Both starvation temperature acclimation had in general little effe





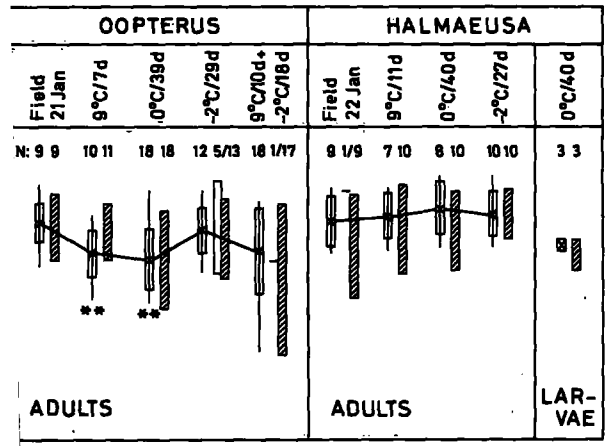


Fig. 1. Mean supercooling points and results of freezing-tolerance tests for adults and larvae of *Perimylops antarcticus*. The specimens were collected in the field from lowland and highland localities, and acclimated under starvation at 9.0 and −2°C in the laboratory. Comparison by *t*-test of mean supercooling points of acclimated specimens with those of corresponding field collected animals are given: $*P < 0.05$, $**P < 0.01$. Other comparisons were not significantly different. *N* number of specimens used for mean supercooling points and surviving/dead specimens from freezing-tolerance tests

Fig. 2. Mean supercooling points and results of freezing-tolerance tests for adults and larvae of *Hydromedion sparsutum*. Details as for Fig. 1

Fig. 3. Mean supercooling points and results of freezing tests for adult specimens of *Oopterus soledadinus* and *Halmaeusa atriceps*. Details as for Fig. 1

freezing-tolerance of lowland adult beetles, and no specimens survived freezing below −7°C.

In larvae from lowland localities a marked effect of acclimation at 0 and −2°C on their supercooling points was observed in both species. Larvae of *H. sparsutum* also lowered their supercooling points during 8 days at 9°C. Following acclimation for 36 days at 0°C five larvae of *H. sparsutum* survived freezing in the range of −5.0 to −8.5°C, indicating that their freezing-tolerance was slightly increased. For technical reasons, since the supercooling points of larvae acclimated at −2°C were all relatively low, freezing above −8.5°C could not be controlled, and all specimens were killed by freezing below this temperature.

Field collected adults of *H. sparsutum* from highland localities had a mean supercooling point of −5.8°C, and adults and larvae of *P. antarcticus* exhibited mean

supercooling points of −5.7 and −6.1 °C, respectively. These values were generally lower than those of corresponding lowland specimens. Since restricted numbers of specimens from highland localities were available, acclimation experiments were performed at 0 °C only. At this temperature the mean supercooling point of adults of *H. sparsutum* was lowered to −10.3 °C, and of adults and larvae of *P. antarcticus* to −12.9 and −14.5 °C, respectively.

From these results it is concluded that, in general, the highland beetles are more coldhardy than the lowland specimens, and they respond faster to decreasing temperatures. These differences are in accordance with the increased severity of the thermal environment experienced by these insects at higher elevations on South Georgia. The level of freezing-tolerance of highland larvae and adult *P. antarcticus* and adult *H. sparsutum* did not differ from the corresponding lowland forms.

In *O. soledadinus* relatively small changes in supercooling points of adult beetles were observed (Fig. 3), although their values were significantly lower after storage at 9 and 0 °C. With the exception of a few specimens acclimated at −2 °C, all beetles were killed by freezing at temperatures below −3 °C. Similarly, adults of *H. atriceps* were susceptible to freezing, and did not survive temperatures below ca. −3 °C (Fig. 3). Their supercooling points remained almost constant regardless of starvation and low temperature acclimation.

Cryoprotective Substances

The only compound present in more than trace amounts in field adults and larvae of *H. sparsutum* was trehalose, the maximum concentration (18 µg mg^{-1} lw) being recorded in larvae from the Gull Lake area. In general, acclimation at low temperatures reduced trehalose levels in both life stages. Glycerol was detected in small amounts (ca. 4 µg mg^{-1} lw) in larvae after 28 days and 35 days at 0 °C.

Similarly, trehalose was present in the highest concentration of all the compounds found in *P. antarcticus,* and was higher in larvae than in adults. Trehalose occurred particularly in field samples collected from both Gull Lake and Mount Hodges (adults 10–12 µg mg^{-1} lw, larvae 16–19 µg mg^{-1} lw), and in specimens acclimated at 0 °C for 8 days (13–20 µg mg^{-1} lw). However, exposure for longer periods, e.g. 36 days at 0 °C resulted in decreased trehalose levels. Trehalose also occurred in concentrations of 10–12 µg mg^{-1} lw in both life stages after 29 days at −2 °C. Maximum glycerol levels were found in both adults and larvae in field samples from Mount Hodges (7–8 µg mg^{-1} lw). Glucose levels of ca. 9 µg mg^{-1} lw were measured in larvae exposed to 0 °C for 9 days.

Trehalose, glycerol and myoinositol were the main substances in adults of *O. soledadinus*. Trehalose peaked after 35 days at 0 °C (17 µg mg^{-1} lw compared to 4–6 µg mg^{-1} lw in other samples), and myoinositol after 29 days at −2 °C (9 µg mg^{-1} lw). The latter corresponded to the pattern for glycerol in this species with a maxim of 12 µg mg^{-1} lw.

In samples of adult *H. atriceps,* myoinosi trehalose and glycerol were detected after acclimatio 0 and −2 °C. Maximum concentrations were 8, 5 a µg mg^{-1} lw respectively.

Anoxia

The results of preliminary anoxia experiments indi that a large proportion of adult *H. sparsutum* an *antarcticus* may survive in a nitrogen atmosphere at for 2 days, but that virtually all are killed in 4 d Slightly higher survival rates were recorded in *soledadinus* in which half of the specimens were after 4 days.

Larval Instars

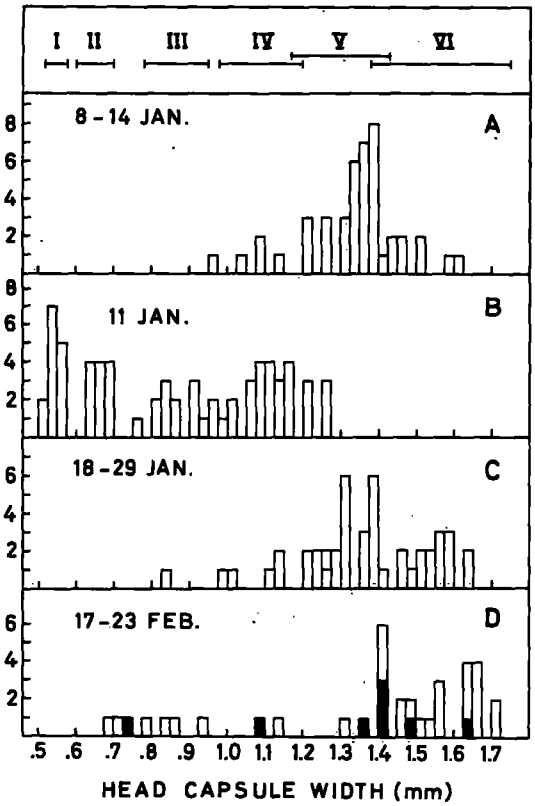
The head capsule widths of *H. sparsutum* are comp to the results of Watt (1970) regarding division instars I–VI (Fig. 4). Larvae sifted from tussock litter near the beach at King Edward Point were m in the I to IV instars (Fig. 4B). Other larvae, h collected from under rocks and moss in the valleys on the mountain slopes, were mostly V and VI i larvae, although a few II–IV were found (Fig. 4A D). The difference reflects the fact that the sm instars are easily overlooked by hand-collecting ir field. With the exception of a small increase in number of VI instar larvae, there was no differen instar composition of the larval collections from tussock grass habitats in early and late January (Fig. C). Towards the end of February this increase in the portion of VI instar larvae was more pronounced 4D). There appeared to be no difference in i composition of lowland and highland larvae collect February (Fig. 4D), but since only a few specimens latter were available, no conclusions may be draw general, it is concluded that all six larval instar present during the summer months, and that ther tendency for an increase in the proportion of VI i larvae towards the end of this period.

Only a small number of hand-collected larvae *antarcticus* were examined (Fig. 5). Most of them w their IV–VI instars, but a few specimens in e instars indicate that all instars of this species also during the summer.

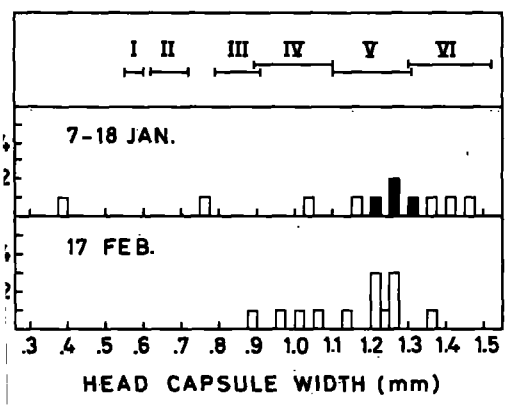
Discussion

Cold Hardiness

The method used to determine freezing-tolerance present study omits consideration of the time fact pointed out by Asahina (1969) and later shown in insect species, mortality due to freezing increase with time and decreasing temperature. For ex adults of the carabid *Pelophila borealis* were kille at −10 °C, while some specimens survived seven at −5 ° and several months at −3 °C (Sømme 1



4. Head capsule measurements of larvae of *Hydromedion sparsu-* collected at South Georgia during January and February 1982. The al instars are shown according to Watt (1970). *A, C* and *D:* Hand- ected from under rocks and mosses, *B:* Sifted from tussock grass r. Open bars represent lowland localities, black bars highland local-



5. Head capsule measurements of larvae of *Perimylops antarcticus* ted at South Georgia during January and February 1982. The instars are shown according to Watt (1970). Open bars represent nd localities, black bars highland localities

s likely that higher mortality rates would have been d for larvae and adult beetles in the present study, if had been left in the frozen state for longer time ds (which was not possible for technical reasons at AS station). Although small differences in rates of val were found among specimens frozen at different eratures, none of the four species possesses a degree ezing-tolerance of any ecological significance. hus, South Georgian beetles depend mainly on su- oling for winter survival. In *H. sparsutum* and *P. antarcticus* the ability to supercool increased during low temperature acclimation, and particularly in specimens from highland localities (Figs. 1 and 2). On steep mountain slopes, where the latter specimens were collected, winter air temperatures are probably much lower, and protection from the sparse vegetation and snow cover much less than in the valleys at lower elevations.

On morphological, taxonomic and ecological grounds, it is thought that *P. antarcticus* survived the Pleistocene on South Georgia, whereas *H. sparsutum* may be a recent immigrant to the island, possibly since the last glaciation (Watt 1970). Although *P. antarcticus* lives at higher elevations than *H. sparsutum,* the present results from summer-collected beetles do not indicate a significant difference in cold hardiness between the two species.

Adults of *H. atriceps* did not increase their cold-hardiness in response to low temperature acclimation and starvation, whilst mean supercooling points of *O. soledadinus* were lowered slightly at 0 and 9 °C (Fig. 3). Both species are found mainly in various types of plant litter in the coastal lowlands and near the seashore, and these habitats are often covered by snow during the winter.

The microclimate of certain lowland terrestrial communities on South Georgia has been studied, especially in respect of the soil and plant litter habitats. Typically, although air temperatures within 1 m of the ground may be as low as ca. −12 °C, the thermal regime near the soil surface in a *Festuca* grassland may be in the 0 to −2 °C zone for approximately four months (May – September). In addition, the depth of snow cover varies according to length of the winter period, type of plant community, aspect, elevation, year, etc. Maximum depths of snow for most lowland areas are generally in the range 30 – 40 cm, although 70 – 80 cm have been recorded on a *Tortula-Rostkovia* site near Gull Lake (D. W. H. Walton, personal communication). Therefore, the supercooling capacity (mean supercooling point range −5 to −8 °C) found in summer beetles would probably afford sufficient protection against extreme winter temperatures for the majority of the populations of the four species examined.

Cryoprotective Substances

In both *H. sparsutum* and *P. antarcticus* the highest concentrations of potential cryoprotectants were found in field animals, where trehalose was the most common substance with glycerol and glucose also occurring. Generally, higher concentrations were measured in larvae than in adults of both species. Acclimation for up to 35 days at 0 °C and for 29 days at −2 °C failed to produce significant increases in any of these substances. However, in *O. soledadinus,* there were indications that such acclimation resulted in increased levels of trehalose, glycerol and myoinositol in the adults compared to field samples. It is concluded that the acclimation procedures, times, and conditions used in the present experiments did not result in the levels of polyols and sugars found in winter field animals (W. Block, unpublished). This was

because either the simulations were inadequate to elicit the response, or, more likely, the beetles were in a summer physiological state and incapable of responding to such conditions.

Myoinositol is an unusual polyol to be implicated in low temperature tolerance of such insects, and its role requires further clarification. The occurrence of trehalose as the dominant compound in summer field animals, the levels of which declined with exposure to temperatures around 0 °C, suggests that it is the likely carbohydrate precursor of any cryoprotectant. It is therefore surprising that glycerol and other polyols were not detected in larger quantities in these beetles.

Anoxia

The ability of adult beetles to survive under anoxia was not well developed, and it may be that these species do not experience an oxygen deficiency of any importance during overwintering. This is in contrast to some species of alpine beetles, which are enclosed by ice for several months during winter, and in which survival under anoxia is an important part of their adaptation to extreme climates (Conradi-Larsen and Sømme 1973; Sømme 1974).

Life Cycles

Compared to several species of beetles from temperate and arctic areas (Zachariassen 1980; Miller 1982; Sømme 1982) the beetles of South Georgia exhibit only a moderate degree of cold hardiness, which is in accordance with the winter climate of their habitats. Judged from the available meteorological data (Smith and Walton 1975), the summers at South Georgia are relatively cold compared to conditions in some arctic and alpine localities (Rosswall and Heal 1975). For beetles and other terrestrial arthropods at South Georgia, special adaptations may be required for continued development and other biological functions during the cold summers.

As pointed out by MacLean (1975) extended and flexible life cycles are important features of adaptation to the environment in arctic and alpine insects. The life cycle durations of *H. sparsutum* and *P. antarcticus* are unknown, but it appears that most larval instars overwinter. Thus, according to Watt (1970), most instars of *H. sparsutum* were present in May and November and III to VI instar larvae of *P. antarcticus* were collected in early spring from September to November. All instars of both species were found during the summer, which is in agreement with the present results. Since there is no clear pattern of larval growth throughout the year, these data suggest that both *H. sparsutum* and *P. antarcticus* have extended life cycles. It seems likely that they overwinter at least twice as larvae before pupation occurs. Possibly the pupae do not overwinter, but adult beetles are present throughout the year (R. K. Headland, personal communication), and deposit their eggs in early spring when conditions become favourable.

Other Adaptations

H. sparsutum and *P. antarcticus* are also adapted to th environment in other respects. In their mountain-si habitats adults and larvae are found in small m clumps, on which they obviously feed, since almost other vegetation is present. Feeding on mosses was a observed in specimens brought into the laboratory. T utilization of moss as a food resource, which is not usu ly consumed by phytophagous insects, permits th beetles to live in habitats that would otherwise be imp sible to colonize.

As pointed out by Mani (1968), wing reduction a flightlessness are closely correlated with high altitude vironments. In correspondence with the cold and win conditions of South Georgia, both *H. sparsutum* and *antarcticus* are brachypterous. *O. soledadinus* has been seen in flight but it has fully developed wings.

Acknowledgements. We are grateful to the British Antarctic Survey logistic support during the 1981 – 82 season, and especially to T. H bronn and R. K. Headland for their assistance. We thank Roger W land and Sarah Barnes (BAS) for skilful technical assistance in resp of the GLC analyses. L. Sømme participated in this project throug grant from the Norwegian Research Council for Science and Huma ties.

References

Asahina E (1969) Frost resistance in insects. Adv Insect Physiol 6:1 –
Block W, Sømme L (1982) Cold hardiness of terrestrial mites at Si Island, maritime Antarctic. Oikos 38:157 – 167
Conradi-Larsen E-M, Sømme L (1973) The overwintering of *Pelop borealis* Payk. 2. Aerobic and anaerobic metabolism. Nor Ento Tidsskr 23:325 – 332
Darlington PJ (1970) Coleoptera: Carabidae of South Georgia. Pac sects Monogr 23:234
Gressitt JL (1970) Subantarctic entomology, particularly of So Georgia and Heard Island. Pac Insects Monogr 23:1 – 374
MacLean SF (1975) Ecological adaptations of tundra invertebrates Vernberg FJ (ed) Physiological adaptations to the environment. text Education, New York, pp 269 – 300
Mani MS (1968) Ecology and biogeography of high altitude insects Junk, The Hague, pp 1 – 527
Miller LK (1982) Cold-hardiness strategies of some adult and imma insects overwintering in interior Alaska. Comp Biochem Ph 73A:595 – 604
Rosswall T, Heal OW (1975) Structure and function of tundra ec tems. Ecol Bull (Stockholm) 20:1 – 450
Smith RIL, Walton DWH (1975) South Georgia, subantarctic. Bull (Stockholm) 20:399 – 423
Sømme L (1974) The overwintering of *Pelophila borealis* Pay Freezing-tolerance. Nor Entomol Tidsskr 21:131 – 134
Sømme L (1982) Supercooling and winter survival in terrestrial ar pods. Comp Biochem Physiol 73A:519 – 543
Steel WO (1970) Coleoptera: Staphylinidae of South Georgia. Pa sects Monogr 23:240 – 242
Sweeley CC, Bentley R, Makita M, Wells WW (1963) Gas-liquid matography of trimethylsilyl derivates of sugars and related stances. J Am Chem Soc 85:2497 – 2507
Watt JC (1970) Coleoptera: Perimylopidae of South Georgia. P sects Monogr 23:243 – 253
Zachariassen KE (1979) The mechanism of the cryoprotective eff glycerol in beetles tolerant to freezing. J Insect Physiol 25:29
Zachariassen KE (1980) The role of polyols and nucleating age cold-hardy beetles. J Comp Physiol 140B:227 – 234

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Ecophysiology of two intertidal mites at South Georgia

Lauritz Sømme and William Block

Sømme, L. and Block, W. 1984. Ecophysiology of two intertidal mites at So Georgia. – Oikos 42: 276–282.

(1) The resistance of *Halozetes marinus* (Cryptostigmata) and *Hyadesia max* (Astigmata) to cold and heat, to submergence in water and to anoxia was studie determine their adaptations to the intertidal environment of the sub-Antarctic.
(2) Supercooling capacities to lower than –20°C exist in both species, and remain unchanged during acclimation at temperatures around 0°C for up to 4 More than 77% of all samples were low group individuals (supercooling poin –15°C). Glycerol and myoinositol were found in maximum concentrations o 10–20 μg mg^{-1} live weight, which together with four other polyols and sugars did influence supercooling.
(3) The probability of inoculative freezing increased with lowered temperature increased time at subzero temperatures, with higher mortality in freshwater tha seawater.
(4) Tolerance to heat (35°C) was greatest in moist rather than dry conditions, losses of 25–30% body weight resulted in ca. 50% mortality in both mites.
(5) Mortality during submersion in freshwater was greater than in seaw suggesting that normal tidal submersion has no effect. Both species also survived under anoxia.
(6) These mites are well adapted to the South Georgian intertidal environme respect of the ecophysiological features examined, and inoculative freezing ma the main mortality factor during severe winters.

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Устойчивость *Halozetes marinus* (Cryptostigmata), *Hyadesia maxima* (Astig mata) к холоду и жаре, к погружению в воду и аноксии исследовали для ис чения их адаптаций к литоральным условиям Субантарктики.
Способность к переохлаждению при температурах ниже –20° имеется у обои видов, и она не меняется при акклимации при температуре около 0°C до 4 дней. Более 77% всех проб содержали необольшие группы особей (точка пе охлаждения ≤ 15°C): глицерол и миоинизитол найдены в максимальных конц трациях, примерно 10–20 μг/мг живого веса, что вместе с четырьмя други полиолами и сахарами не влияет на переохлаждение.
Возможность инокулятивного замерзания повышается при понижении темпера ры и увеличении периода отрицательных температур с более высокой смерт стью в пресной воде, нежели в морской.
Устойчивость к жаре (35°C) наибольшая во влажных, нежели в сухих услов ях; потеря 25–30% веса тела приводит к пости 50% смертности у обоих ви Смертность во время погружения в пресную воду выше, чем в морской воде означает, что нармальное приливное погружение в воду не оказывает влия Оба вида выживают также при аноксии в течение 16 дней.
Эти клещи хорошо адаптированы к литоральным условиям Св. Георгия в отн шении исследованных экофизиологических особенностей, и инокулятивное з зание – возможно основной фактор смертности в течение суровой зимы.

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ıtroduction

tively few air-breathing arthropods live in marine al habitats (Cheng 1976). Apart from a suitable substrate, other limiting factors may include lack tygen and freshwater, together with salinity and erature effects. The intertidal zone is probably one e most physiologically stressful environments for ɔpod colonisers from the land. Such animals have lerate heat and cold, desiccation, submergence in ıter, and on occasions, freshwater, often with po- ılly anoxic conditions. In addition, freezing by in- tion may occur in certain situations. In the interti- ɔne, regular fluctuations occur in several of these ːal conditions, whilst others will change irregu- Information on the adaptations employed by ar- ɔds living in littoral habitats is thus of considerable ɡical and physiological interest.

s paper reports the results of an experimental in- ation of the effects of selected physical factors on ıysiology of two littoral-dwelling mites, *Halozetes us* (Lohmann) (Cryptostigmata, Podacaridae) and *sia maxima* Fain, Sømme and Block (Astigmata, siidae), of which the latter has been described ly by Fain et al. (1983). Both species inhabit the l zone along sheltered coasts on the island of Georgia in the sub-Antarctic, occurring in large rs in small cracks and crevices in rocks on the re. The distribution of both species is intertidal ey are found from just below high water mark to one third the depth of the intertidal zone. ed rocks are those covered, at least partially, by filamentous algae (mainly *Enteromorpha* spp.). ıs are found together with adults in the crevice ations.

aims of the study were to examine resistance of nites to cold and heat, including inoculative g and desiccation, to submergence in water, both ınd salt, and to determine their responses to conditions. Conclusions may then be drawn con- ; the adaptations of such micro-arthropods to the e physical conditions of the intertidal habitat, nay suggest the possible mechanisms utilised and e the understanding of the ecology of such ani-

ıods

d collection

l for experiments was collected from two main Cumberland Bay, South Georgia during January h in the austral summer of 1981–82. The mites iginally discovered on rocks on the shore at n, and later, collections were made at sites near luff (ca. 1 km north of Hope Point) close to the Antarctic Survey station Grytviken on King Edward Point. The mites were collected by scraping the rocks and crevices with a needle or toothpick, fresh algae being added to the cultures in glass vials as food. The three nymphal instars and adults of *H. maxima* were collected in this way together with adults and mainly deuto- and trito-nymphs of *H. marinus*.

The effects of starvation and low temperature on the supercooling capacity of both species were studied by enclosing groups of mites in small glass vials with mesh lids without food and placing them in temperature cabinets at 0 ± 0.5°C and −2 ± 0.5°C in a saturated atmosphere for various time periods.

2.2. Supercooling

Supercooling points (SCP) of both field fresh animals and those acclimated to low temperatures and starvation were measured using copper-constantan thermocouples (30–36 swg) and a Linseis L 2061 six-channel continuous recorder. Techniques were essentially as described by Block and Sømme (1982), except that controlled cooling at ca. 1°C was achieved using cooled ethanol and CO_2 ice in a thermos flask (Block and Sømme 1983). Supercooling points were read from the recorder charts as the point of origin of the temperature rise due to the release of latent heat that accompanied freezing. Examination of the individual supercooling point data for both mites suggested a division in the frequency distribution around −15°C, which separated those individuals having food material in their guts and those without. Previous work (Young and Block 1980, Block and Sømme 1982) showed that gut contents increase the probability of nucleation in micro-arthropods when supercooled. Examination of field specimens after supercooling point determinations of *H. maxima* confirmed this, but observation of gut contents was more difficult in *H. marinus*.

2.3. Polyols and sugars

Three samples of *H. maxima* and four samples of *H. marinus* were taken from each field collection and experimental treatment for chromatographic analysis of polyols and sugars. Sample fresh weights ranged from 1.4 to 8.6 mg (*H. maxima*) and 1.5 to 11.0 mg (*H. marinus*), and consisted mainly of adult specimens but with some trito- and deuto-nymphs included. Each sample was homogenised in 1 ml of 70% ethanol to extract polyols and sugars, then stored below 0°C during transport from South Georgia to the UK. Analyses were undertaken at the BAS laboratories in Cambridge using GLC techniques after derivatives were prepared with a trimethylsilyl reagent with pyridine (Sigma Sil-A) according to Sweeley et al. (1963). Chromatography was carried out as described in Block and Sømme 1983), using at least four replicates per sample or treatment. Mean concentrations of identified substances were derived in $\mu g\ mg^{-1}$ live weight (lw) of mites.

2.4. Inoculative freezing

For tests of inoculative freezing 15–21 adults of *H. marinus* or a similar number of adults and juveniles of *H. maxima* were placed in Petri dishes on filter paper moistened with seawater or freshwater. There was abundant moisture present in the dishes so that the mites were covered by a film of water and therefore were in direct contact with ice during its formation, when the dishes were placed in temperature cabinets at ca. –3.5°C, ca. –5.5°C or ca. –8°C. The dishes were removed from the cabinets at regular intervals, and the number of dead and surviving mites counted at room temperature. Dead mites were assumed to have been killed by inoculative freezing. It is well known that seawater and freshwater yield different amounts of ice on freezing, and this was the reason for undertaking this experiment.

2.5. Desiccation and heat tolerance

Tolerance to heat was tested under dry and humid conditions in a temperature cabinet at 35 ± 0.5°C. The mites were kept in vials closed by a lid with a fine mesh screen in the centre. The vials were placed in an outer container with silica gel or wet tissue paper, giving a very dry or a moist atmosphere respectively. Each vial contained 15–20 adults of *H. marinus* or a similar number of adult and juvenile *H. maxima.* Survival rates were calculated at intervals up to 24 h, and 5–12 replicates were used per time interval.

Desiccation was studied in separate samples of mites kept on dry silica gel at 35°C. Each sample contained 30 mites. Weight loss was estimated from weighing the mites on a microbalance. One series of 6 replicates of each species was weighed after 1, 4, 8 and 24 h, and another series after 2, 6, 10 and 24 h. In this way frequent handling was avoided, which could have affected the results.

2.6. Submergence in water

Tolerance to submersion in water was tested in a simple experiment in which the mites were placed in half dram vials of seawater and freshwater at room temperature and at 0°C. Each vial contained 12–16 adults of *H. marinus* or a similar number of adults and juveniles of *H. maxima.* Each series consisted of two or three vials, from which mortality was recorded and dead mites removed at regular intervals.

2.7. Anoxia

Anaerobic conditions were produced in 5 mm diameter glass tubes (Sømme and Conradi-Larsen 1977, Block and Sømme 1982), which were flushed and then filled with nitrogen and sealed by melting both ends after the introduction of 25–30 mites. The tubes were stored for various time intervals at 0°C, after which they broken, and the mites removed to a normal atmos on moist filter paper in a Petri fish. Their rec within 24 h at room temperature was observed an centage mortality calculated.

3. Results

3.1. Supercooling

Mean supercooling points of field and acclimated ples of both species did not differ greatly (Fig. 1). increase in mean LG supercooling points occurred *marinus* after acclimation at 0°C for 27 to 46 d, b trend was not continued at –2°C after 27 d. *H. m*

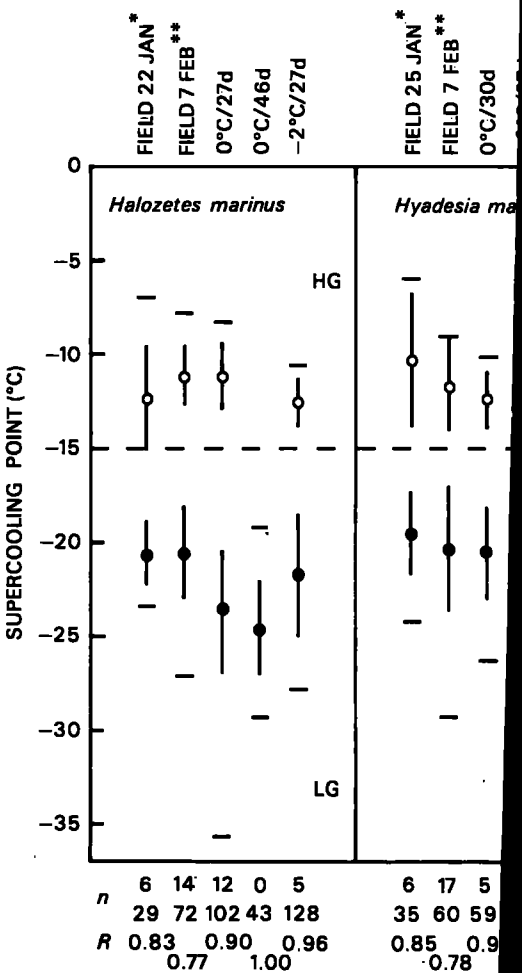
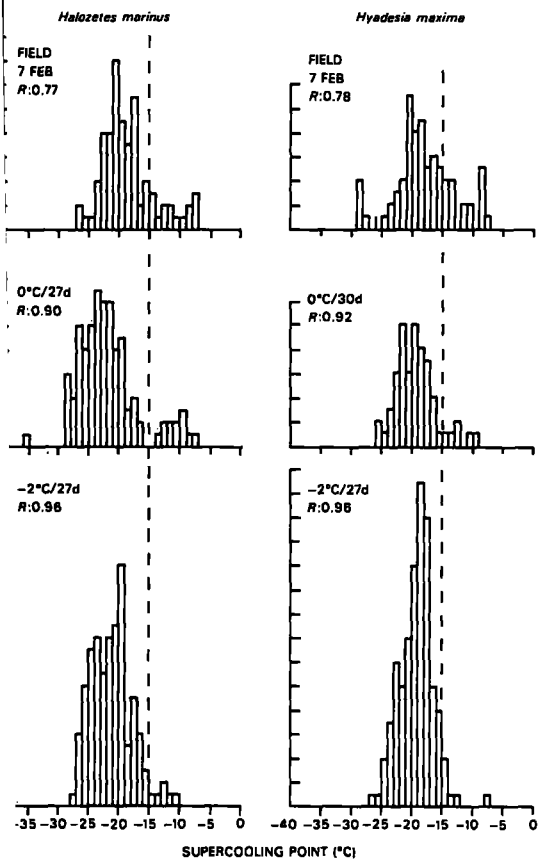


Fig. 1. High group (HG) and low group (LG) mea supercooling points and ranges of *Halozetes mar Hyadesia maxima* for field-fresh mites and for samp mated at 0 and –2°C for various times. n: number of s in the HG and LG, R: LG/(HG + LG) ratio with th between the groups being at –15°C. *Maiviken Cove Bluff.



Supercooling point distributions for *Halozetes marinus* *adesia maxima* from field samples and after acclimation d –2°C for various times. R: LG/(HG + LG) ratio with ision being at –15°C.

ot exhibit any significant changes in mean LG ooling points during the experiments, but HG in- als tended to lower their mean supercooling point ower acclimation temperatures and longer time ired to field animals. However, the HG data com- only a small number of observations. The lowest lual supercooling point was –36.6°C in *H. s* and –29.3°C in *H. maxima*. Although both HG G were present in samples from both field sites ken and Sooty Bluff), the proportion of individu- he LG was always high (77–85%). This propor- icreased during the acclimation experiments to or both species, resulting in a slightly changed ition of supercooling points (Fig. 2) with loss of HG individuals.

concluded that although a considerable capacity ercooling exists (to greater than –20°C) in both of intertidal mites, this is not altered by experi- exposure to temperatures around 0°C. Small s of individuals form a residual HG in both ions.

3.2. Polyols and sugars

Analyses were undertaken on extracts of samples taken from field mites, and after acclimation at 0°C for 27 d, and at –2°C for 28 d.

Glycerol, glucose, trehalose, ribitol and myoinositol were found in field and low temperature acclimated samples of both mites, whilst erythritol was detected in *H. maxima* in addition. The concentrations of most compounds were less than 1% of live weight, while in some samples glycerol and myoinositol occurred in larger quantities. Glycerol levels increased in *H. marinus* at 0°C for 27 d to a maximum of 21 μg mg^{-1} lw compared to 7 μg mg^{-1} lw in field mites. However, acclimation for similar periods at –2°C produced only trace amounts of glycerol. In *H. maxima*, highest concentrations (ca. 5 μg mg^{-1} lw) of glycerol were measured in field samples. Myoinositol was found in both species at 10–19 μg mg^{-1} lw only after acclimation at 0°C for 29 d, and in low concentrations in all other samples.

These results accord with those for the supercooling capacity of the mites, in that few changes occurred in composition of the polyols and sugars with acclimation at 0 and –2°C, and the increased levels of glycerol and myoinositol were so small (maximum ca. 2% lw) as not to affect supercooling.

3.3. Inoculative freezing

In *H. marinus* frozen in contact with seawater more than half of the mites survived up to 8 d at –3.5 and –5.5°C, while mortality appeared to be higher at –8°C (Fig. 3). Of those frozen in contact with freshwater more than 60% were killed even after two days at –3.5°C and still higher mortality rates were recorded at

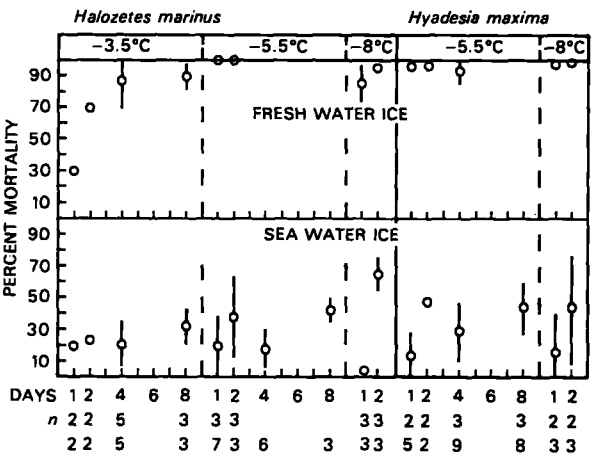


Fig. 3. Mortality rates of *Halozetes marinus* and *Hyadesia maxima* with time due to inoculative freezing from contact with ice formed from freshwater and seawater at various subzero temperatures. Mean (± SD) percentage mortality is shown. n: number of samples in freshwater and seawater ice.

–5.5 and –8°C. Similar results were obtained with *H. maxima* tested at –5.5 and –8°C, although fewer experiments were carried out with this species (Fig. 3).

The considerable differences in mortality that occurred between seawater and freshwater, may have been due to the different freezing properties of the liquids. Although there was variation between dishes, the results indicate an increase in mortality in both mites with decreased temperatures and with increased time at subzero conditions.

3.4. Desiccation and heat tolerance

Mortality at 35°C increased gradually during 24 h of exposure in both *H. marinus* and *H. maxima* (Fig. 4). Mortality rates were higher in mites exposed to a dry atmosphere, compared to those maintained in a water saturated condition. Tolerance to moist heat was highest in *H. maxima*, where about 50% of the mites survived 24 h of exposure. Heat intolerance was aggravated by desiccation. Water loss rates at 35°C over 24 h were similar in the two species (Fig. 4), and a reduction

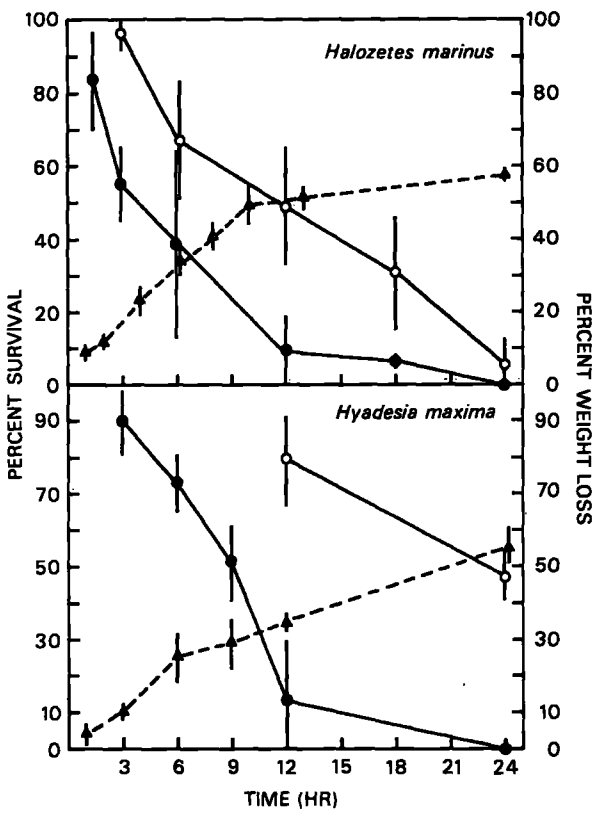


Fig. 4. Survival rates of *Halozetes marinus* and *Hyadesia maxima* in water saturated conditions (○—○) and in a dry (silica-gel) atmosphere (●—●) at 35°C. The dashed line (▲– – –▲) shows weight loss under dry conditions. Mean (± SD) values are given.

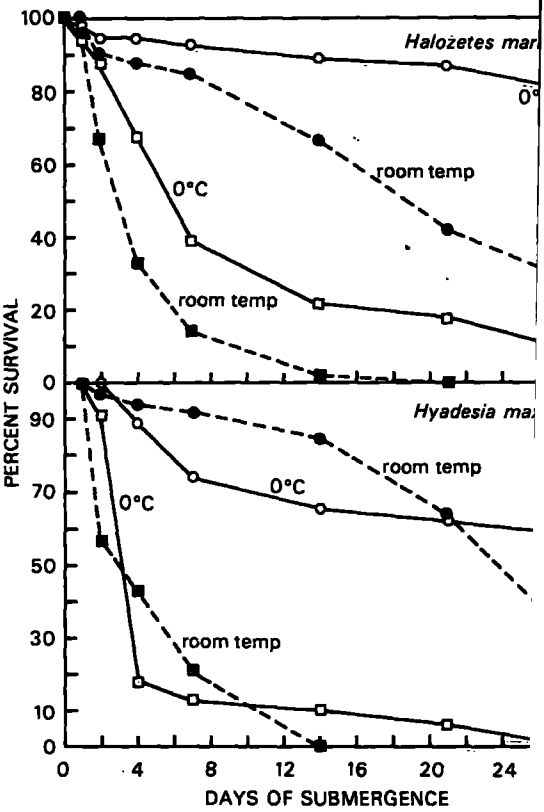


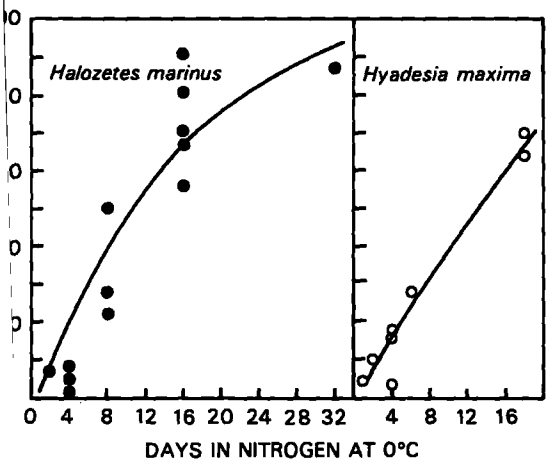
Fig. 5. Survival rates of *Halozetes marinus* and *H. maxima* during submergence in seawater (○, ●) and fr ter (□, ■) at 0°C (——) and room temperature (– – – point represents the mean of three replicates (n = 12–

of ca. 30% body weight corresponded to aroun mortality of both mites at 0% RH. The total weig was 56% in *H. maxima* and 58% in *H. marinu* 24 h.

3.5. Submergence in water

Survival rates of mites submerged in seawat freshwater are presented in Fig. 5. Some specin both species survived periods of several days or in sea water. In *H. marinus* mortality was hi room temperature than at 0°C, while in *H. maxi* temperature effect was not that pronounced. Th tality of specimens submerged in fresh water w siderably higher, probably due to osmotic effects were observed in the swelling of the mites. A temperature all mites were killed in 2–3 wk i water, while higher survival rates were recorded in particular in *H. marinus*.

It is concluded that tidal submersion or longer in sea water due to wave action will have littl effect on the mites. In nature, submergence in r ter will only be experienced for a short time b



). Mortality of *Halozetes marinus* and *Hyadesia maxima* stored in nitrogen at 0°C for various times. Each point sents a sample of 25–35 mites. Lines were fitted by eye.

tides, and is unlikely to cause any significant mor-

noxia

nortalities of *H. marinus* and *H. maxima* kept in en at 0°C are shown in Fig. 6. Very little mortality red after 2–4 d, and a large proportion of both s survived 16 d under these conditions. The re- trongly suggest that the mites will survive under l conditions if submergence in water or enclosure should result in an oxygen deficiency.

cussion

nature the intertidal zone has a very stressful nment, where organisms are adapted to a com- f terrestrial and marine conditions. Intertidal sms often have to tolerate more extreme condi- han other marine organisms because they are ed to widely fluctuating environmental condi- Vernberg and Vernberg 1972, Newell 1979). The ving in the upper part of the intertidal zone may sidered as terrestrial animals invading a marine ment, in which a suite of resistence adaptations to have been evolved to ensure their survival. o species studied at South Georgia are well l to such fluctuating environmental conditions of -Antarctic climatic regime.

levels of supercooling were in the range of –10 C for the HG and ca. –20°C for the LG of both It is unlikely that LG animals would be exposed temperatures on South Georgia as the absolute erature range is –19 to 24°C (Smith and Walton However, if HG animals are present during the winter, they will be at risk when minimum air temperatures at sea level approach –20°C. Concomitant with there being little or no requirement for their supercooling ability to increase during cold seasons, relatively insignificant amounts of polyols and sugars were found in the mite extracts. Freezing due to inoculation by ice probably remains the major mortality factor for such intertidal animals during severe winters at South Georgia.

In the laboratory both *H. marinus* and *H. maxima* survived extended periods of submergence in sea water, indicating that high tides and flooding by sea water will not result in high mortalities of these animals. Submergence in freshwater is more physiologically demanding, due to the effects of water gain which probably leads to disruption of water balance in the mites. However, a large proportion of both species can tolerate such conditions for several days (Fig. 4). It is not known to what extent *H. marinus* and *H. maxima* are able to absorb oxygen from the water, but their ability to survive under anoxia for several days indicates that they are able to tolerate an oxygen deficiency during submersion in water. Plastron respiration has been reported in secondarily aquatic gamasid mites (Hinton 1971, Krantz 1974) and in an aquatic oribatid species (Krantz and Baker 1982). The gamasids utilise plastron beds derived from peritremes whereas oribatids, in the absence of external peritrematic grooves, have specialised areas of cuticular extrusions contiguous with stigmata that connect with the internal tracheae. It seems that *H. marinus* may utilise a plastron mechanism to take up oxygen from water during submersion. Although plastrons have not been reported in astigmate mites, a similar process may operate in *H. maxima*, as the species have similar survival rates in seawater.

From the laboratory experiments it also appears that the two species of mites are well adapted to terrestrial life under the climatic conditions of South Georgia. This implies both heat tolerance during summer and cold hardiness during winter. The degree of resistance to desiccation found in the two species indicates that they are well able to survive when the rocks are warmed by radiative heating.

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References

Block, W. and Sømme, L. 1982. Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. – Oikos 38: 157–167.

– and Sømme, L. 1983. Low temperature adaptations in beetles from the sub-Antarctic island of South Georgia. – Polar Biol.
Cheng, L. (ed.) 1976. Marine insects. – North-Holland, Amsterdam.
Fain, A., Sømme, L. and Block, W. 1983. *Hyadesia maxima* spec. nov. (Acari, Hyadesiidae) from South Georgia. – Soc. belge d'Entomol. in press.
Hinton, H. E. 1971. Plastron respiration in the mite, *Platyseius italicus*. – J. Insect Physiol. 17: 1185–1199.
Krantz, G. W. 1974. *Phaulodinychus mitis* (Leonardi 1899) (Acari: Uropodidae) an intertidal mite exhibiting plastron respiration. – Acarologia 16: 11–20.
– and Baker, G. T. 1982. Observations on the plastron mechanism of *Hydrozetes* sp. (Acari: Oribatida: Hydrozetidae). – Acarologia 23: 273–277.
Newell, R. C. 1979. Biology of intertidal animals, 3rd ed – Marine Ecological Surveys, Faversham.
Smith, R. I. L. and Walton, D. W. H. 1975. South Ge subantarctic. – Ecol. Bull. (Stockholm) 20: 399–423
Sømme, L. and Conradi-Larsen, E.-M. 1977. Anaerobic overwintering collembolans and oribatid mites windswept mountain ridges. – Oikos 29: 127–132.
Sweeley, C. C., Bentley, R., Makita, M. and Wells, W 1963. Gas-liquid chromatography of trimethylsilyl de tives of sugars and related substances. – J. Am. chem 85: 2497–2507.
Vernberg, W. B. and Vernberg, F. J. 1972. Environm physiology of marine animals. – Springer, New York
Young, S. R. and Block, W. 1980. Experimental studies c cold tolerance of *Alaskozetes antarcticus*. – J. Physiol. 26: 189–200.

COMPARATIVE STUDY OF INVERTEBRATE SUPERCOOLING AT SIGNY ISLAND, MARITIME ANTARCTIC

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ABSTRACT. The capacity for supercooling and the cryoprotective contents of 19 species of invertebrates collected from inshore marine (eleven species), freshwater (two species) and terrestrial (six species) habitats in summer 1981–82 were examined at Signy Island. All the species tested were freezing susceptible and individuals died at their supercooling points. Aquatic species generally exhibited poor supercooling ability (−5 to −9°C) compared with the terrestrial arthropods (−8 to −12°C), of which four species were high capacity supercoolers (<−20°C). Potential cryoprotectants were in lower concentrations (mostly <0.1% of fresh weight) in aquatic species than in terrestrial forms, where a four-component (glycerol, myo-inositol, glucose and trehalose) profile was identified. Summer levels of cryoprotectants were not thought to influence individual supercooling in any species. Considering the annual temperature range for each of the habitat categories (*c.* 3 deg for inshore marine, *c.* 5 deg for freshwater lakes and *c.* 62 deg (−26.5 to +35.8°C) for terrestrial sites), it is unlikely that any of the aquatic invertebrates tested would be at risk from freezing in maritime Antarctic conditions. Most of the terrestrial species avoid lethal freezing by extensive supercooling, but nucleation by food retained in the gut will increase the probability of freezing even in summer acclimatized animals. The high incidence of freezing susceptibility in the Antarctic fauna, especially that of the land, may indicate that supercooling confers a selective advantage on potential colonists over freezing tolerance.

INTRODUCTION

wo strategies for overcoming the problems caused by freezing temperatures have
adopted by invertebrate poikilotherms (see review by Block (1982)). Some
ies are freezing tolerant, being able to survive extracellular ice formation, while
rs are freezing susceptible and avoid ice crystallization by supercooling (the
city to maintain their body fluids in the liquid phase below the freezing point).
zing tolerant forms frequently have poor supercooling ability and ice nucleators
ent in the haemolymph in winter aid protective extracellular freezing in the
erature range from *c.* −2 to −12°C (Zachariassen and Hammel, 1976).
pounds such as glycerol may confer a degree of protection from ice crystals
g freezing and thawing in such animals. In freezing susceptible species,
cooling may be enhanced by low molecular weight solutes (polyhydric alcohols,
s, etc.), depending on their concentration in the body fluids, thereby avoiding
ing, which is always lethal. Nucleating agents (possibly proteins or peptides)
also be present in freezing suceptible animals but these are either removed or
ed within the intercellular matrix during supercooling (Zachariassen, 1982).
emperature at which whole-body freezing occurs in the supercooled state is
d the supercooling point.

wever, the situation is not always clear-cut and freezing tolerant insects
cularly Coleoptera) with relatively low supercooling points have been found in
and alpine habitats (Miller, 1982; Ring, 1982).

he Antarctic, previous investigations concentrated on land arthropods in which
ng susceptibility is widespread (Block and Sømme, 1982; Sømme and Block,

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1982). A single species of insect, the Antarctic midge *Belgica antarctica* Jacobs, freezing tolerant but only in the larval stage (Baust and Edwards, 1979). Freezi resistance has been little studied in marine invertebrates (Rakusa-Suszczewski a McWhinnie, 1976) and not at all in the freshwater fauna. The purpose of the pres study was to compare the potential for avoiding freezing by supercooling in a range invertebrates representative of terrestrial, freshwater and inshore marine habita The work was undertaken during the austral summer 1981–82 at Signy Island, wh is typical of much of the maritime Antarctic zone (Holdgate, 1977), where freeze-tolerant species had been discovered. The aims of the study were to relate supercooling capacity of selected species to their normal habitat temperatures and determine the levels of any possible cryoprotectants that occur.

Methods

Fauna

A total of 19 invertebrate species was examined, all except two being arthropo They comprised six terrestrial species, two freshwater and eleven marine forms, latter including an intertidal annelid (Enchytraeidae) and a gastropod mollusc. T taxa are listed in Table I, each being referred to by the generic name throughout paper except the enchytraeid, which was not determined, but appears to be refera to one species (B. Christensen, pers. comm.)

Samples of animals were collected in the field by hand sorting and micro-aspirat (terrestrial habitats), by vertical-haul netting and water bottle sampling (freshwa habitats), and by hand collection of sea-weeds, etc. by SCUBA diving techniq (inshore marine habitats). The terrestrial species were obtained from sites aro Factory Bluffs, Cemetery Flats and Gourlay Peninsula, the freshwater species fr Sombre Lake and a pool at Hillier Moss (near Signy Island Reference Site 2), w the marine forms were from sites in Borge Bay, in particular near Bare Rock water between 10 and 20m deep. All specimens for experimental work w maintained in their appropriate medium either at *c.* 0°C (aquatic species) or at 3– (terrestrial species) for up to 8h before being used. Specimens were tested sho after field collection in order that the results would be representative of field anir as far as possible.

Supercooling points

Supercooling points of individuals of all species were measured following method of Block and Sømme (1982) using a freezing mixture (1.5:1v/v $CaCl_2.6H_2O$ and snow to produce a cooling rate of *c.* 1 deg min^{-1}. A six-cha Linseis recorder and various sizes of copper–constantan thermocouples 40s.w.g.) monitored the body temperature of the experimental animals. supercooling point was read as the point of origin of the small, but significant, ri body temperature that occurred through latent heat emission during spontan freezing. All the aquatic specimens were damp-dried on filter paper be attachment to the thermocouples. For the larger species, e.g. amphipods, iso pycnogonids, etc., each individual was located in the base of a small polythene with the thermocouple tip being lowered to make a firm contact on the ve surface.

Cryoprotectants

Extracts of polyhydric alcohols and sugars were prepared for chromatograp macerating, in 70% ethanol, single individuals of most of the larger species (a marine taxa except the enchytraeid) and samples composed of several individua

Table I. Invertebrate taxa tested for supercooling potential from terrestrial, freshwater and inshore marine habitats at Signy Island. Live weights of individuals of some taxa are indicated. nd: not determined.

Habitat category	*Group*	*Species*	*Live weight (mg) per individual*	*Habitat*
Terrestrial	Insecta, Collembola	*Cryptopygus antarcticus*	$2–120 \times 10^{-3}$	Ubiquitous
		Parisotoma octooculata	$3–61 \times 10^{-3}$	Guano-enriched areas
		Archisotoma brucei	nd	Shore-line
	Arachnida, Acari	*Stereotydeus villosus*	nd	Moist areas with some plant cover
		Gamasellus racovitzai	$10–145 \times 10^{-3}$	Mosses, fellfields; predator
		Alaskozetes antarcticus	$13–197 \times 10^{-3}$	Rocky areas (enriched) preferred
Freshwater	Crustacea, Anostraca	*Branchinecta gaini*	4–11	Lakes, nekton
	Crustacea, Copepoda	*Pseudoboeckella poppei*	nd	Lakes, pools
Marine	Oligochaeta, Enchytraeidae	nd	1–5	Intertidal
	Crustacea, Amphipoda	*Oradarea bidentata*	81–187	Epifauna on rocks and weeds
		Oradarea ocellata	nd	,,
		Bovallia gigantea	nd	,,
		Paraphimedia integricauda	nd	,,
		Paradexamine fissicauda	nd	,,
		Cheirimedon femoratus	nd	Infauna of sediments
	Crustacea, Isopoda	*Serolis polita*	51–92	Sandy substrates
		Glyptonotus antarcticus	nd	,,
	Arachnida, Pycnogonida	*Nymphon orcadense*	101–292	Bottom dwelling
	Gastropoda, Opisthobranchiata	*Philine* (?) *gibba*	nd	Sediments

terrestrial and freshwater species together with the enchytraeid worm). The range fresh weights obtained using a Cahn electro-balance for the former animals is giv in Table I, while the latter micro-faunal samples were all slightly greater than 1 r fresh weight. A minimum of three samples per taxon was assayed but five to s samples were possible for larger specimens. GLC techniques were applied af derivatizing the samples in trimethylsilyl reagent with pyridine (Sigma Sil- (Sweeley and others, 1963), using a Pye-Unicam GCD instrument with a Chrompa CP[tm] Sil 5 non-polar capillary column and internal standards. A Hewlett-Packa Integrator 3380A was also used (see Block and Sømme (1982) for details).

Results

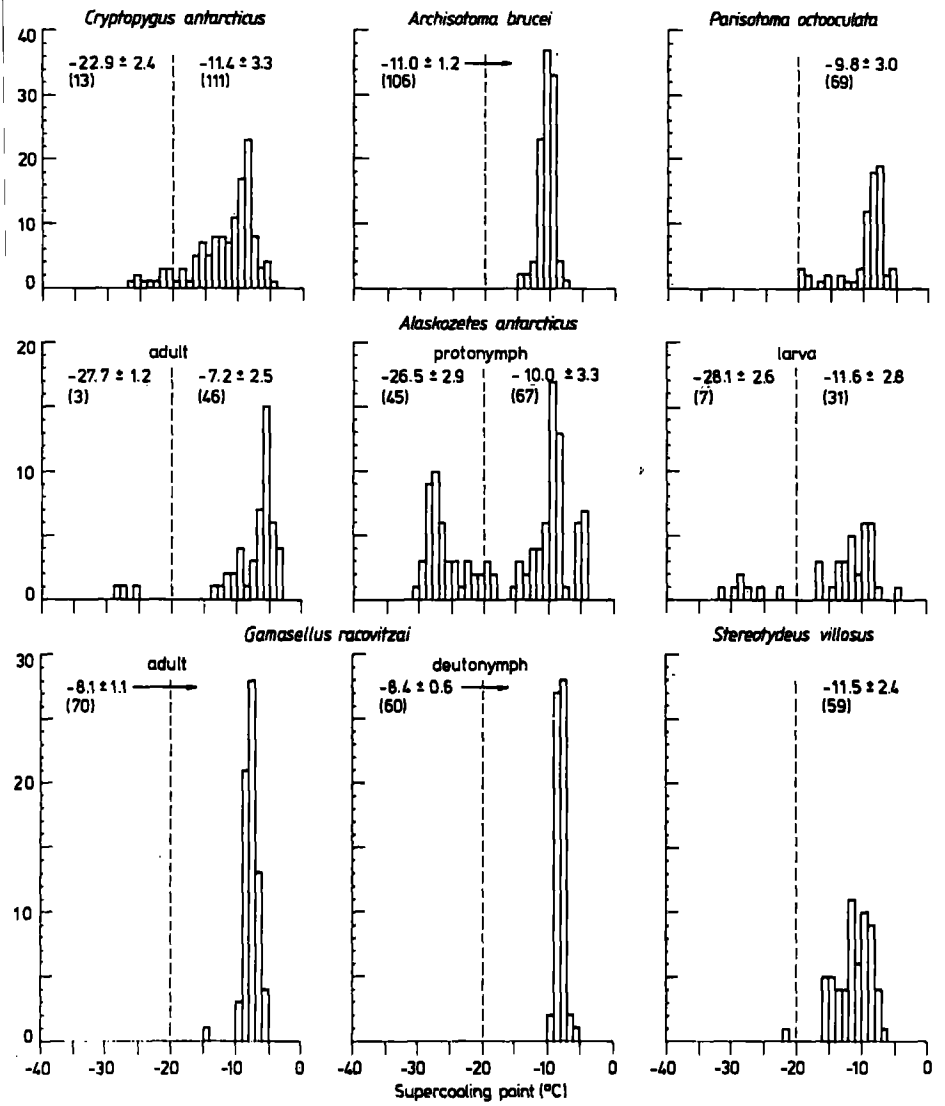
Supercooling capacity

Frequency histograms of individual supercooling points for the six terrestr species are shown in Fig. 1. Those for the two freshwater crustaceans are given in F 2 together with the data for three of the marine arthropods and the interti enchytraeid worm. Separation of the data into a high group (HG) (>−20°C) an low group (LG) (<−20°C) was undertaken following earlier work on Antar micro-arthropods (Bløck and Sømme, 1982). The division between the two gro was at −20°C.

In the terrestrial invertebrates (Fig. 1), the shape of the supercooling pc distribution varies considerably. Of the three collembolans, only *Cryptopygus* capable of supercooling below −20°C and the mean supercooling points of the did not vary significantly between species. Of the three mite species, only oribatid *Alaskozetes* was able to resist temperatures below −20°C by supercoolin all its life stages. This species possessed both a HG and a LG in the samp examined, whereas the mesostigmatid *Gamasellus* and the prostigm *Stereotydeus* (with one slight exception) exhibited only a HG in their supercoo point distributions. The mean supercooling points of all the HGs in the mites w not significantly different and the mean LG supercooling points of the various stages of *Alaskozetes* were also similar. Similarly, the two life stages of *Gamase* had almost identical supercooling ability with the majority of the measured po falling within a narrow 2–3 deg band. This contrasts with most of the o terrestrial species, which showed a broader range of supercooling powers (with exception of *Archisotoma*).

The aquatic species, both marine and freshwater (Fig. 2), show a consis presence of a HG in their unimodal distributions. Individuals in the arthr samples had a remarkable similarity of supercooling ability with mean supercoo points ranging from −5.7 (the pycnogonid *Nymphon*) to −8.9°C (the cope *Pseudoboeckella*). Data for amphipods, other than *Oradarea bidentata*, were few and generally similar to those of *O. bidentata* (mean supercooling p ranging from −2.8 for *Cheirimedon femoratus* to −8.5°C for *Bovallia gigan* that they are not considered further. Only the enchytraeid showed any extensi the supercooling range below −20°C (but only in three individuals in a total of the overall mean being −11.9°C.

A comparison of mean (± SD) supercooling points for the invertebrates stu at Signy Island is made in Fig. 3. For *Alaskozetes* and *Gamasellus*, mean v were calculated from the data for all life stages tested. The species are gro according to major habitat categories: terrestrial, freshwater and inshore mari can be seen that LG supercooling points (<−20°C) occurred only in four o terrestrial species and that the supercooling points of their HGs (overall mean −10°C) were generally lower than the aquatic species (overall means of *c.* −



1. Supercooling point distribution histograms for six species of terrestrial arthropods (three Collembola and three Acari) at Signy Island during December–January of the 1981–82 austral summer. The mean (±SD) supercooling points and the number of observations (n) are shown for the high group (HG) and low group (LG) with the division at −20°C.

C for freshwater and marine respectively). These forms have the greatest acity for avoiding freezing by supercooling. Most (four species out of six) of the estrial invertebrates showed evidence of an ability to shift their supercooling ge to below −20°C (i.e. LG), and these clearly have a greater capacity to avoid al freezing when it occurs. The exception in the aquatic species was the nytraeid with an overall mean supercooling point of *c.* −12°C. The freezing eptibility of the Antarctic enchytraeid is in contrast to the freezing tolerance layed by intertidal invertebrates of arctic and temperate regions (Aarset, 1982).

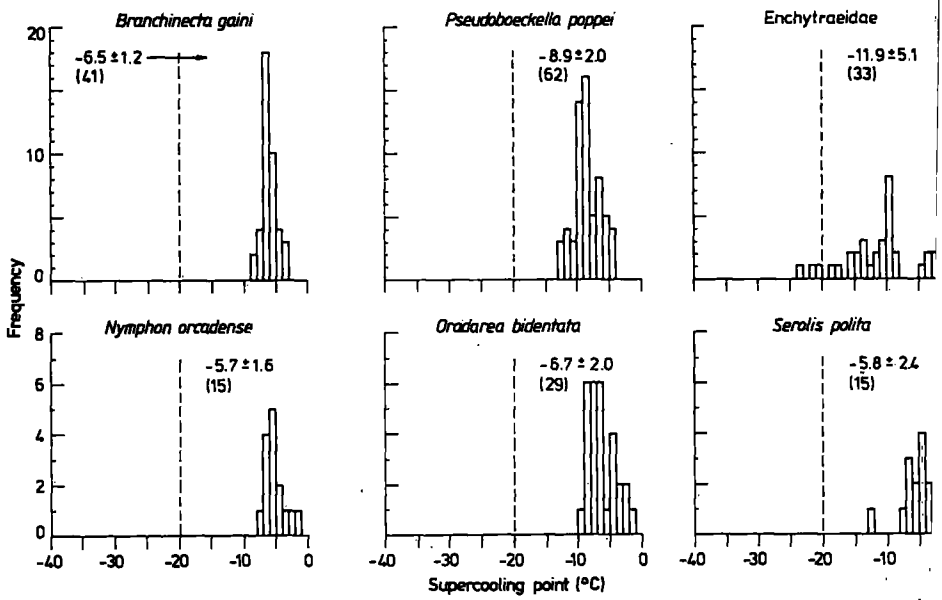


Fig. 2. Supercooling point distribution histograms for six taxa of aquatic invertebrates (two freshwa crustaceans, two marine crustaceans, one pycnogonid and one intertidal enchytraeid) at Si Island during December–January of the 1981–82 austral summer. The mean (± SD) supercool points and the number of observations (*n*) are shown for the HG.

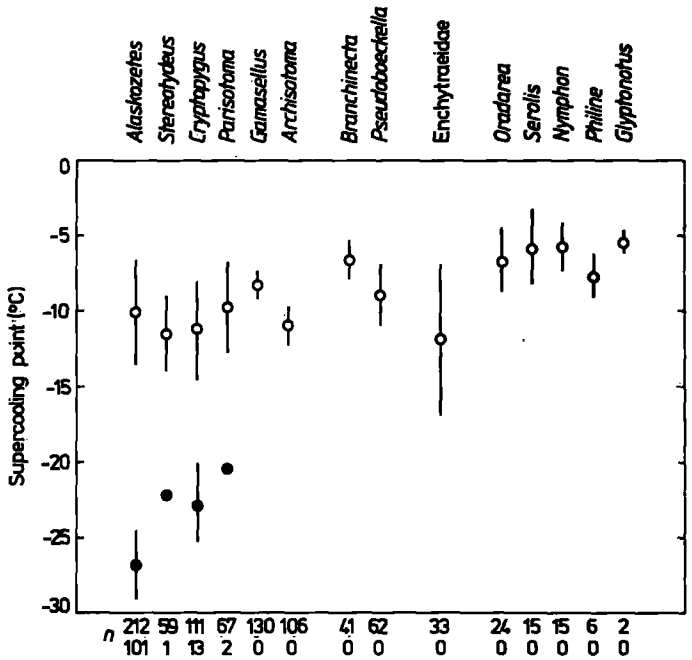


Fig. 3. Comparison of the mean HG and LG supercooling points of 14 invertebrate taxa from terres freshwater and inshore marine habitats at Signy Island in the austral summer 1981–82. *n:* nu of data points in the HG and LG respectively.

ıtential cryoprotectants

Three polyhydric alcohols (polyols) and three sugars were detected in extracts of elve species examined (Table II). No compound was found in a concentration in cess of 1.1% of fresh weight, which was the average level of glucose in the chytraeid samples. Mean concentrations of most compounds were <0.1% of fresh ight, although some increased to 0.4% by weight. Glycerol, glucose and trehalose re found in all samples from all the taxa, whilst ribitol and fructose occurred in ven species. Myo-inositol was found in eight taxa. On a species basis, there is no tinct pattern of occurrence of cryoprotectants but the terrestrial species appear to ssess a four-component cryoprotectant profile, consisting of glycerol, myo-ısitol, glucose and trehalose. Each of these were in excess of 0.1% by weight. This ıge of compounds contrasted with the aquatic taxa in which only glycerol was ected at concentrations >0.1% of fresh weight in only two of the five species. The hytraeid was, again, unusual in having 11μg mg^{-1} fresh weight of glucose in lition to ribitol, myo-inositol and fructose, all >0.1% by weight.

The compounds found in the present study do not reflect the profiles reported lier from field mites and Collembola (Block and Sømme, 1982; Sømme and ck, 1982), except in the case of *Alaskozetes*. Here, the 1979–80 summer samples broadly similar to the 1981–82 results (Table II). The conclusion that there is a re diverse spectrum of potential cryoprotectants available to terrestrial ertebrates than is found in either freshwater or marine forms, supports the erimental evidence that the former have a much greater capacity for ercooling.

Discussion

reezing was lethal to 19 species of invertebrates from three major habitats at ıy Island and individuals rely entirely on supercooling as an avoidance hanism. In samples from field populations, collected in summer, the average ercooling was between −6 and −12°C (Fig. 3), although in four terrestrial species viduals were able to extend their supercooling to well below −20°C. None of the atic forms from both freshwater and inshore marine systems exhibited a LG (low ıp) in terms of supercooling. Although the present data are derived from summer

e II. Concentrations of sugars and polyols in extracts of twelve invertebrates from terrestrial, freshwater and marine habitats at Signy Island in 1981–82. −, no trace; +, trace but <0.1% fresh weight; *, >0.1%; **, >0.2%; ****, >0.4%; *****, >1.0%.

n	*Glycerol*	*Ribitol*	*Myo-inositol*	*Glucose*	*Fructose*	*Trehalose*
topygus	+	−	+	**	+	**
otoma	+	+	−	+	+	+
isotoma	+	+	*	+	+	+
ɔtydeus	+	+	+	*	+	*
ɪsellus	+	+	****	*	+	+
:ozetes	**	+	*	*	−	+
:hinecta	+	+	−	+	+	+
loboeckella	*	+	+	+	+	+
ytraeidae	+	*	*	*****	*	+
ɪrea	*	+	+	+	+	+
s	+	+	−	+	+	+
)hon	+	+	−	+	+	+

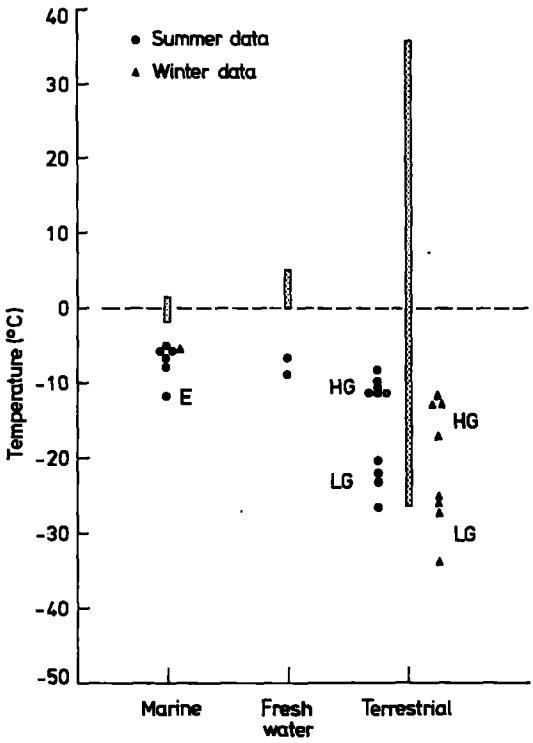
acclimatized animals, it is important to relate the results to the environment temperatures experienced by the fauna in the field and also to winter levels supercooling where data exist.

The annual temperature range (absolute maximum and minimum) recorded Borge Bay (D. G. Bone, pers. comm.) where the marine animals were collected, th average mid-depth water temperature in three freshwater lakes (Heywood, 196 and that at the surface of a moss turf community (Walton, 1982) at Signy Island a depicted in Fig. 4. Mean supercooling points for species from each of the habit categories are shown for comparison. The terrestrial arthropods are subdivided in the two supercooling groups and data from winter samples are included. The aquat habitats at Signy Island have relatively narrow annual temperature ranges, with th inshore marine environment experiencing only *c.* 3.3 deg change compared to th lakes where *c.* 5 deg is usual. Terrestrial communities undoubtedly experience th largest variation in temperature of all the habitats throughout the year (*c.* 62 deg Although the duration of a particular low (or high) temperature level may be sho species here probably have to survive such a range and extremes at least once with their life cycle. In terms of supercooling, both the inshore marine fauna and the la and pool invertebrates have a sufficient capacity, even in summer, to avoid freezi over a temperature range representative of the annual one. The position f terrestrial invertebrates is more complex in that, due to feeding activity and t retained food in the arthropod gut promoting, in effect, self-nucleation under cert conditions, a bimodal separation of individual supercooling points results (Fig. Temperatures below $-5°C$ are unlikely to occur even on the ground surface duri November–March at Signy Island (Walton, 1982) and, therefore, the supercooli ability demonstrated for summer specimens in this study would ensure survival the majority of their populations. In winter, both supercooling point groups sho downward shift relative to summer levels and the LGs of most species would av lethal freezing, some to $<-30°C$. The HGs would be more at risk from freezing winter, and some individuals would succumb.

A single sample of *Nymphon orcadense* (Pycnogonida) collected in winter 1 had a mean ($\pm$ SD) supercooling point of $-5.4 \pm 1.2°C$ ($n = 23$) (A. D. Hemmi pers. comm.), both this and its cryoprotectant profile being very similar to summer sample. The enchytraeid, occupying an intertidal habitat, will experie lower temperatures than benthic and other marine invertebrates and its supercool capacity reflects this in being intermediate between the truly aquatic species and terrestrial forms.

It is concluded that, although there is a graded response across the habitat subzero temperatures, the aquatic species are well protected by their power supercooling to avoid freezing. The terrestrial invertebrates, on the other hand, be subjected to much greater thermal variation during the year and supercooling be inhibited by the presence of gut contents even at times in winter when a propor of their populations may be at risk from freezing.

Supercooling is a widespread phenomenon in invertebrates (see review by Søn (1982)) and is apparently a successful strategy for a wide range of species inhabi low temperature environments where winter survival is linked to toleranc avoidance of freezing temperatures. Few freezing tolerant species have b recorded (Block, 1982). In the Antarctic, freezing susceptibility is commo invertebrates but they also exhibit considerable powers of supercooling, which manifest in the mostly terrestrial fauna studied to date. This may be due to the that the land fauna of the Antarctic region is grossly impoverished by compa with other continents and the immigration routes of potential colonists from wa



4. Comparison of the mean supercooling points of 18 species of invertebrates with the annual temperature range for inshore marine, freshwater and terrestrial habitats at Signy island. ●, summer data; ▲, winter data; E, enchytraeid; HG, high group; LG, low group.

thern areas are long and rigorous. Supercooling may thus be more advantageous a species colonizing an environment colder than whence it originated. No novel siological or biochemical adaptations appear to be required, merely the nsion and development of existing mechanisms. An example of this is provided he chironomid midge (*Eretmoptera murphyi* Schaeffer), which was accidentally oduced to Signy Island from either the Falkland Islands or South Georgia (Block others, 1984). Its life stages, especially the larva, have sufficient supercooling acity to have survived for 17 years in the new habitat and reproduction by henogenesis occurs. It may be more difficult for freeze tolerant forms to become nizers. In this strategy, particular proteins are required to perform the eating function as temperature declines (ice nucleating proteins, cf. Duman and rs, 1982; Zachariassen, 1982). It is essential to the survival of such animals that eation takes place at relatively high subzero temperatures.

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References

AARSET, A. V. 1982. Freezing tolerance in intertidal invertebrates (a review). *Comparative Biochemis and Physiology*, **73A**, 571–80.

BAUST, J. G. *and* EDWARDS, J. S. 1979. Mechanisms of freezing tolerance in an Antarctic midge *Belg antarctica*. *Physiological Entomology*, **4**, 1–5.

BLOCK, W. 1982. Cold hardiness in invertebrate poikilotherms. *Comparative Biochemistry a Physiology*, **73A**, 581–93.

BLOCK, W., BURN, A. J. *and* RICHARD, K. J. 1984. An insect introduction to the maritime Antarc *Biological Journal of the Linnean Society* (in press).

BLOCK, W. *and* SØMME, L. 1982. Cold hardiness of terrestrial mites at Signy Island, maritime Antarc *Oikos*, **38**, 157–67.

DUMAN, J. G., HORWATH, K. L., TOMCHANEY, A. *and* PATTERSON, J. L. 1982. Antifreeze agents terrestrial arthropods. *Comparative Biochemistry and Physiology*, **73A**, 545–55.

HEYWOOD, R. B. 1968. Ecology of the fresh-water lakes of Signy Island, South Orkney Islands: Physical and chemical properties of the lakes. *British Antarctic Survey Bulletin*, No. 18, 11–

HOLDGATE, M. W. 1977. Terrestrial ecosystems in the Antarctic. *Philosophical Transactions of the Ro Society of London, Series B*, **279**, 5–25.

MILLER, L. K. 1982. Cold-hardiness strategies of some adult and immature insects overwintering interior Alaska. *Comparative Biochemistry and Physiology*, **73A**, 595–604.

RAKUSA-SUSZCZEWSKI, S. *and* MCWHINNIE, M. A. 1976. Resistance to freezing by Antarctic fau supercooling and osmoregulation. *Comparative Biochemistry and Physiology*, **54A**, 291–3

RING, R. A. 1982. Freezing-tolerant insects with low supercooling points. *Comparative Biochemistry Physiology*, **73A**, 605–12.

SØMME, L. 1982. Supercooling and winter survival in terrestrial arthropods. *Comparative Biochemi and Physiology*, **73A**, 519–43

SØMME, L. *and* BLOCK, W. 1982. Cold hardiness of Collembola at Signy Island, maritime Antarc *Oikos*, **38**, 168–76.

SWEELEY, C. C., BENTLEY, R., MAKITA, M. *and* WELLS, W. W. 1963. Gas–liquid chromatography trimethylsilyl derivatives of sugars and related substances. *Journal of the American Chem Society*, **85**, 2497–507.

WALTON, D. W. H. 1982. The Signy Island terrestrial reference sites: XV. Micro-climate monitor 1972–74. *British Antarctic Survey Bulletin*, No. 55, 111–26.

ZACHARIASSEN, K. E. 1982. Nucleating agents in cold-hardy insects. *Comparative Biochemistry Physiology*, **73A**, 557–62.

ZACHARIASSEN, K. E. *and* HAMMEL, H. T. 1976. Nucleating agents in haemolymph of insects tolerar freezing. *Nature, London*, **262**, 285–7.

ical Journal of the Linnean Society (1984), 23: 33–39

insect introduction to the maritime tarctic

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lthough several invertebrates have been introduced by Man into the Antarctic, no olometabolous insects have survived to colonize terrestrial habitats successfully. Data are presented n the survival of populations of a chironomid midge, together with an enchytraeid worm, for 17 ears in a maritime Antarctic site at Signy Island, South Orkney Islands. Both species are thought have been introduced on plant material transplanted from either South Georgia or the Falkland lands or both in 1967. Population densities average 25 718 m^{-2} for the dipteran larvae and 43 m^{-2} for the worms. Successful completion of the midge's life cycle was indicated by emergence brachypterous adults and oviposition (the population is parthenogenetic with only females esent). Although both taxa are capable of supercooling to between −13 and −26°C, this pacity may not be sufficient in a severe winter to avoid lethal freezing. Four potential yoprotectants were found in insect extracts, but in concentrations (< 1% fresh weight) unlikely to fluence cold hardiness. Both invertebrates appear to be pre-adapted for survival in much harsher nditions than they normally experience, by the extension of existing physiological mechanisms. It concluded that the main limitations to invertebrate colonization of suitable Antarctic land areas soil-dwelling species are geographical.

EY WORDS:—Colonization – Antarctic – holometabolous insect – enchytraeid – supercooling – eze tolerance – pre-adaptation.

CONTENTS

INTRODUCTION

diversity and number of species of insects decline south of the Antarctic rgence with an abrupt change between the sub-Antarctic and maritime tic zones (Block, 1984). For example, the island of South Georgia ntarctic) is known to have just under 100 species of free-living terrestrial pods, of which 41 are insects and 55 are mites, whilst Signy Island me Antarctic) possesses only 13 species of free-living arthropods (four and nine mites). All the indigenous insects at Signy Island are

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Collembola, there being no holometabolous forms. It is generally thought barriers to colonization of the Antarctic Region by terrestrial arthropods ar geographical isolation and the biological problems of establishment and sur under the severe climate. Evidence suggests that much of the maritime continental Antarctic arthropod fauna derives from relic populations v survived the Pleistocene, although there may have been immigration fron north after this period (Wallwork, 1973). More recent colonizations have facilitated by man and frequent accidental and deliberate introductio plants and animals have been made to several sub-Antarctic islands (Edwar Greene, 1973; Jenkin *et al.*, 1982; Massé, 1982). Accidental introductions t maritime Antarctic have been fewer in number, and only two plant specie known to have survived for more than 2 years (Smith, 1984). Se temperate arthropods, chiefly Acari and Coleoptera, have been recorded i maritime zone, but as they are confined to areas of human habitation and populations have not become established, they are considered as temp introductions (Balfour-Brown & Tilbrook, 1966; Goddard, 1979).

The problems of initial colonization and establishment of arthropo Antarctic land habitats are severe. Survival of the physical and biolo conditions imposed by the environment is paramount, whilst some modifica of the species' biology and physiology may be required for establishment successful reproduction. There are no known instances of successful breedi recent arthropod colonists in maritime Antarctic habitats. Records of succ colonization by insects and other invertebrates are significant from viewpoint of understanding the processes of colonization of south polar areas, and for assessing the colonization potential that may exist in organisms. They also afford an insight into the ways and extent to which species may be pre-adapted for survival under more extreme conditions they normally encounter. This paper reports the discovery of a s established, reproducing population of a chironomid midge, together enchytraeid worms at Signy Island (60°43'S 45°38'W), in the South O Islands, maritime Antarctic. These alien taxa, accidentally introduced in material from either or both of the Falkland Islands and South Georgia, survived at least 17 years in the one site, and evidence is presented successful reproduction by the midge and its adaptation to cold temperat

FIELD OBSERVATIONS

On 27 September 1980, peat and moss samples were collected during th spring thaw from the base of Factory Bluffs close to the British Antarctic S station on Signy Island. Hand sorting of these cores revealed consid numbers of dipteran larvae and enchytraeid worms. These invertebrates restricted to a small site, *c.* 1 m^2 in area, situated on a 20° NNE facing sl 13 m asl, which had been subjected to a plant introduction experiment i (Edwards & Greene, 1973; Edwards, 1980).

Twelve specimens of 11 vascular plant species, which had been collec 17 November 1967 from the neighbourhood of Mount Challenger Falkland Islands, were transplanted into a native peat and mineral soil m at this site on Signy Island on 23–24 December 1967. By the following (November-December 1968) all the transplants had died. A total

imens of 14 vascular plant species, collected from three locations on South rgia in early December 1967, had been transplanted into the same site at y Island later in that month. Most of the South Georgian transplants died ng the following (1968) winter, but *Poa flabellata* was the most successful of e introductions, one plant continuing to grow for $4\frac{1}{2}$ years after its duction. All introduced plant material was removed and destroyed in uary 1973. As the soil in the original 1967 transplant site was from Signy d, and although subsequently it has been partly invaded by the moss *richum alpestre* and surface-growing lichens, all native to the island, it is luded that the dipteran and enchytraeids were introduced on the plants from either or both of the Falkland Islands and South Georgia. The duced forms appear to have survived in this habitat from 1967 to 1984, a d of 17 years.

he chironomid is *Eretmoptera murphyi* Schaeffer (Cranston, in press), which been recorded from moss at low altitudes on South Georgia (Brundin, 1970). currently being redescribed (Cranston, in press). *'Eretmoptera' murphyi* described from a male specimen collected at South Georgia, and the Signy d specimens are parthenogenetic with only females occurring (see below). recise taxonomic position is of considerable significance for the biological es concept concerned with potentially inter-breeding populations. The ytraeids belong to an undescribed species and probably a new genus, eneric with two specimens collected from Lynch Island (also in the South ey Islands) and Deception Island (South Shetland Islands off the Antarctic nsula) (B. Christensen, pers. comm.).

parallel series of transplants to Signy Island from the Falkland Islands and h Georgia were made into pots of vermiculite in 1967, and into native soil 68 (Edwards, 1980). No alien invertebrates have been found in any of these which are close to the one described above.

e field populations of both invertebrates at Signy Island have been tored regularly since their discovery in 1980. Estimates of summer lation densities average 25 718 m^{-2} for the midge larvae, and 3243 m^{-2} for nchytraeid worms, both species being highly aggregated. The midge larvae in greatest numbers within a few centimetres of the peat surface and close e mosses, especially *Polytrichum alpestre*, and lichens (mainly *Cladonia* spp.), as the pupae are located in small lacunae within the older peat matrix from living plants. The enchytraeids are found chiefly at 3–4 cm depth ssociated with areas of mixed fine organic and mineral debris. Extensive ination of the ground immediately adjacent to the site has produced little nce of spread by either taxon. A single larva of *E. murphyi* was found from the edge of the site in 1982, whilst six adults were seen on moss *c.* from the site in the following year.

ring the austral summer 1981–82, field observations were undertaken at te, and both female pupae and adult female midges were discovered. No have been found. Five small emergence traps, operated on the site for of December and January, collected nothing. However, on 6 January during a period of relative calm and sunny weather, when air ratures at screen height exceeded 4°C during the day, the brachypterous midges were observed for the first time on Signy Island. They were active g daylight for five days, when weather conditions were favourable. At such

times the temperature at the peat surface was in the range 11.9–12.8°C atmospheric relative humidity fluctuating from 77 to 84%. Temperatu 3 cm depth in the peat substrate of the site were similar to those at th surface. During this period, female midges were observed emerging from cases, crawling over the ground surface and holding firmly against wind cur Little migration seemed to occur. Oviposition took place and large, sph gelatinous egg masses were found on the site, from which larvae emerged ten days incubation at 5°C in the laboratory. Larval body lengths ranged 1.5 to 5.0 mm, whilst pupae were between 2.5 and 4.5 mm and adults 2 3.0 mm in length. Live weights of field insects were in the following ra 0.46–4.76 mg (larva), 1.01–2.04 mg (pupa), 0.18–1.16 mg (adult) ($N > 17$ in case). A further adult emergence was recorded on 6 January 1984 (Collett, pers. comm.).

LABORATORY EXPERIMENTS

An examination of the possible mechanisms for overwinter survival of invertebrates was undertaken at the BAS station on Signy Island in Jan 1982. Supercooling points were measured by monitoring the body temper (Block and Sømme, 1982) of individual Diptera and enchytraeids o temperature range of 5 to −30°C at a cooling rate of *c.* 1°C min^{-1} (Tab Both invertebrates appeared to be susceptible to freezing, i.e. unde experimental conditions freezing was lethal, although partial recove individual midge larvae and worms after freezing was observed on s occasions. Pupae of *E. murphyi* had the greatest capacity for supercooling the pupal data clearly divide into two groups at *c.* −20°C with supercooling points of −11.1°C ($N = 16$) and −22.9°C ($N = 20$) respect Individual adult supercooling points, although spanning a similar temper range, have a unimodal distribution. Summer-collected larvae, together the enchytraeids, had the poorest supercooling ability. Larval midges, col from the site in October 1982, had supercooling points in the region of (Table 1). Acclimation of both forms at 5°C for *c.* 6 months did not supercooling ability, with mean freezing points of -4.3 ± 0.1°C, $N = 24$ (larvae) and -4.5 ± 0.1°C, $N = 14$ (enchytraeids). Larval recovery t

Table 1. Mean (±S.D.) supercooling points and freezing ranges fo introduced terrestrial invertebrates at Signy Island, maritime Antarc January and October 1982

Month	Taxon	Life stage	N	Supercooling point (°C)	Freezing ra (°C)
January	Chironomidae				
	Eretmoptera murphyi	Larva	41	-7.2 ± 3.0	−2.4 to −
	Eretmoptera murphyi	Pupa (♀)	36	-17.6 ± 6.6	−6.2 to −
	Eretmoptera murphyi	Adult (♀)	51	-10.5 ± 4.7	−4.7 to −
	Enchytraeidae	—	27	-7.2 ± 2.3	−3.0 to −
October	*E. murphyi*	Larva	24	-5.0 ± 2.1	−1.6 to −

le 2. Mean (±S.D.) concentrations (μg mg^{-1} fresh weight) of polyols and rs detected in extracts of the midge, *Eretmoptera murphyi,* in January 1982 at Signy Island, maritime Antarctic

age	*N*	Trehalose	Glucose	Fructose	Glycerol
	14	6.59±5.37	2.96±2.21	1.66±1.26	0.94±0.68
(♀)	17	2.61±2.35	6.64±4.06	0.84±0.48	0.96±0.10
(♀)	17	0.87±0.39	2.61±1.59	3.03±2.13	1.41±1.12

lity after freezing has been recorded and appears to vary seasonally . C. Cannon pers. comm.).

hole body extracts of polyhydric alcohols and sugars in insect samples were ed by gas-liquid chromatography in Cambridge (Block & Sømme, 1982). compounds were found in all life stages of the midge: trehalose, glucose, ose and glycerol, but all were present in low concentrations (< 1% of fresh weight) (Table 2) compared to species of native arthropods. Trehalose the highest concentration (0.7% of fresh weight) in pupae and fructose % fresh weight) in adult females. Traces of mannitol, myo-inositol, ribitol rythritol were also detected in larval extracts. In spite of the small amounts nt, changes were observed in the levels of some of these compounds with ng. Comparison of trehalose levels in field fresh (unfrozen) larvae and e with individuals that had been experimentally supercooled and frozen led a reduction in concentration by a factor of 3–6 after freezing. This tion correlated with increases in glycerol and glucose concentrations.

DISCUSSION

e two invertebrates have not been found elsewhere in terrestrial habitats at Island and, in view of their restricted distribution there, their association ntroduced material from either the Falkland Islands or South Georgia, or and the fact that the dipteran has been recorded on South Georgia, it is t certain that both invertebrates were introduced to Signy Island in 1967 fore. Although colonization has been assisted by Man in this, the first ce of a holometabolous insect and an enchytraeid worm becoming ished in the Antarctic Region, both populations have survived a erable time (17 years after their introduction). Their estimated field ation densities, and their wide but aggregated distribution within the site tes that both have increased in numbers and spread locally since their uction. Oviposition by parthenogenetic females confirms that the midge is o complete its life cycle under maritime Antarctic conditions, and this of reproduction clearly helps to maintain its population at Signy Island. It e that sexual reproduction by fragmentation or parthenogenetic means, of many soil-dwelling enchytraeids, would ensure a similar success for the

ival of immediately sub-zero temperatures by individuals of both taxa is ercooling. Larvae of *E. murphyi* show similarity with ~~in contrast to~~ the ther terrestrial midge found in the Antarctic, *Belgica antarctica,* which is g tolerant (Baust, 1980). Although mean supercooling points of summer-

acclimatized specimens from the Signy Island site ranged from −5 to −1 some individuals froze at lower temperatures (−13°C for enchytraeids −26°C for *E. murphyi*). However, such a capacity for supercooling ma insufficient to ensure survival by avoiding freezing in severe winters at S Island, when extreme minimum temperatures at the surface of moss t exceptionally approach −25 to −30°C (Walton, 1982). The small amoun polyhydroxy compounds found would not significantly improve supercooling, but their biochemical profile may alter at the onset of wi Thus, a capacity to withstand freezing when it occurs in the larva would c a significant advantage in terms of survival on such a species introduced i more climatically severe environment. The field evidence indicates that species survives sufficiently well in the maritime Antarctic to complete it cycle and reproduce asexually to increment the population numbers. T activities have occurred despite a shorter time for development and grow summer and much colder winter temperatures than experienced on either S Georgia or the Falkland Islands. However, it should not be assumed tha dipteran population produces adults or that oviposition occurs each year.

Both taxa exhibit features of pre-adaptation for survival in conditions harsher than those from which they originated. In terms of cold hardiness results support the hypothesis that colonization and survival in environments has not always necessitated the evolution of novel ada features, but often the extension and development of existing mechanisms proposed that the major limitations to colonization of terrestrial habitats maritime Antarctic, especially by soil-living invertebrates, are prin geographical rather than biological. The data presented here confirm suitable physiological mechanisms already exist in some forms, and that if are available, the main obstacle to potential colonists is the geogra isolation of Antarctic sites from faunal sources in the southern cold tem zone.

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REFERENCES

BALFOUR-BROWNE, J. & TILBROOK, P. J., 1966. Coleoptera collected in the South Orkney a Shetland Islands. *British Antarctic Survey Bulletin, 9:* 41–43.

BAUST, J. G., 1980. Low temperature tolerance in an Antarctic insect: a relict adaptation? *Cryo-* 360–371.

BLOCK, W., 1984. Terrestrial microbiology, invertebrates and ecosystems. In R. M. Laws (Ed.) Ecology: 163–236. London, New York: Academic Press.

BLOCK, W. & SØMME, L., 1982. Cold hardiness of terrestrial mites at Signy Island, maritime *Oikos, 38:* 157–167.

BRUNDIN, L., 1970. Diptera: Chironomidae of South Georgia. *Pacific Insects Monograph, 23:* 276.

CRANSTON, P. S., in press. *Eretmoptera murphyi* Schaeffer (Diptera: Chironomidae), an a parthenogenetic *Antarctic Survey Bulletin, 67.*

Antarctic midge. British λ

ARDS, J. A., 1980. An experimental introduction of vascular plants from South Georgia to the maritime tarctic. *British Antarctic Survey Bulletin, 49:* 73–80.
ARDS, J. A. & GREENE, D. M., 1973. The survival of Falkland Island transplants at South Georgia d Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin, 33 & 34:* 33–45.
DARD, D. G., 1979. Biological observations on the free-living mites of Signy Island in the maritime tarctic. *British Antarctic Survey Bulletin, 49:* 181–205.
IN, J. F., JOHNSTON, G. W. & COPSON, G. R., 1982. Introduced animal and plant species on acquarie Island. *Comité national françaises des recherches antarctiques, 51:* 301–313.
É, L., 1982. Les introductions végétables dans les Terres Australes et Antarctiques Françaises. *Comité ional françaises des recherches antarctiques, 51:* 333–336.
H, R. I. L., 1984. Terrestrial plant biology. In R. M. Laws (Ed.), *Antarctic Ecology:* 61–162. London, w York: Academic Press.
WORK, J. A., 1973. Zoogeography of some terrestrial micro-Arthropoda in Antarctica. *Biological iews, 48:* 233–259.
ON, D. W. H., 1982. The Signy Island terrestrial reference sites: XV. Micro-climate monitoring, 2–74. *British Antarctic Survey Bulletin, 55:* 111–126.

Arthropod Interactions in an Antarctic Terrestrial Community

W. BLOCK[1]

Summary. A functional analysis of a low-diversity terrestrial arthropod community in the maritime Antarctic is made, especially in relation to the flux of energy and predation. Although net primary production of the main plants – mosses is 392–409 g m^{-2} yr^{-1} (dw), most arthropods feed on epiphytic algae, micro-flora and detritus. Invertebrates other than Protozoa contribute < 1% to total heterotroph respiration. Invertebrate carnivores utilize very little of primary consumer production (< 0.5%). The abundant collembolan herbivore *Cryptopygus antarcticus* alters its energy budget depending on food quality and temperature, but its grazing may have a significant impact only at algal dominated sites. The single arthropod predator *Gamasellus racovitzai* feeds on three species of arthropod, the principal one during summer being *C. antarcticus*, which forms the greatest proportion of available prey. It is non-selective with regard to prey when feeding during summer, and does not feed extensively in winter. It is unlikely that such a predator ever has a shortage of food in bryophyte habitats. It is concluded that: the principal grazing chain in such communities is ectothermic, being based entirely on invertebrates and regulated by algae and micro-flora production; Antarctic and temperate terrestrial systems differ in the pathways of energy flux with contrasting ecological efficiencies for both herbivores and carnivores; on current evidence the functional position of invertebrate predators such as *G. racovitzai* appears anomalous; and, several correlates of adversity or A-selection are found in Antarctic communities, which may preclude their recovery from perturbations.

1 Introduction

Notwithstanding the variation in tundra communities throughout the world, those of the Arctic and Antarctic regions have some features in common and many that are dissimilar. Their commonality resides in the limitation by their low temperature environments of the rates of most biological processes, the relatively short season for biological activity and the frequent occurrence of permafrost. The major differences are the rates of net primary production, especially the cryptogam component, their micro-floral biomasses, the amount of herbivory, the composition of the invertebrate community and utilization of the annual detritus input. In particular, Antarctic terrestrial habitats accommodate invertebrate communities of relatively low species diversity, and this is especially the case for arthropods, the majority of which are Acari and Collembola. Such a community composition with few interacting species, but often comprising large numbers of individuals (D.G. Goddard 1979; Block 1982), allows a functional analysis which is impossible at present elsewhere. Most other terrestrial communities are richer both in species and population numbers, and, hence, present too complex a suite of interactions for such analysis. Antarctic communities therefore provide an unrivalled opportunity for an attempt to understand some of the fundamental ecological processes governing species and energy interactions, and to test general ecological theory.

This paper is a first attempt at a functional analysis of a low-diversity terrestrial arthropod community at Signy Island in the maritime Antarctic (Holdgate 1977). As part of the analysis, the flux of energy through key species is examined, together with the role of predation in the community. Most of the basic data are derived for bryophyte-dominated communities (e.g., the Signy Island Reference Sites (Tilbrook 1973), but observations comparative with other terrestrial habitats such as fellfields are made where appropriate.

2 Community and Trophic Structure

In terrestrial communities of the maritime Antarctic, organic matter resides in three compartments; autotrophs (primary producers), heterotrophs (secondary producers) and dead organic matter. The primary producers are chiefly mosses, liverworts and lichens (consumed as dead material by heterotrophs) together with both uni- and multi-cellular algae (consumed as live material by heterotrophs). The secondary producers are comprised of saprotrophs (bacteria, yeasts, and filamentous fungi), primary consumers (protozoa, rotifers, tardigrades, nematodes, mites, and springtails), and secondary consumers (three carnivorous species: a nematode, *Coomansus gerlachei*, a tardigrade, *Macrobiotus furciger*, and a mite, *Gamasellus racovitzai*). The dead organic matter pool receives contributions from both auto- and heterotrophic components, but consists mainly of dead plant material.

The arthropods of such communities are all micro-forms (135–1,250 μm in body size), do not include higher insects and consist entirely of Acari (six to nine species) and Collembola (three to four species) (Tilbrook 1967; D.G. God-

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Antarctic Nutrient Cycles and Food Webs (ed. by W.R. Siegfried, P.R. Condy, and R.M. Laws)

1. The diet of terrestrial arthropods at Signy Island

	Algae	Mosses, liverworts lichens	Micro-flora	Dead organic matter	Micro-arthropods
nbola					
ɔtopygus tarcticus	⊕	–	⊕	+	–
ɔotoma to-ulata	+	–	⊕	⊕	–
kozetes arcticus	⊕	⊕	+	+	–
ɔdes nutus	⊕	–	+	–	–
netes cquari-is	⊕	–	+	–	–
otydeus ɔsus	⊕	–	–	–	–
ɔrchestes arcticus	⊕	–	–	–	–
us rooki	⊕	+	+	–	–
ɪsellus ɔvitzai	–	–	–	–	⊕

(–) not observed in gut contents; (+) low proportion (< 40%) contents; and, (⊕) high proportion (> 50%) of gut contents

979; Usher and Booth 1984). A generalized synopsis diet of the main species of arthropods is presented le 1 (after D.G. Goddard 1982; Burn 1984). Four al food resources can be distinguished. The domi-oods for such micro-arthropods are algae, both and macro-forms, which comprise a highly diverse ily assimilated food resource. Broady (1979) recorded ls of 162 species of algae from a range (122) of ter-habitats at Signy Island. A second-order resource is cro-flora, with yeasts and fungi being the main items. ird food component is dead organic matter, and the resource is entirely animal material as prey for the rthropod predator. Mosses, liverworts and lichens are nsumed by the arthropods to any significant extent % of their net primary production being utilized by mary consumers according to Davis (1981). Hence, suitable environmental conditions, the majority of yte and lichen production passes directly into the ganic matter pool and accumulates as peat, a process s characteristic of the maritime Antarctic. Thus algae, r with the micro-flora and detritus, provide the main ı of the diet of many of the primary consumers, ly the micro-arthropods.

weight biomass of micro-algae growing epiphytically riety of mosses in summer ranged from ca. 4 to ^{2} (Broady 1975), equivalent to a dry wt. biomass of 4 g m^{-2}. Net production estimates for algae were in ge 13-15 g m^{-2} yr^{-1} dry wt. (Davis 1981). These data contrast markedly with average values in the maritime Antarctic for total moss standing crop of these communities of 180-604 g m^{-2} dry wt. and a calculated net production of 392-409 g m^{-2} yr^{-1} dry wt.

3 Energy Flux

Few functional analyses of Antarctic terrestrial communities have been made (Smith 1977 in the Sub-Antarctic; Davis 1981 in the maritime Antarctic). Figure 1 shows a generalized energy flow diagram for the bryophyte-dominated ecosystems typical of the maritime Antarctic. Although the majority of the plant biomass is made up of mosses and liverworts (and sometimes lichens), the importance of algae, and to a lesser extent the micro-flora, in the functioning of such systems must be stressed. Davis (1981) estimated that in moss turf and carpet communities the consumption of algae by primary consumers (invertebrates) exceeded algal net production by between 8 and 77 times, respectively. In the same instance, the dietary demands of the invertebrates are largely transferred to the heterotrophic micro-flora with between 40 and 80% of micro-floral production being utilized in this way.

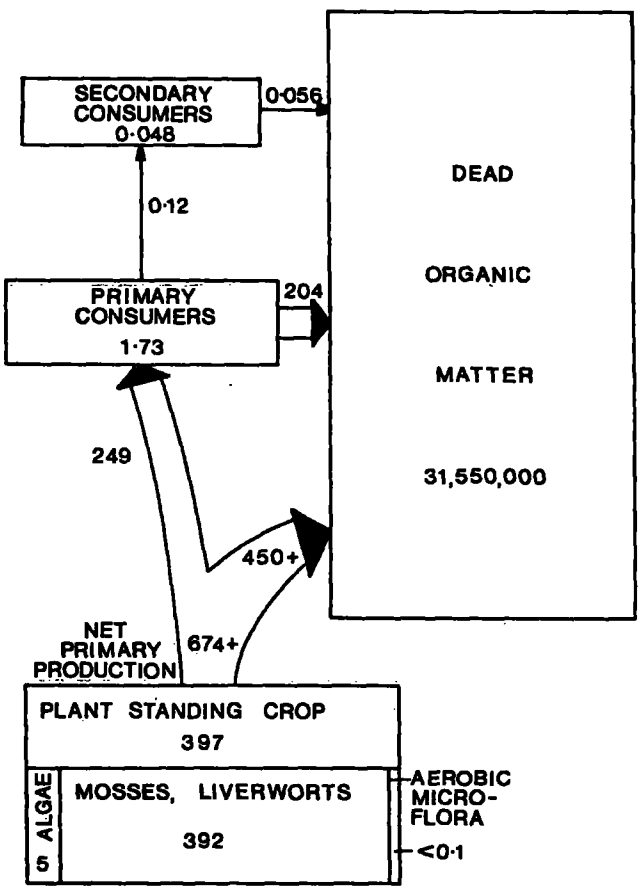


Fig. 1. Generalized diagram of energy flux in bryophyte-dominated ecosystems of the maritime Antarctic (After Davis 1981). Units are g m^2 yr^{-1} dry wt.

Since < 0.1% of the net primary production (bryophytes) is eaten by primary consumers, the consumption of algae by some invertebrate species is the only significant herbivory in such moss-dominated systems. The saprotrophs are functionally the most important heterotrophic organisms and may control decomposition processes to a large extent. Their dominant role is reflected in the proportion of total heterotrophic respiration: the micro-flora respire 81%–89% compared to 11%–19% by the Protozoa, and 0.4%–0.5% by the remainder of the invertebrates (Davis 1981). The reduced role of the invertebrates other than the Protozoa in such Antarctic ecosystems contrast with Arctic and temperate upland studies, where they contribute between 1% and 23% of the total heterotroph respiration (Whitfield 1977; Coulson and Whittaker 1978). However, Antarctic communities are greatly impoverished in respect of invertebrates compared to those of Arctic and upland systems, in which insect larvae, lumbricids, enchytraeids, etc., are often found. The reduced invertebrate component, together with low microbial activity, may contribute to the slow decomposition rates measured in Antarctic bryophyte communities (Davis 1980).

The supposed poor quality of bryophytes as food resources for many terrestrial invertebrates in conjunction with the overall limiting effects of their low temperature environment may account for their small part in energy flux. The low efficiency of utilization of primary consumer production by invertebrate carnivores is less easy to understand. Efficiencies of 0.3%–0.5% [(carnivore consumption/primary consumer production) × 100] have been calculated (Davis 1981), but these are very low compared with Arctic systems where efficiencies of 12%–33% have been estimated (Whitfield 1977; MacLean 1980).

It is appropriate to examine in detail the processes of herbivory and predation in Antarctic ecosystems in an attempt to clarify these anomalies. For this, attention will be confined to recent work on selected species of micro-arthropods at Signy Island.

4 Herbivory

The isotomid collembolan, *Cryptopygus antarcticus*, is very abundant in communities throughout the maritime Antarctic. Field populations in summer ranged from 19,000 (moss turf) through 39,000 (fellfield) to 180,000 (algal site) individuals m^{-2} at Signy Island (Burn 1984) with annual mean values of ca. 49,420 (moss turf) individuals m^{-2} (Block 1982). It feeds on unicellular green algae, dead moss material and fungal hyphae (in order of preference). Using a radioisotope C^{14} label, Burn (1984) measured feeding rates and individual growth rates on these three common field foods for two size classes of *C. antarcticus*. The interval between moults was similar on all foods for both sizes, and the dry weight increase per moult for the larger animals was similar on each food type. However, the growth rates of the smaller

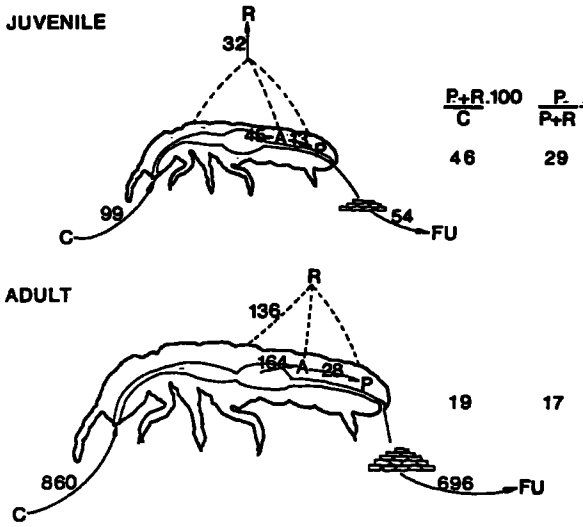


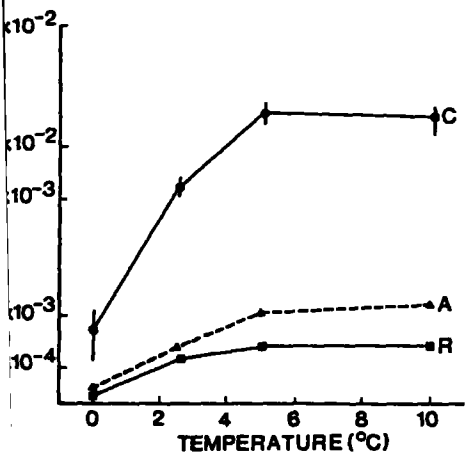
Fig. 2. A schematic representation of the energy budget for ju and adult individuals of *Cryptopygus antarcticus* when fed o at 5 °C, together with assimilation and production efficiencies. Burn 1984). *C* consumption, *A* assimilation, *P* production, *R* r tion, and *FU* rejecta. Units are J × 10^3 per individual per moul val

collembolans fed on fungi were significantly slower compared to those fed on algae and homogenized mos

A schematic representation of the energy budgets oped for both young and mature individuals of *C. anta* is given in Fig. 2. At 5 °C, this species consumed 24% of its body weight on moss peat, but only 7%–13% o food. Of particular note in the energy budgets are diffe in assimilation [100(P+R)C]* and production (P+R)]* efficiencies between young and mature indiv In the mature animal, both these efficiencies are those of the young instars. The range of both these en efficiencies is low compared to data for temperate s Both age classes assimilated algae better than moss p though individuals fed more rapidly on the latter, wh a larger indigestible component, thereby compensat a lowered assimilation efficiency and achieving simil of growth on both substrata. The energy balance of *arcticus* was influenced further by temperature o range 0°–10 °C (Fig. 3). The ingestion rates sugge adaptation by maintenance of a positive energy bal low temperatures. In turn, feeding rates changed over 0°–5 °C, corresponding with previously r changes in metabolic rate (Block and Tilbrook 1975)

In terms of population energetics, it was estima *C. antarcticus* would consume between 7 (moss t 26 (algae) g m^2 yr^{-1} dry wt. (Burn 1984). This has a negligible effect on the net primary production of t phyte communities, but feeding of this species ma more influential role in algae-dominated sites, wh

* P = production; R = respiration; C = consumption



Influence of temperature on the energy budget of juvenile *pygus antarcticus* fed on moss peat (Burn 1984). *C* consump- S.E.M., *A* assimilation, and *R* respiration

mption may reach 135 g m^2 yr^{-1} dry wt. and plant ction may be limited locally.

s detailed approach to the feeding ecology and ener- of an abundant species confirms the general low level ɔivory in such situations, and the importance of algae, available, as a nutritious and comparatively readily as- ed, energy-rich substratum. The influence of food on individual energy budgets and growth rates is nd, and will be reflected in the population dynamics *ntarcticus* (Block 1982).

dation

e arthropod predator in these simple communities is sostigmatid mite, *Gamasellus racovitzai*, which has bserved to feed on eight monospecific prey arthro- ecent studies have enabled the identification of the ırgest and most abundant prey items in extracts of ıal predators by their characteristic esterase band pat- ısing polyacrylamide gel electrophoresis (Lister, to .). The data presented here are qualitative and based on the occurrence of prey traces. Food traces remain identifiable in the predator gut for up to 19 d at 5 °C.

Ignoring minor between-site differences, there are clear seasonal changes in the proportion of the predator population with detectable food or prey traces. Only about 18% of the population at Signy Island is non-feeding during summer (November–March), whereas no evidence of feeding was found in *G. racovitzai* throughout the winter (May–September). The proportions of two of the three prey species in *G. racovitzai* diet occur with the same frequency as their field abundance in the sites examined (Fig. 4). However, the mite *Alaskozetes antarcticus* appears to be underrepresented in the diet of the predator, probably as a result of its heavy sclerotization especially in the later nymph and adult stages making predation by a similar sized mite difficult. There is no evidence for active selection by *G. racovitzai* between potential prey species in the field.

There are no data available on predation rates of *G. racovitzai* under experimental or field conditions, but from preliminary observations at Signy Island it seems unlikely that starvation due to prey shortage would ever occur during summer. Comparison of population estimates for both the predator and its main prey species, *C. antarcticus*, shows that over the 2-yr study period, the prey population was, on average, over 100 times more numerous than the predator in a moss turf habitat. *Gamasellus racovitzai* is randomly distributed and generally found in the top 30 mm of the vertical profile, whereas *C. antarcticus* is strongly aggregated and is part of the green moss community in the upper 15 mm of the turf (D.G. Goddard 1979; Usher and Booth, to be published). It appears, therefore, that the predator has a super-abundance of potential food, and its extremely low utilization efficiency of herbivore production is brought about by other factors such as behavioural or physiological constraints.

6 Discussion

The absence of above-ground herbivores and the reduced invertebrate component of the fauna have profound effects

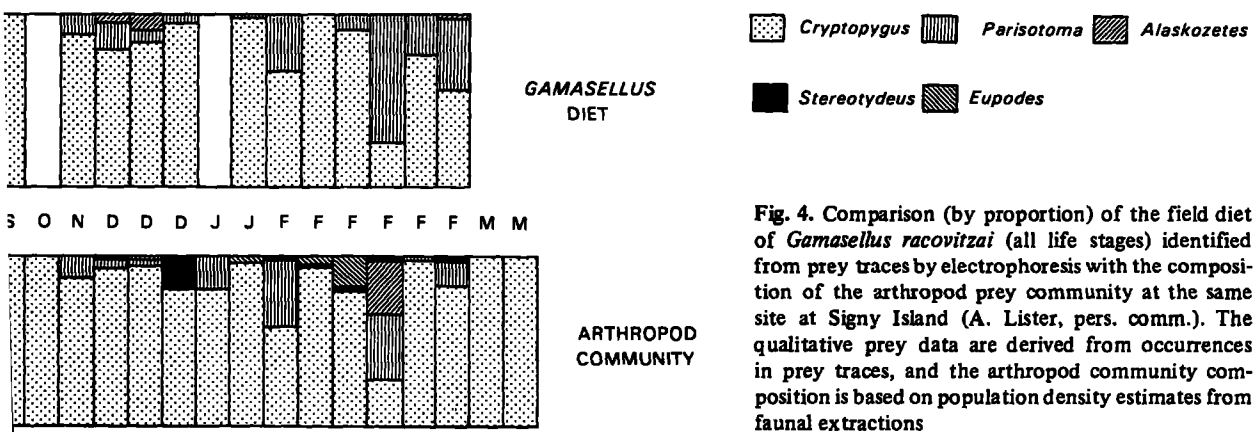


Fig. 4. Comparison (by proportion) of the field diet of *Gamasellus racovitzai* (all life stages) identified from prey traces by electrophoresis with the composition of the arthropod prey community at the same site at Signy Island (A. Lister, pers. comm.). The qualitative prey data are derived from occurrences in prey traces, and the arthropod community composition is based on population density estimates from faunal extractions

on both the structure and functioning of terrestrial ecosystems. It shifts the emphasis of energy flux onto smaller organisms in the below-ground-soil sub-system. This, in turn, greatly enhances the role of the micro-flora, especially in polar ecosystems, and the micro-flora-invertebrate interface is one that warrants further study under these conditions. Mammalian grazers tend to control net primary production and phytomass in communities where they occur. Invertebrates, on the other hand, appear less sensitive to annual variations in primary production, completing their life cycles when environmental conditions permit, and, hence, they may be more efficient at exploiting low temperature habitats. Thus, the principal grazing chain in the maritime Antarctic is ectothermic and invertebrate based.

The ecological efficiencies (Ricklefs 1973) for herbivores in the moss communities studied are 7%–9%, which lie within the range of temperate values (Davis 1981). However, the pathways of energy flux differ between Antarctic and temperate systems. Very little of the net primary production of mosses is eaten by primary consumers directly. Instead, the micro-flora assimilate dead organic matter and convert it to a form more readily metabolized by invertebrates. In this way, the soil fauna annually consume an amount equivalent to ca. 58% of the annual net primary production (after Davis 1981), which is very different from that which occurs in Arctic tundra where exploitation efficiencies are $< 1.5\%$ (Whitfield 1977). On the other hand, carnivore efficiency is slight, being 0.3%–0.5% of primary consumer production, which is in contrast to 15%–33% calculated for Arctic tundra. The major regulator of this type of herbivory in the maritime Antarctic is therefore the autotrophic micro-flora (mainly algae) which form one of the main herbivore food sources. Such a functional difference between northern and southern terrestrial systems was postulated by Holdgate (1977), on the basis that less invertebrate material was produced in the maritime Antarctic compared with the prediction of the model of Heal and MacLean (1975).

The position of invertebrate predators in the simple Antarctic communities is not clear. In the unique, single-predator arthropod community at Signy Island, *G. racovitzai* has a broad diversity of potential prey, but apparently exercises no selectivity and the proportions of the three main species in its diet fluctuate with their field abundance. These are characteristics more of a random rather than a prudent predator (Slobodkin 1974). There are no indications of the regulation of any of the herbivore populations by this predator under maritime Antarctic conditions. Invertebrate predators usually exhibit high basal metabolic rates, and therefore might be at a disadvantage in a low temperature environment compared to low metabolic rate herbivores (S.J. Goddard 1979). It is difficult to envisage how an extended life cycle could have evolved in such a predator without the interpolation of a diapause to conserve energy and withstand periods of stress. *Gamasellus racovitzai* has a high basal metabolism compared to the herbivorous and detritivorous mites of the maritime Antarctic (D.G. Goddard 1977); its life cycle is at least 2 yrs in duration, but no pause has been found.

The idea of the habitat templet was advanced by So wood (1977), in which habitat favourableness was assu to be the converse of a stressful or adverse situation, imparted a durational stability to the system through predictability. To the concept of r- and K-selection added adversity or A-selection, which favours the conse tion of adaptations to environments which are consiste severe but nevertheless predictable. Several correlate A-selection (Greenslade 1983) are found in Antarctic restrial habitats where relatively simple communities in harsh environments, and these include the poor migra ability of species, extended life cycles and low reprodu rates. In the present analysis, the inability of the inverte herbivores to consume bryophytes and the way in w this is circumvented are related features. Furthermore, habitats are species poor and many of the adaptation to the physical rather than the biological environment. environmental stability and predictability allow the sp to adapt closely, whilst environmental severity res competitors. Interspecific competition appears to be existent, and in dietary terms, generalists predominate specialists. The Antarctic populations appear to remain below habitat carrying capacity. However, the pred low reproductive rates of certain species in such commu suggest a limited capacity for recovery after a decrease ability of these arthropod communities to adjust to ph perturbations or to counter the introduction of new sp whether accidentally by man (Block et al. 1984) or n ally by colonization, may not be adequate.

Acknowledgements. I appreciate the stimulus provided by t portunity to study Antarctic systems, and the helpful critic many colleagues in the British Antarctic Survey in the prepa of this paper. I am indebted to Drs R.C. Davis, A.J. Burn, and A. for the use of unpublished information, and to my wife May f ful drawing.

References

Block W (1982) The Signy Island terrestrial reference sites Population studies on the Collembola. Br Antarct Surv I 55:33–49

Block W, Tilbrook PJ (1975) Respiration studies on the A collembolan *Cryptopygus antarcticus*. Oikos 26:15–25

Block W, Burn AJ, Richard K (1984) An insect introductio maritime Antarctic. Biol J Linn Soc 22:

Broady PA (1975) Studies on the terrestrial algae of Signy South Orkney Islands. PhD thesis, University of Bristol, U

Broady PA (1979) The terrestrial algae of Signy Island, South Islands. Br Antarct Surv Sci Rep No 98:1–117

Burn AJ (1984) Energy partitioning in the Antarctic coll *Cryptopygus antarcticus*. Ecol Entomol 9:11–21

Coulson JC, Whittaker JB (1978) Ecology of moorland ani Heal OW, Perkins DF (eds) Production ecology of Britis and montane grasslands. Springer, Berlin Heidelberg Ne pp 52–93 [Ecological Studies 27]

Davis RC (1980) Peat respiration and decomposition in A terrestrial moss communities. Biol J Linn Soc 14:39–49

is RC (1981) Structure and function of two Antarctic terrestrial moss communities. Ecol Monogr 51:125–143
dard DG (1977) The Signy Island terrestrial reference sites: VI. Oxygen uptake of *Gamasellus racovitzai* (Trouessart) (Acari: Mesostigmata). Br Antarct Surv Bull No 45:1–11
dard DG (1979) The Signy Island terrestrial reference sites: XI. Population studies on the terrestrial Acari. Br Antarct Surv Bull No 48:71–92
dard DG (1982) Feeding biology of free-living Acari at Signy Island, South Orkney Islands. Br Antarct Surv Bull No 51:290–293
dard SJ (1979) The population metabolism and life history tactics of *Neobisium muscorum* (Leach) (Arachnida: Pseudoscorpiones). Oecologia (Berl) 42:91–105
nslade PJM (1983) Adversity selection and the habitat templet. Am Nat 122:352–365
OW, MacLean SF (1975) Comparative productivity in ecosystems – secondary productivity. In: van Dobben WH, Lowe-McConnell RH (eds) Unifying concepts in ecology. Dr W Junk, The Hague, pp 89–108
gate MW (1977) Terrestrial ecosystems in the Antarctic. Philos Trans R Soc Lond B 279:5–25
r A (to be publ.) Predation in an Antarctic micro-arthropod mmunity. Proc VI Int Cong Acarology (Edinburgh)
MacLean SF (1980) The detritus-based trophic system. In: Brown J, Miller PC, Tieszen LL, Bunnell FL (eds) An Arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson and Ross, Pennsylvania, pp 411–457 [US/IBP Synthesis Series 12]
Ricklefs RE (1973) Ecology. Thomas Nelson, London
Slobodkin LB (1974) Prudent predator does not require group selection. Am Nat 108:665–678
Smith VR (1977) A qualitative description of energy flow and nutrient cycling in the Marion Island terrestrial ecosystem. Pol Rec 18:361–370
Southwood TRE (1977) Habitat, the templet for ecological strategies? J Anim Ecol 46:337–365
Tilbrook PJ (1967) The terrestrial invertebrate fauna of the maritime Antarctic. Philos Trans R Soc Lond B 252:261–278
Tilbrook PJ (1973) The Signy Island terrestrial reference sites: I. An introduction. Br Antarct Surv Bull Nos 33/34:65–76
Usher MB, Booth RG (1984) Arthropod communities in a maritime Antarctic moss-turf habitat: three dimensional distribution of mites and Collembola. J Anim Ecol 53:427–442
Whitfield DWA (1977) Energy budgets and ecological efficiencies on Truelove Lowland. In: Bliss LC (ed) Truelove Lowland, Devon Island, Canada: a high Arctic ecosystem. University of Alberta Press, Edmonton, pp 607–620

Cryo-Letters 6, 73-80(1985).
Published by Cryo-Letters, 7, Wootton Way, Cambridge CB3 9LX, U.K.

LOSS OF SUPERCOOLING ABILITY IN CRYPTOPYGUS ANTARCTICUS (COLLEMBOLA: ISOTOMIDAE) ASSOCIATED WITH WATER UPTAKE

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UMMARY

Individuals of an Antarctic springtail mostly showed supercooling oints (SCP) below -20°C, when taken directly from the field during winter, ut when placed at 5°C for short periods (3 and 7 d) in the presence of vailable distilled water (DW), a substantial loss of supercooling ability ccurred. Control treatments without DW (dry), showed no loss of super- ooling ability. In one experiment supercooling ability was inversely orrelated with body water content, which was low (37%) in field specimens id after the dry treatment, but high (68%) in the DW treatment. These indings are discussed in relation to nucleation and gut-clearing, and it is iggested that physiological changes occur in this species that result in a ehydrated over-wintering state.

Y WORDS

Supercooling, nucleation, cold hardiness, gut-clearing, dehydration.

INTRODUCTION

All species of Collembola investigated to date, depend upon supercooling of their freezable body water, to survive sub-zero winter temperatures[1]. A correlation between extent of supercooling and gut conten was demonstrated for Tetracanthella wahlgreni Linnaniennii[2]. The authors concluded that the ability to supercool increased when guts are emptied and glycerol is accumulated. Two species of Collembola at Signy Island (60°43'S, 45°38'W) in the maritime Antarctic provided further evidence for the relation between supercooling and feeding status[3]. For one species, Crytopygus antarcticus Willem, fed on a diet of purified green algae, it wa suggested that increased supercooling ability resulted from a lack of nucleators in this food. In contrast another batch of Cryptopygus, fed on diet of moss turf homogenate, showed poor supercooling ability, which indicated the presence of efficient nucleators. Burn[4] studied the feeding activity of Cryptopygus on Signy Island, and found that feeding activity in the field declined with the onset of sub-zero temperatures. The absence of gut contents in winter-collected specimens was correlated with enhanced survival at -15°C in the laboratory, which resulted from improved supercooling ability. Seasonal changes in supercooling potential of field collected Cryptopygus generally correspond with the annual temperature cycl on Signy Island (W. Block, unpublished data), although rapid changes in supercooling ability occur when temperatures exceed 0°C for short periods winter. Abrupt changes in the numbers of fed Cryptopygus during spring freeze-thaw cycles suggest that a rapid gut emptying response occurs.

In the course of a preliminary series of experiments at Signy Island, it was observed that Cryptopygus individuals acclimated to -15°C for 14 d and allowed to recover at 5°C for c. 3 d, showed a rapid loss of cold hardening (i.e. supercooling potential) if given access to distilled water but this did not occur when the insects were deprived of water. To confir this observation, two fully controlled experiments were undertaken using field-fresh winter-collected Cryptopygus in 1983 and 1984. The aim of the experiments was to quantify the rate and extent of these changes in supercooling ability and water contents, which occur as a result of the presume uptake of distilled water. The results are discussed in relation to the role of nucleators in determining freezing, and also to the physiology of over-wintering Cryptopygus.

MATERIALS AND METHODS

The use of heat extraction methods to obtain collembolans from soil samples can result in a loss of cold-hardiness[5]. In the present study, over-wintering Cryptopygus were obtained in the field by suction (aspirator) and brushing from icy surfaces, usually underlying flat rocks (quartz-mica schist). On two occasions (14 October 1983 and 10 August 1984) collections were made near a moss-dominated site, close to a penguin rookery (unoccupied) on the Gourlay Peninsula of Signy Island. During the winter months the site is mainly encased in frozen ground water and overlaid by a variable thickness (<50 cm) of snow. Sampling involved removing the snow layer and chipping out the iced-in rocks to expose aggregations of immobile Cryptopygus on the ice glazed soil surface beneath. The minimum air temperatures during the 24 h periods immediately prior to sampling on 14 October 1983 and 10 August 1984, were c. -4 and -12°C respectively.

The bulked samples of field collected insects were transported to the laboratory in dry plastic petri-dishes, i.e. without contact with moisture, and placed at 5°C for sorting. On 10 August 1984 (only) five samples each of ten individuals (mixed sizes) were weighed immediately after collection. They were immobilised (some recovery had occurred) by rapid cooling of the containment vials using an aerosol spray. The samples were reweighed after oven drying at 50°C for 48 h, thus providing an estimate of water content. Both supercooling points (SCP) and water contents of field-fresh specimens (treatment a) were determined within 4 h of collection.

To obtain SCP, the insects were attached by a grease film to fine (30-36 swg) copper-constantan thermocouples, the outputs of which were recorded on a 6-channel, mains-operated Linseis L2001 chart recorder. Insects of a wide size range (c. 600-1800 μm) were attached in groups of 10-12 per thermocouple, avoiding contact between individuals. A cooling rate of c. 1 deg min^{-1} was obtained using the method of Block & Somme[6], and SCP were measured and analysed using similar techniques.

Two experimental treatments (b and c) were set up, identical in all respects other than the presence (in c) and absence (in b) of double distilled water. The collembolans were placed in small (25 ml) plastic pots; these had mesh-covered ventilation holes in the lids which allowed gaseous exchange, but prevented the insects from escaping. The pots contained shreds of nylon mesh, which in treatment c were wetted to provide a thin film of available distilled water; the surface tension being lowered to aid the dispersion of the film across the mesh. The pots were placed inside larger (500 ml) screw-top glass jars; moistened filter-paper in the bases of

these jars provided a saturated atmosphere in the pots. The jars were kep at 5°C in continuous light conditions for 7 d (14 October 1983 sample) and 3 d (10 August 1984 sample). Following the treatment periods, SCP and wat contents were determined: both treatments (b and c) within c. 2 h of each other. Prior to SCP determination, insects (all treatments) were placed o dry filter paper for c. 10–20 min. Microscopic inspection confirmed that all individuals were dry, when attached to thermocouples.

Smoothed frequency distributions of the SCP data were plotted (see Fig. 1) using 3-point running means[7], with individual SCP summed over 1 de intervals. The terms high group (HG) and low group (LG) refer to modal groups of SCP which in this case are divided at a critical temperature (-20°C), such that LG < -20°C < HG. Thus for each distribution there are two means (± S.D.) (see Table 1), for values either side of -20°C. Howeve the median values given (Table 1) are for the complete distributions per treatment.

RESULTS

The smoothed frequency distributions for the two experiments (1 and 2 with treatments (a, b and c) are shown together (Fig. 1) to enable comparisons. The median SCP (M), is indicated on each distribution. The mean SCP are given separately for HG and LG (Table 1), and R-values, the proportion of individual SCP in the LG, are also presented.

For the 14 October 1983 sample 63% of field collected individuals had individual SCP in the LG (i.e. < ~ 20°C), whereas in the 10 August 1984 sample the proportion was 98%. This initial difference is probably carrie over to some extent in the subsequent treatments, although the nature of t changes produced in the two experiments are similar.

In both experiments the dry treatment (b) did not result in large changes in supercooling ability, compared to the field collected animals (a). This was particularly apparent in Expt. 2, where nearly all field collected individuals had SCP in the LG, suggesting that the insects were a fully winterised state. In Expt. 1, the proportion of SCP in the HG decreased slightly in treatment b, although the mean HG location did not alter greatly (Table 1). There was also a slight downward shift of the L in this treatment (Expt. 1b), which is clearly suggested by the median (Table 1). This, albeit small affect, may also have been because the 14 October 1983 sample was not taken during mid-winter.

TABLE 1

Mean (± S.D.) and Median (M) supercooling points (SCP) for Cryptopygus antarcticus (mixed sizes) in two separate experiments (1 and 2), and mean (± S.D.) water contents (experiment 2), using the same three treatments: a) field collected; (b) dry; (c) distilled water. n = number of insects in LG (low group) and HG (high group) (see text). R = LG/(HG + LG).

	Mean (± S.D.) supercooling points (°C)		
Experiment 1.			
4 Oct 1983	(a)	(b)	(c)
G SCP	−14.6 ± 3.0	−13.9 ± 4.1	−6.1 ± 3.7
n	27	6	46
G SCP	−25.4 ± 1.4	−26.2 ± 3.1	−23.7 ± 3.0
n	45	24	5
R	0.63	0.80	0.10
M	−24.3	−26.5	−5.7
Experiment 2.			
Aug 1984	(a)	(b)	(c)
SCP	−19.0	−15.4 ± 2.0	−10.7 ± 2.3
n	1	2	32
SCP	−30.7 ± 1.4	−29.6 ± 1.9	−22.9 ± 1.3
n	39	38	27
R	0.98	0.95	0.46
M	−30.6	−30.3	−18.5
ter contents (%)	37.0 ± 4.5	37.0 ± 6.0	68.4 ± 1.3

The distilled water treatments (c) are a striking contrast to the dry eatments (b) in that they show a considerable loss of supercooling ability ing the short duration of the experiments. These differences, which are t apparent in the longer experiment (1), are illustrated by the smoothed quency distributions (Fig. 1) and are reflected in the medians and R-ues. The appearance of the majority of the SCP at temperatures ediately below 0°C, suggests that profound changes occurred in the ects where distilled water was available.

The mean water contents for insects in Expt. (2) (Table 1), show a similar pattern to the SCP: the low levels (37%) that occurred in field collected specimens (a) were maintained during the dry treatment (b), but increased markedly (to 68%) during the DW treatment (c), suggesting an uptake of distilled water.

DISCUSSION

Both experiments revealed that the availability of distilled water alone can cause a substantial loss of cold hardiness (i.e. supercooling ability) in overwintering Cryptopygus, in contrast to dry treatments where no loss occurred. The second experiment (2) suggested that the loss of col hardiness was the result of an increase in water content, which implies an uptake of water by the insects. This may occur via the ventral tube, whicl as well as enabling Collembola to adhere to surface films of water, is alsc concerned with water absorption[8]. The most important feature of the distilled water-associated decrease in supercooling ability, is the appearance of HG SCP normally produced by feeding[3]. The upward shift in SC was most marked in the 7 d experiment (1), which suggests that the duratio (3 d) of Expt. 2 was insufficient to effect the same degree of change.

Although the dry treatments were at 5°C, there was not loss of cold hardiness, in fact there was a slight improvement in Expt. 1. This might have been because cryoprotectants are not involved in this phenomenon. In acclimation experiments on Cryptopygus[9], little evidence was found for changes in glycerol concentration in the short term, although an increase in most cryoprotectants (especially glycerol) after acclimation at -5°C fo 28 d has been documented[3]. In view of a possible dehydration mechanism in overwintering Cryptopygus, it could be that such increases are the result a concentration effect. Further studies are needed to resolve the role of cryoprotectants in this species.

In a laboratory experiment, individual Cryptopygus were repeatedly frozen and rewarmed[10]. Although all insects died after the first freezing a significant increase in supercooling ability of the dead specimens occurred, probably as a result of dehydration. However, these experiments did not produce a significant shift of SCP from HG to LG, and it seems fr other evidence[3,4] that an active, behavioural response (i.e. gut-clearing is required to achieve this.

The elevation of SCP that occurred in treatment (c) resulted from an increase in internal nucleation at higher sub-zero temperatures, and was caused by innoculative freezing from surface moisture. Apart from the

ventral tube, the collembolan cuticle is strongly hydrofuge, and is not readily wetted. Either fresh nucleators were introduced with the double distilled water, or nucleators already present in the insect were reactivated (or unmasked). If nucleators are present in such liquids, then they must occur in all substances entering the insect gut, and it is difficult to envisage how an insect could remove all such particles, especially over the short time scale. However, if a gut-clearing response involved physiological changes such as nucleator masking, then re-activation by distilled water is clearly possible.

It is known that a reduction in gut volume occurs in some collembolans experiencing drought conditions[11], and it may be that a similar mechanism operates in overwintering Cryptopygus. In which case, potential nucleators remaining inside the gut would be isolated from free water elsewhere in the insect (i.e. the haemocoel). The removal of free water from nucleation sites other than the gut, is a subject for further investigation. If water uptake is via the ventral tube in Cryptopygus, then water will enter the haemocoel directly, bipassing the gut. The extent to which nucleators remain in insect guts that are apparently empty is a central issue. It may be that gut-clearing, or simply a cessation of feeding, leads to a removal of water from the gut, and as feeding reintroduces water (with or in food), correlation between full guts and poor supercooling ability will occur[2,12].

REFERENCES

1. L. Sømme, Comp. Biochem. Physiol. 73 A, 519 - 543 (1982).
2. L. Sømme and E.-M. Conradi-Larsen, Oikos 29, 118 - 126 (1977).
3. L. Sømme and W. Block, Oikos 38, 168 - 176 (1982).
4. A.J. Burn, C.N.F.R.A. 51, 219 - 225 (1981).
5. H.P. Leinaas and L. Sømme, Oikos 43, 197 - 206 (1984).
6. W. Block and L. Sømme, Oikos 38, 157 - 167 (1982).
7. R.W. Salt, Can. J. Zool. 48, 205 - 208 (1970).
8. J. Noble-Nesbitt, J. exp. Biol. 40, 701 - 711 (1963).
9. R. Schenker, Rev. Ecol. Biol. Sol. 21, 205 - 220 (1984).
10. R.J.C. Cannon, J. Insect Physiol. 29(8), 617 - 624 (1983).
11. E.N.G. Joose, Pedobiologia 25, 217 - 234 (1983).
12. W. Block and J. Zettel, Ecological Entomology 5, 1 - 9 (1980).

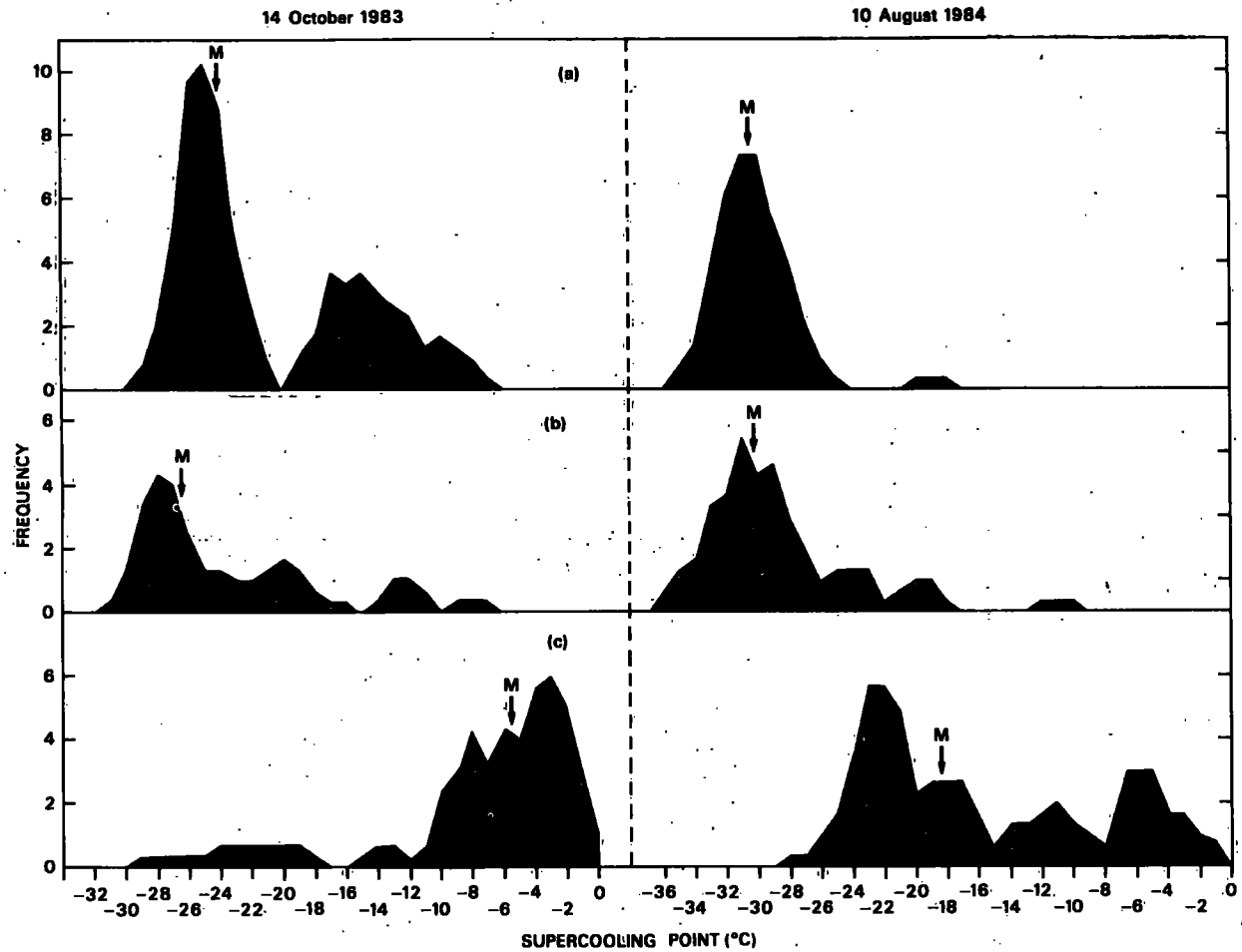

FIG. 1. Supercooling point distributions for Cryptopygus antarcticus in two separate experiments (1. 14 October 1983 and 2. 10 August 1984) using the same three treatments: (a) field collected; (b) dry; (c) distilled water.

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SURVIVAL AND WATER LOSS IN SOME ANTARCTIC ARTHROPODS

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Abstract—Seven species of Antarctic micro-arthropods (4 mites and 3 collembolans) were examined to determine their resistance to dehydration and their survival under dry conditions. Water loss at r.h. 5% at temperatures in the range −10 to 45°C was measured gravimetrically using a recording micro-balance. Survival of samples of mites was monitored after exposure to r.h. 5% and temperatures in the range 0–20°C. Rates of water loss ranged from 0 to about 30% fresh weight h^{-1} depending on temperature and species. The 3 Collembola were least resistant and the 2 oribatid mites were most resistant to dehydration under the experimental conditions. The optimal survival temperature of the mite *Alaskozetes antarcticus* was around 10°C under 5% r.h.; there were no significant differences in rate of water loss between temperatures. The results are discussed in terms of possible control mechanisms and the type of habitat occupied by each species.

Key Word Index: Water loss, Antarctic micro-arthropods, dehydration, survival

INTRODUCTION

environment of Signy Island (60°43′S, 45°38′W) he maritime Antarctic presents the indigenous ulations of micro-arthropods with severe physical straints. In particular, freezing temperatures and ccating conditions may not occur together. The ority of Antarctic arthropods, and the 7 species ided in this study, survive sub-zero temperatures avoiding freezing with extensive supercooling er than being freezing tolerant. They utilize two esses to improve their cold-hardiness. These are he clearance of their gut contents including food water to reduce the probability of heterogeneous eation when supercooled, and (2) improving their rcooling ability by the accumulation of poly- ic alcohols such as glycerol. A bimodal distri- on of individual supercooling points occurs in ples of fed animals, and studies of their high p and low group composition have been made k and Sømme, 1982).

uch research has focused on the production of reeze compounds by cold-hardy arthropods and nvironmental triggers for their synthesis. Young Block (1980) showed that dehydration stimulated rol accumulation in the Antarctic mite *Alas- es antarcticus* (Michael). Recent studies on other rctic micro-arthropods indicate that a decrease dy water content accompanies the onset of r concomitant with the synthesis of glycerol, l is possibly triggered by low atmospheric dities (Cannon, 1986). However, the roles of spheric and body water in the physiology of animals are unclear.

e aims of this study were: (1) To determine the y of a range of polar micro-arthropods to withstand dehydration, (2) to measure the level of dehydration that could be survived by individuals, (3) to investigate possible dehydration control mechanisms.

MATERIALS AND METHODS

Seven species of micro-arthropods were used for the determination of water loss at Signy Island. These included 2 species of oribatid mites, *Alaskozetes antarcticus* (Michael) and *Halozetes belgicae* (Michael), a predatory mesostigmatid mite, *Gamasellus racovitzai* (Trouessart), a prostigmatid mite, *Stereotydeus villosus* (Trouessart) and 3 collembolans, *Cryptopygus antarcticus* (Willem), *Parisotoma octooculata* (Willem) and *Archisotoma brucei* (Carpenter). For simplicity these taxa will be referred to by their generic names in this paper. Three life stages of *Alaskozetes* were examined: adult, tritonymph and deutonymph. Mature (>1000 μm in length) and juvenile (>400 < 1000 μm in length) *Cryptopygus* were differentiated, but for all other species mature adults were used. For the survival experiments, only adult *Alaskozetes* were used. All samples, with the exception of *Halozetes*, were collected within 200 m of the British Antarctic Survey station on Signy Island, South Orkney Islands, during the austral summer of 1983–84. Due to the sparseness of *Halozetes* close to the station, sufficient specimens for the experiments were collected from a site 3 km away from the laboratory and maintained at 5°C in a saturated atmosphere for periods of up to 24 h before experimentation.

All specimens were collected in the field with an aspirator and, except for *Halozetes*, were placed in the experimental chamber within 10 min of collection, sorting being carried out at 5°C.

hom correspondence should be addressed.

Water loss experiments.

Changes in live weight of individual micro-arthropods with time were measured using a recording micro-balance (C.I. Electronics) in an arrangement similar to that used by Vannier (1982), but with a weighing accuracy of $\pm 0.5\,\mu g$ (Fig. 1). Single live specimens were enclosed in an aluminium foil container consisting of two parts which were sealed together. The upper part was perforated with about 30 holes each of 200 μm dia, to allow adequate ventilation. The assembled container weighed 26.5 ± 5 mg and this was tared off prior to the experiment. Individual micro-arthropods were pre-weighed on a Cahn micro-balance to determine their absolute live weight before being placed on the balance pan in the experimental chamber. The chamber consisted of a brass cylinder surrounded by a jacket through which temperature controlled (± 0.1°C) ethanediol (40%) was circulated. A neoprene "O" ring formed a seal between the sample chamber and the vertical extension tube of the micro-balance. A dry atmosphere (r.h. of 5 ± 1%) was maintained within the balance chamber using silica gel. The temperature of the air surrounding the sample in the experimental chamber was monitored using a copper-constantan thermocouple, connected to an electronic thermometer (Comark) and the relative humidity was measured by a capacitative probe and meter (Vaisala HMP 13). The weight of the animal was continuously monitored using a Euroscribe chart recorder (100 μg full scale deflection).

Normally, the weight loss of 6–10 individual replicates was recorded for each species at each temperature over a period of 1–2 h, followed by an 8 h overnight recording in each case. Weight loss of individual arthropods was equated to water loss over the duration of the recording. Although other processes, such as defaecation, may contribute to weight loss, they are not considered to be significant in the experimental procedures adopted, and of little importance when comparing species. At the end of each recording the individual was reweighed on the Cahn microbalance and its dry weight measured after in an air oven at 60°C.

Survival experiments

Batches of 20 adult *Alaskozetes* were so weighed and placed in glass vials with perforated (volume 3.5 ml). Groups of 12 vials were place sealed jars containing silica gel to provide a atmosphere (r.h. 5 ± 1%), each group being i bated at a set temperature (0, 5, 10, 15 and 20 Vials were then removed at various time inter which were selected to cover the period until survivors remained. On removal from the vial batch of mites was weighed before being giv standard recovery period of 24 h at 5°C in an al saturated atmosphere (r.h. 95–98%). Survival assessed by observation of the animals und binocular microscope at × 25 magnification. Indi uals showing signs of movement were counted as Finally the batch was dried, as in the prev experiment, and reweighed to obtain the dry we

RESULTS

Water loss experiments

A summary of the results from the 7 species an stages is presented in Fig 2. Plots of weight los hour in dry air on temperature show large differe between species in their ability to withstand d dration. The 3 Collembola species exhibited the est rates of water loss at low temperatures (− 10°C). *Parisotoma* lost water at the rate of 20% at −10°C, whilst *Cryptopygus* lost 5% h^{-1} a same temperature. *Archisotoma*, the third lembolan, lost about 8% h^{-1} at −10°C rising to at 0°C. In contrast the oribatid mites dehydrat a slower rate (*Halozetes* lost $< 1\%\ h^{-1}$ at peratures in the range −10 to 20°C) and, in the of *Alaskozetes*, only 5% h^{-1} at 35°C. The orib appear to have a threshold temperature above the rate of water loss increased sharply, possibl to the breakdown of any cuticular wax layer at h

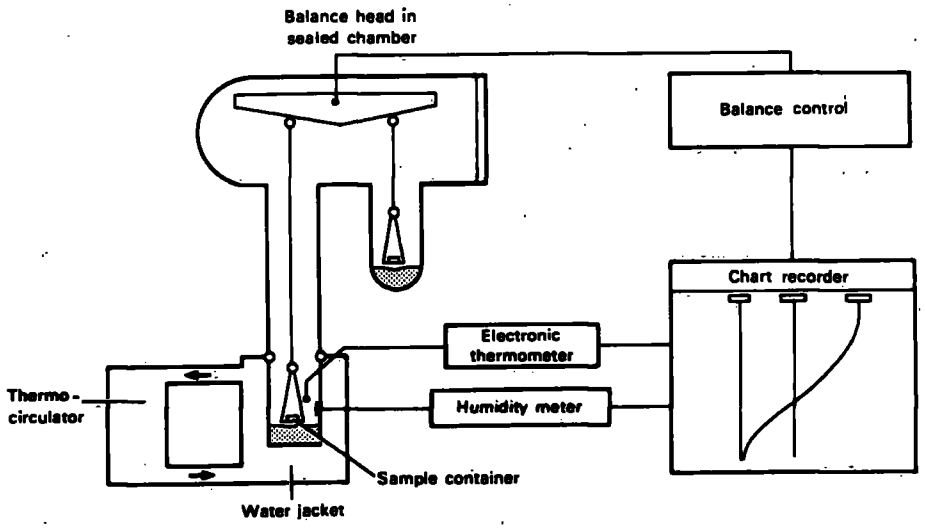

Fig. 1. Schematic diagram of apparatus used to measure water loss in micro-arthropods (after Vannier 1982). ▩: silica gel.

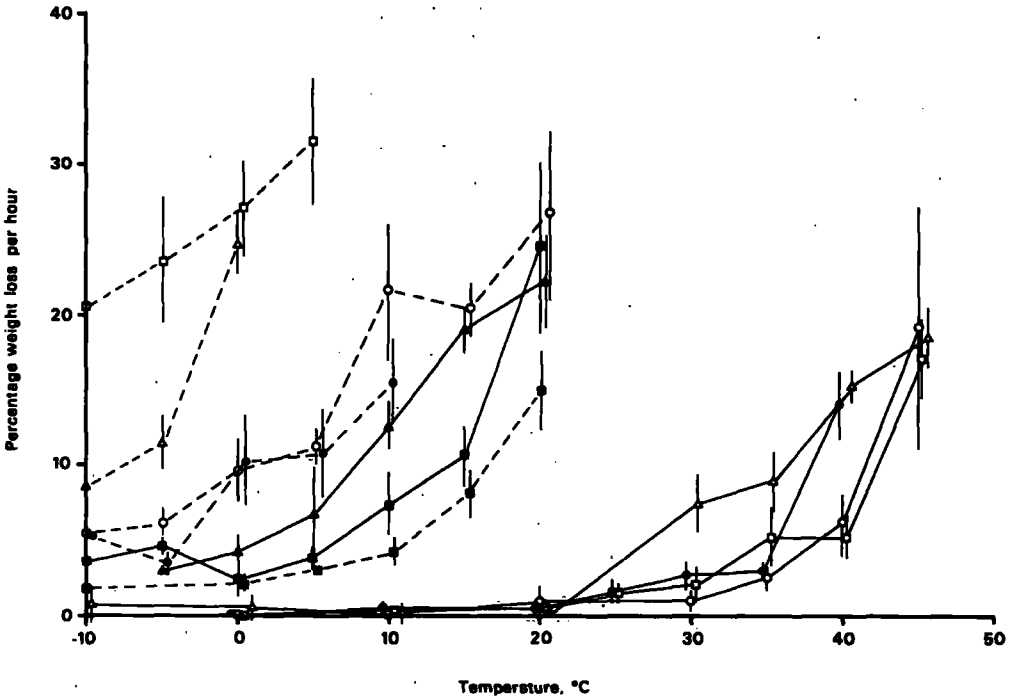

Fig. 2. Rates of weight loss of 7 micro-arthropods under desiccating conditions (r.h. = 5 ± 1%) at controlled temperatures.

Alaskozetes antarcticus adults (●——●)
Alaskozetes antarcticus deutonymphs (□——□)
Alaskozetes antarcticus tritonymphs (○——○)
Halozetes belgicae adults (△——△)
Stereotydeus villosus adults (▲——▲)
Gamasellus racovitzai adults (■——■)
Gamasellus racovitzai deutonymphs (■----■)
Cryptopygus antarcticus mature (○----○)
Cryptopygus antarcticus juvenile (●----●)
Parisotoma octooculata mature (□----□)
Archisotoma brucei adults (△----△)

eratures. This threshold was about 5°C lower for t *Alaskozetes* (35°C) than the juvenile stages to- and trito-nymphs at 40°C). This difference een stages was statistically significant at 0.01 (Student's *t*-test). *Gamasellus* and *Stereo-us* form an intermediate group, but were able to ve at 0°C with water losses of around 4.5% h^{-1}. ch experiment the rate of water loss after the l 5 min was constant until approx 85% of the water content had been lost. During the initial d of the experiment a rapid loss representing % of the sample weight, was recorded. This was nainly to the evaporation of surface water on the men and sample pan, and it was not included in nal calculations. No sporadic weight losses were ded by the micro-balance which may have indi- the operation of a control mechanism.

val experiments

e survival of adult *Alaskozetes* under desiccating itions at various constant temperatures showed verse sigmoid relationship with weight loss. Both ic and Gompertz curves, relating survival to the ithm of percentage weight loss, were fitted to the using the generalized linear model facility of tat (Alvey *et al.*, 1983). There was little ence between the 2 models but as the Gompertz yielded a smaller deviance, suggesting a mar- y better fit to the data, this model was used as is for comparing the results at different temperatures. The differences between the slope coefficients of the 5 curves were not statistically significant (likelihood ratio test; $\chi^2_4 = 8.01$, $P > 0.05$), so this parameter was held constant in the final model to show the ordered differences between survival at the various temperatures. The resulting fitted lines are shown in Fig. 3. No mortality occurred at any of the temperatures until the sample had lost between 14–18% of the fresh weight. Mean survival over the experimental period was higher at 10°C than at all other temperatures. This is emphasized by the inset graph (Fig. 3) of survival at 35% weight loss on temperature which clearly shows an optimum between 5 and 15°C.

DISCUSSION

The seven species of micro-arthropods studied occupy different terrestrial habitats and, with the exception of *Halozetes*, are common at Signy Island. All the species over-winter as adults and some also as juveniles using supercooling to avoid lethal freezing (Block *et al.*, 1982). The temperature and atmospheric humidity regime that they experience in the field will depend upon the habitat, but at Signy Island in the maritime Antarctic a wide range of conditions occur due to the polar climate being ameliorated by the influence of the surrounding ocean. Diurnal ranges for r.h. of 37–100% and temperatures of −1 to 15°C were recorded under stones of a fellfield in

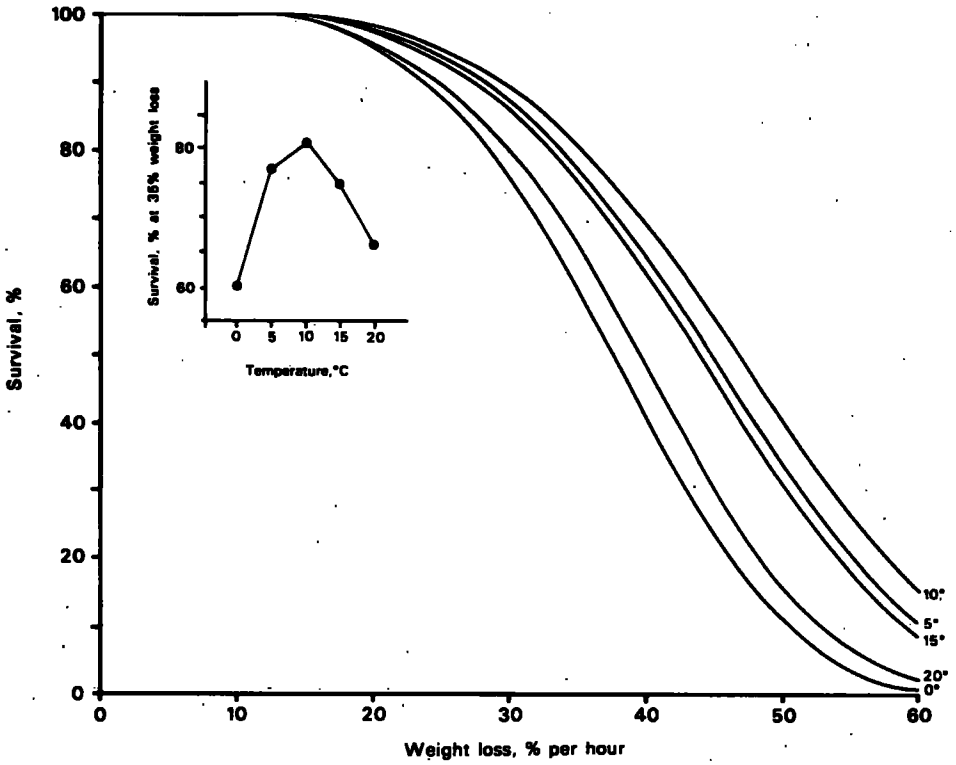

Fig. 3. Percentage of adult *Alaskozetes antarcticus* surviving against percentage weight loss at different temperatures. Lines were fitted to the data using the Gompertz model (see text). Inset: data extracted for 35% weight loss showing the optimum temperature for survival.

summer. Table 1 attempts to relate the ability of some of the terrestrial arthropods to resist dehydration to the type of habitat occupied by each species. In terms of dehydration resistance the 7 Antarctic species fit the classification proposed by Eisenbeis (1983), which is based on water loss rates expressed on a total water basis, and not total body weight as in the present study. *Parisotoma* and *Archisotoma* are humid-air forms (classified as "hygric"), whilst *Halozetes* and *Alaskozetes* are dry-air anim (termed "mesic" by Eisenbeis). The transitional s cies are represented by *Cryptopygus*, *Stereoty* and *Gamasellus* in the Signy Island fauna by bei mixture of both humid-air and dry-air forms. proposed classification is based on transpiration r at 0% r.h. at 22°C, whereas the present data are 5% r.h. at 5°C. Notwithstanding the tempera difference, the Antarctic species studied corresp

Table 1. Relationship of habitat to dehydration resistance in 7 species of micro-arthropods at Signy Island

Species	Type of habitat	Dehydration resistance [mean (±SD)% water loss h^{-1} at 0°C and 5% r.h.
Alaskozetes antarcticus	Underside of rocks particularly in barren but enriched fellfield communities; feeds on exposed surfaces of lichens and algae especially the thallose macro-alga, *Prasiola crispa*	<0.5
Halozetes belgicae	On rocks and stones situated above the intertidal zone; feeds on crustose lichens	0.7 ± 0.9
Gamasellus racovitzai	Amongst rocks with mosses and lichens, expecially in guano enriched areas; feeds mainly on Collembola especially *C. antarcticus*	2.1 ± 0.6
Stereotydeus villosus	In rock scree habitats and in moist plant material particularly peat and mosses	4.1 ± 0.8
Cryptopygus antarcticus	Abundant on underside of rocks, stones and beneath patches of algae (*P.crispa*), and in association with organic material, mosses and most plant cover	9.1 ± 2.2
Parisotoma octooculata	Beneath moss clumps in damp scree and under stones on enriched mineral soil near sea bird colonies	10.1 ± 3.7
Archisotoma brucei	Under large rocks on the seashore and dispersed in fine sand/silt in the intertidal zone; often submerged by seawater	24.6 ± 2.1

art of the range of transpiration rates tabulated Eisenbeis and Wichard (1985).

laskozetes takes advantages of warm periods n it feeds on rock surfaces and forms dense egations on the macro-alga, *Prasiola crispa* htf.) Menegh. Its black, waxy cuticle will absorb r radiation probably causing its body tem- ture to rise above the maximum soil temperature C at a depth of 4.5 cm) recorded (Walton, 1977). differences in threshold temperature between lt and juvenile *Alaskozetes* cannot be explained in is of habitat, but it is known that juveniles are e cold resistant than adults (Young and Block,)). *Halozetes* occupies a similar habitat to *Alas- tes*, but is much less abundant on Signy Island. non and Schenker (1985) concluded that *Halo-* is slightly more cold hardy than *Alaskozetes* rally with a lower supercooling point (−38°C) a lower chill-coma temperature (−5.2 ± 0.9°C). *asellus* is the only arthropod predator on Signy id, and is normally found in damp habitats but, g relatively mobile, it seeks its prey on the surface ocks for short periods under favourable condi- . This species is not particularly cold hardy ng a winter mean supercooling point of only ± 1.2°C (Block *et al.*, 1982) with most individ- being in the high group of the supercooling point ibution; and having a chill-coma temperature of °C (Schenker, 1984). Its mobility suggests it is to avoid the physiologically stressful parts of its ical environment in both summer and winter. e 3 species of Collembola each exhibited ent characteristics of resistance. *Cryptopygus Parisotoma* occupy similar habitats, co-existing ly in damp mineral soil and plant material, while *isotoma* is found along the shore line, amongst and under rocks, being submerged at high tide. *otoma* is more fragile than *Crytopygus*, being damaged by handling. Weight losses of h^{-1} were measured at −10°C rising to 30% h^{-1} C in dry air for *Parisotoma*. These rates appear exceptionally high considering the lower atmo- ic humidity experienced by it in the field, and may have been exaggerated under the experi- al conditions. Alternatively, these results may t the possible temperate characteristics of this s compared to *Cryptopygus* (Burn, 1984). *Ar- oma* is restricted to the intertidal zone where it ably experiences relatively stable conditions of rature and relative humidity, especially in win- en this habitat will be covered by ice and snow. *ytydeus* shows a similar dehydration response to *sellus* but with an increased rate of water loss. urvival strategy of *Stereotydeus* may be similar *masellus*, relying on its mobility to avoid unsuit- conditions (Schenker, 1984). The mechanism d the resistance to dehydration in *Alaskozetes* is ully understood. A clear relationship exists en its ability to survive dehydration and tem- ure with an optimum at around 10°C, which sts there may be an active mechanism control- ater loss (Fig. 2). *Alaskozetes* can survive losses to 20% of its body water and regain it by ption of free water (Block, 1981). During the the water content of field-fresh adult *Alas- s* was 61.5 ± 0.4%, and a small proportion (15%) of the population samples survived weight losses of 60% at 10°C (see Fig. 3). One possible explanation is the utilization of chemically combined water from organic molecules such as glycerol, which can absorb water at any humidity (suggestion by Diamond quoted in Noble-Nesbitt, 1978). Glycerol is the most abundant of several polyhydric alcohols detected in *Alaskozetes* and other micro-arthropods (Block, 1984). Levels of glycerol have been shown to increase in *Alaskozetes* with cold conditions in the field (Block *et al.*, 1982), and by acclimation to low temperatures in the laboratory (Block and Sømme, 1982). The body water content of *Alaskozetes* shows seasonal fluctuations, declining with the onset of winter as glycerol levels increase (Block, 1981). Such polyols may therefore play a significant role in the dehydration resistance of these Antarctic micro-arthropods.

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REFERENCES

Alvey N. G., Banfield C. F., Baxter R. I., Gower J. C., Krzanowski W. J., Lane P. W., Leech P. W., Nelder J. A., Payne R. W., Phelps K. M., Rogers C. E., Ross G. J. S., Simpson H. R., Todd A. D., Tunnicliffe-Wilson G., Wedderburn R. W. M., White R. P. and Wilkinson G. N. (1983) *The Genstat Manual.* Rothamsted Experimental Station. The Numerical Algorithms Group Ltd, Oxford.

Block W. (1981) Terrestrial arthropods and low temperature. *Cryobiology* **18**, 436–444.

Block W. (1984) A comparative study of invertebrate supercooling at Signy Island, maritime Antarctic. *Br. Antarct. Surv. Bull.* No. 64 pp. 67–76.

Block W. and Sømme L. (1982) Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. *Oikos* **38**, 157–167.

Block W., Worland M. R. and Richards K. J. (1982) Seasonal variations in cold resistance of Antarctic land arthropods. Abstract, Symposium on Invertebrate Cold Hardiness, Oslo. *Cryo-Lett.* **3**, 308.

Block W. and Young S. R. (1979) Measurement of supercooling in small arthropods and water droplets. *Cryo-Lett.* **1**, 85–91.

Burn A. J. (1984) Life cycle strategies in two Antarctic Collembola. *Oecologia* **64**, 223–229.

Cannon R. J. C. (1986) Effects of contrasting relative humidities on the cold tolerance of an Antarctic mite. *J. Insect Physiol.* **32**, 523–534.

Cannon R. J. C., Block W. and Collett G. D. (1985) Loss of supercooling ability in *Cryptopygus antarcticus* (Collembola: Isotomidae) associated with water uptake. *Cryo-Lett.* **6**, 73–80.

Cannon R. J. C. and Schenker R. (1985) Cold tolerance of a cryptostigmatid mite at Signy Island, maritime Antarctic. *Br. Antarct. Surv. Bull.* No. 67, pp. 1–5.

Eisenbeis G. (1983) Kinetics of transpiration in soil arthropods. In *New Trends in Soil Biology* (Ed. by Lebrun P., André H. M., De Medts A., Gregoire-Wibo C. and Wauthy G.,), pp. 626–627. Dieu-Brichart, Louvain-la-Neuve.

Eisenbeis G. and Wichard W. (1985) *Atlas fur Biologie der Bodenarthropoden.* Gustav Fisher, Stuttgart.

Noble-Nesbitt J. (1978) Water vapour uptake by *Thermobia domestica* and other insects. In *Comparative Physiology: Water Ions and Fluid Mechanics* (Ed. by Schmidt-Nielsen K., Bolis L., Madrell S. H. P.) pp. 53–67. Cambridge University Press, London.

Schenker R. (1984) Effects of temperature acclimation on cold-hardiness of Antarctic microarthropods. *Rev. ecol. Biol. Sol.* **21**, 205–220.

Vannier G. (1982) Caractérisation des principaux stades de developpement d' *Anatalanta aptera*, Eaton 1875 (Insecte diptère des îles subantarctiques) par leur diagramme de transpiration. [Colloque sur les Ecosystèmes Subantarctiques, Paimpont.] *C.N.F.R.A.* No. 51, pp. 193–207.

Walton D. W. H. (1977) Radiation and soil temperat 1972–74. Signy Island terrestrial reference sites. *Br. arct. Surv. Data*, No. 1.

Young S. R. and Block W. (1980) Experimental studie the cold tolerance of *Alaskozetes antarcticus*. *J. I Physiol.* **26**, 189–200.

MICRO-ARTHROPOD ACTIVITY IN THREE CONTRASTING TERRESTRIAL HABITATS ON SIGNY ISLAND, MARITIME ANTARCTIC

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ABSTRACT. The activity of micro-arthropods was monitored at Signy Island during summer over periods of 48 h by sticky surface traps in three field plots: a fellfield, a *Prasiola–Deschampsia* community and a mossbank. The temperature regime of selected micro-sites within the three 1 m² plots was measured at the same time. Arthropod abundance was determined at the end of the period by extraction from substrate samples. An index of activity, corrected for abundance, was developed. The micro-climates were different for the three plots, which influenced the numbers trapped of the five common species (two Collembola, three Acari). Arthropods (four species) were most abundant in the *Prasiola–Deschampsia* plot, whereas only *Cryptopygus antarcticus* occurred to any extent in the other two sites. Locomotory activity is discussed in terms of habitat structure, micro-climate and temperature as a resource.

INTRODUCTION

he activity of terrestrial ectotherms is largely dependent on the temperature regime ieir habitats. In polar terrestrial environments, particular sheltered micro-sites buffered micro-climates ensure the survival of small arthropods (principally Acari Collembola in the Antarctic). This is particularly important during winter in the time Antarctic, where ground surface minimum temperatures of −21 to −27°C r under shallow snow cover (Walton, 1982).

ntarctic land arthropods have evolved various strategies to aid their survival ck, 1980), e.g. increased cold resistance during winter, elevation of metabolism, h allows activity at low temperatures, and adjustment of their breeding and lopment rates. These result in an extension of life cycles and differing growth rates energy utilization between some species (Burn, 1984). Therefore, as much of their ity is confined to the summer period, when habitat conditions are optimal, an sment of their locomotory activity in relation to environmental temperature and r factors is important. Because the frequency of freeze–thaw cycles increases ig the austral summer (Walton, 1982), the influence of these physical processes unal field activity needs evaluation.

is paper reports the results of field experiments undertaken at Signy Island, South ey Islands (60° 43′ S, 45° 36′ W) in the 1982–83 summer to monitor both the dance and activity of the micro-arthropod populations in three contrasting sites ation to their micro-climates. The results allow an ecological interpretation of es field activity under maritime Antarctic conditions and provide a further step derstanding the interactions governing the colonization and occupation of such habitats.

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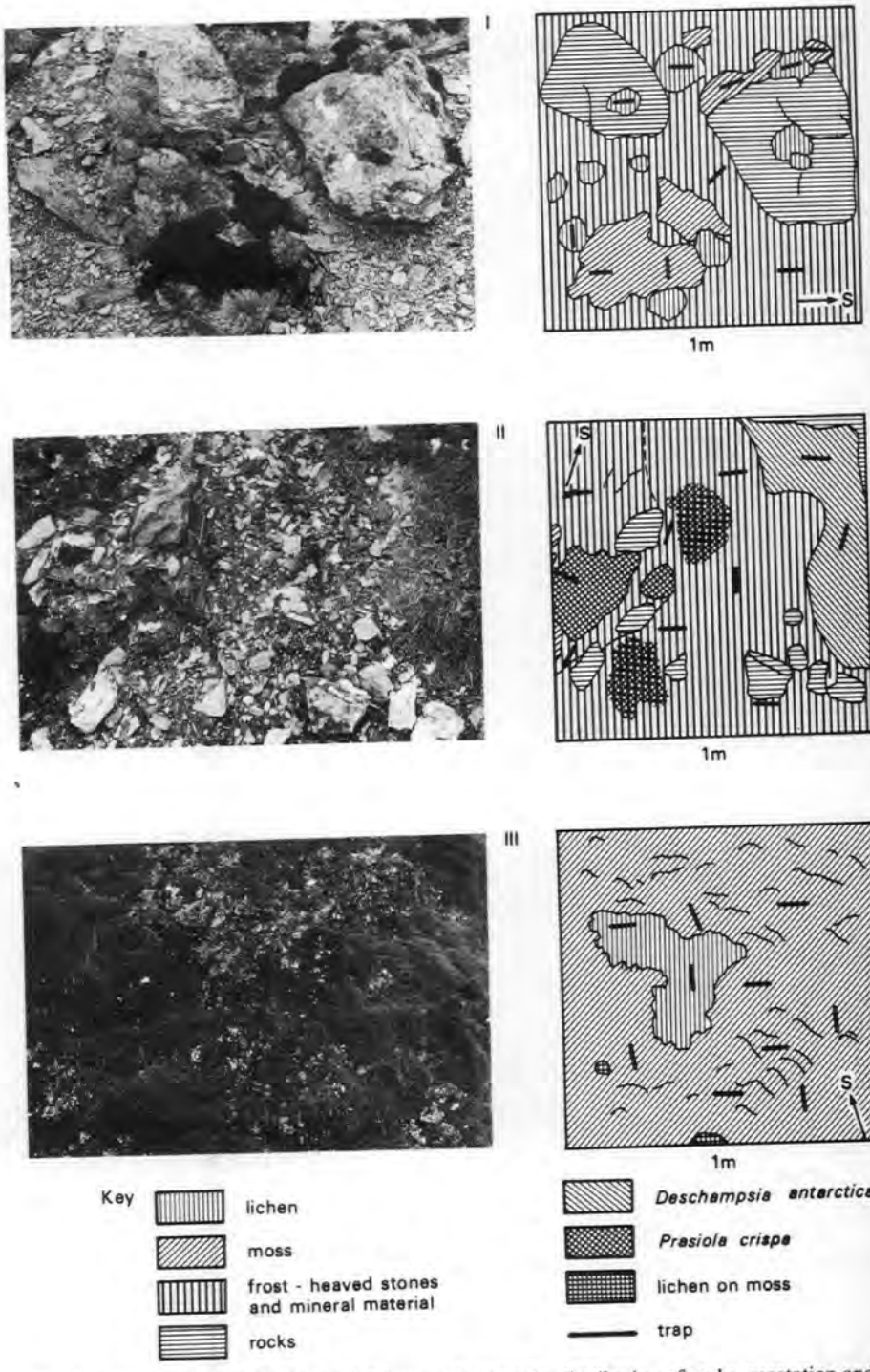


Fig. 1. Photographs of field plots and diagrams showing the distribution of rocks, vegetation and a traps. I, fellfield site; II, *Prasiola-Deschampsia* site; III, mossbank site.

Study Sites

Plots of 1 m² area were staked out in three contrasting habitats: a rocky fellfield, n alga-grass (*Prasiola-Deschampsia*) community and a moss bank, on the eastern side f Signy Island. The fellfield site (I) was situated at the north end of Moraine Valley ear Cemetery Bay at 40 m a.s.l. It faced west with a 28% slope. The substrate mprised frost-heaved stones and mineral soil with sparse vegetation consisting of e mosses *Andreaea regularis* and *A. depressinervis*, and the lichens *Usnea fasciata* and *. antarctica*. The distribution of the rocks and vegetation is shown in Fig. 1. The ga-grass site (II) was beneath Factory Bluffs at 25 m a.s.l. on a north facing slope f 56%. The habitat is diverse and it is fertilized by guano from Cape Pigeons (*Daption pense*) nesting on the cliffs above. A small run of frost-heaved stones on mineral il covered with the green alga *Prasiola crispa* cuts through the plot. The stone run bordered by a patch of the grass *Deschampsia antarctica* on one side and mosses *olytrichum alpina*, *Xantheria* sp., *Candelaria* sp. and *Dicranoweisia grimmiaceae* on e other side (Fig. 1). The mossbank (III) was close to Factory Bluffs, being rth-facing on a 34% slope at 30 m a.s.l. It is composed of *Polytrichum alpestre* and *alpinum*, which in places are overgrown by the lichens *Usnea antarctica*, *Cornicularia uleata* and *Alectoria chalybeiformes* (Fig. 1).

Methods

Micro-arthropod locomotory activity on the ground surface was monitored at the ree sites by using sticky traps. The traps were glass microscope slides (38 × 76 mm) ated on one side with a thin film of insect glue ('Sticktite'). The slides were inserted rtically into the substrate with their long axes parallel to the surface. Using two slides ck-to-back animals were trapped on both sides and, after separation, each slide was amined separately at × 50 and the animals identified and counted.

Ten traps of two slides each were inserted in each plot at characteristic and resentative micro-sites (Fig. 1). A two-day period was used for each experiment, rting and ending at 1200 h local time (GMT less 3 h), with the traps being changed ry four hours. Experiments were conducted at site I from 27 to 29 December 1982, site II from 28 to 30 January 1983 and at site III from 19 to 21 February 1983.

The trapped animals on the slides were identified and counted for each 4 h trapping iod. After each two-day experiment, the substrate (*c.* 250 cm³ with surface area) cm²) around the traps was carefully removed and the arthropods separated from samples in a portable heat extractor (Usher and Booth, 1984). The arthropod nts were standardized to the number of individuals per 100 cm³ of sample material comparison.

Micro-arthropod activity is expressed (1) as the number of individuals caught per interval and (2) as the probability of an individual being trapped during that iod. The latter was calculated from a summation of all animals extracted and pped, and assumed no significant immigration/emigration at the micro-site

$$I_{act} = \frac{n_1}{n_2 - n_3},$$

re I_{act} = index of activity; n_1 = number of individuals trapped in a given 4-h iod; n_2 = total number of individuals trapped over 48 h + total number extracted n 250 cm³ substrate at end of the 48-h trapping period; n_3 = cumulative total of viduals trapped in all previous 4-h periods. This index was used $n_1+n_2+n_3) > 50$, because rare species, of which only a few individuals were pped and extracted, inflated the index artificially.

Weather data were used from the Signy Island Meterological Station (SIMS) t
relate to the micro-climate measurements at the study plots. The latter consisted c
spot temperature measurements using thermistors at various micro-sites (see Figs. 2
b and c) and an overall measure of atmospheric relative humidity (RH) by means
wet and dry bulb thermometers. The micro-sites were mostly close to the groun
surface of each plot, in plants and soil, under rocks, etc. Relative temperatures fo
each micro-site were derived from a comparison with those measured at 2 cm dept
in moss (sites I and III) and in grass (site II), where the majority of micro-arthropo
occur (Tilbrook, 1973; Goddard, 1979). Therefore, they are not presented as absolu
temperatures but as the difference between the micro-site and that at 2 cm depth
the substrate.

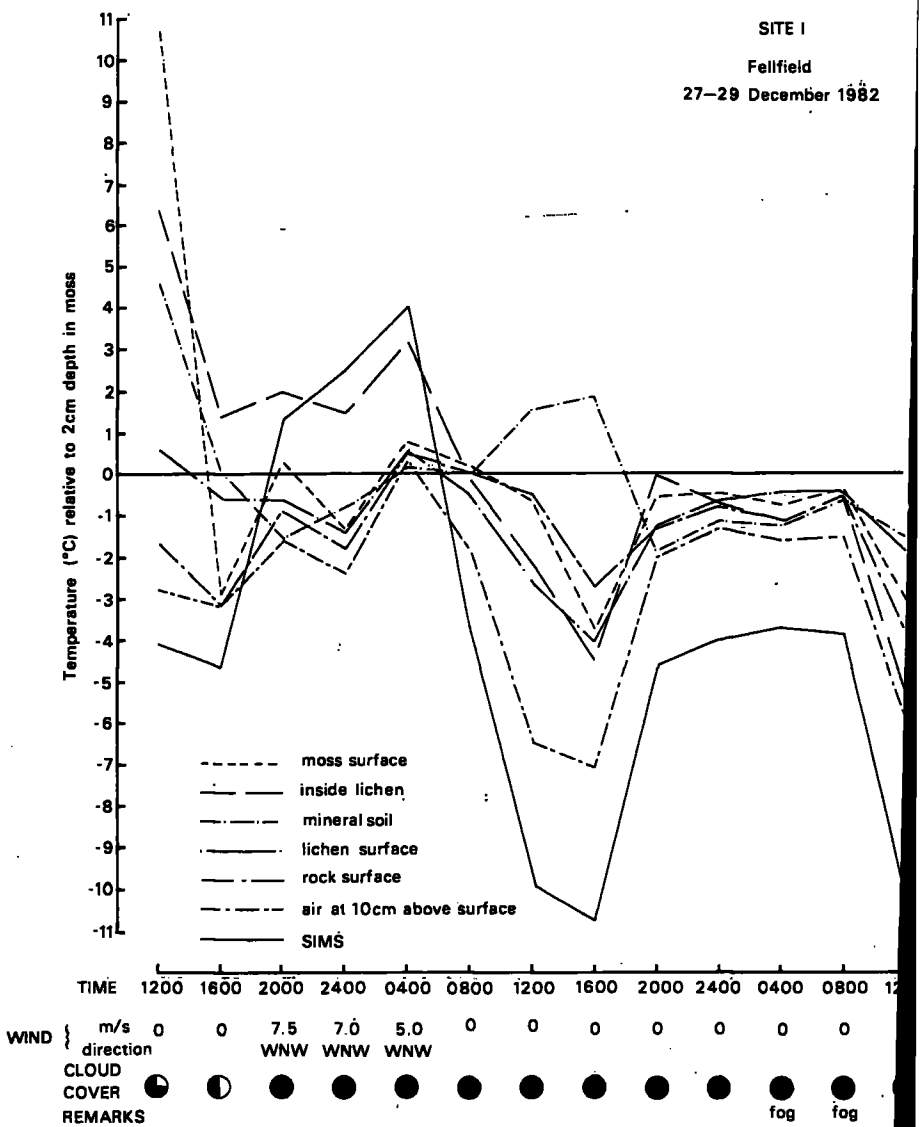


Fig. 2a. Relative temperatures at the fellfield site (site I).

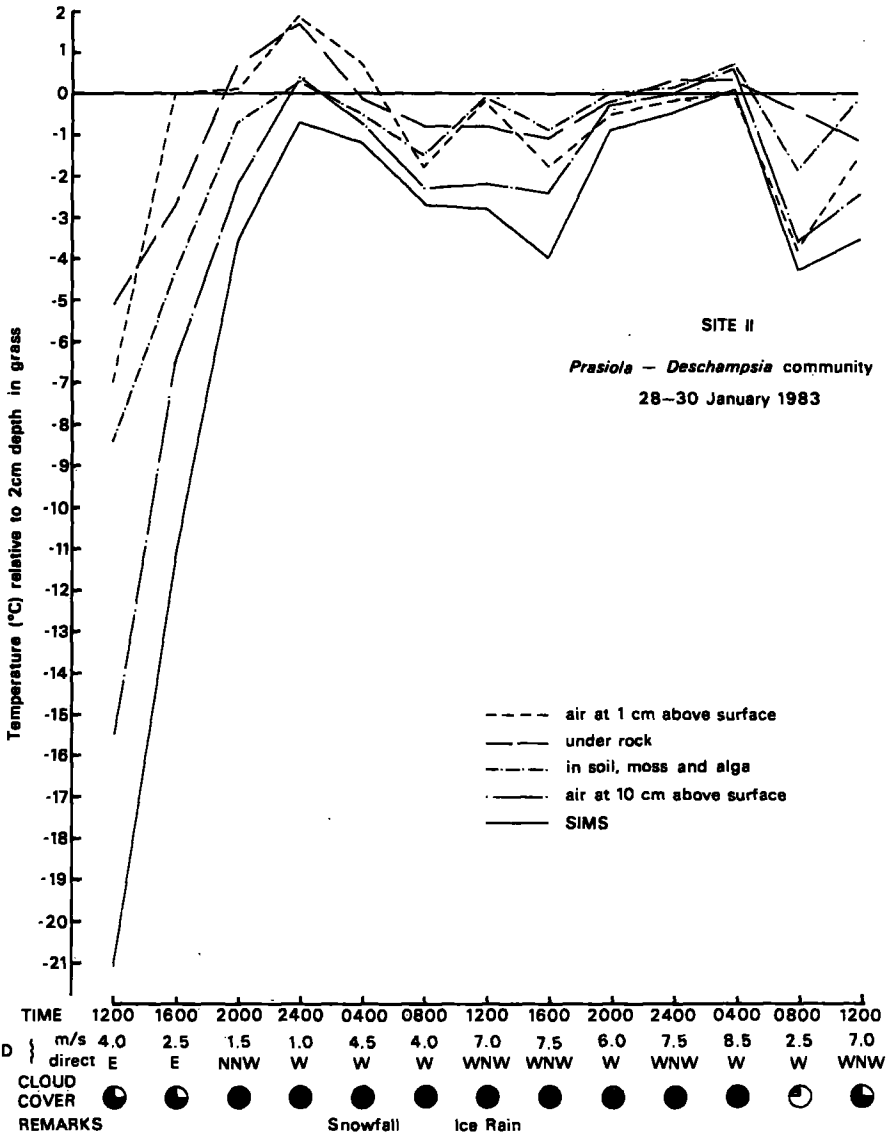


Fig. 2b. Relative temperatures at the *Prasiola-Deschampsia* site (site II).

RESULTS

bitat micro-climate

There were no large differences between mean (and range) in either air temperature atmospheric humidity between the study periods (Table I). All the data were typical a maritime Antarctic summer season. Also, the study sites experienced similar ditions, in general, to those of the Signy Island Meteorological Station which was .75 km in distance away from them. The dynamics of micro-site temperatures tive to the substrate and to SIMS data are shown in Figs. 2a, b and c. Neither

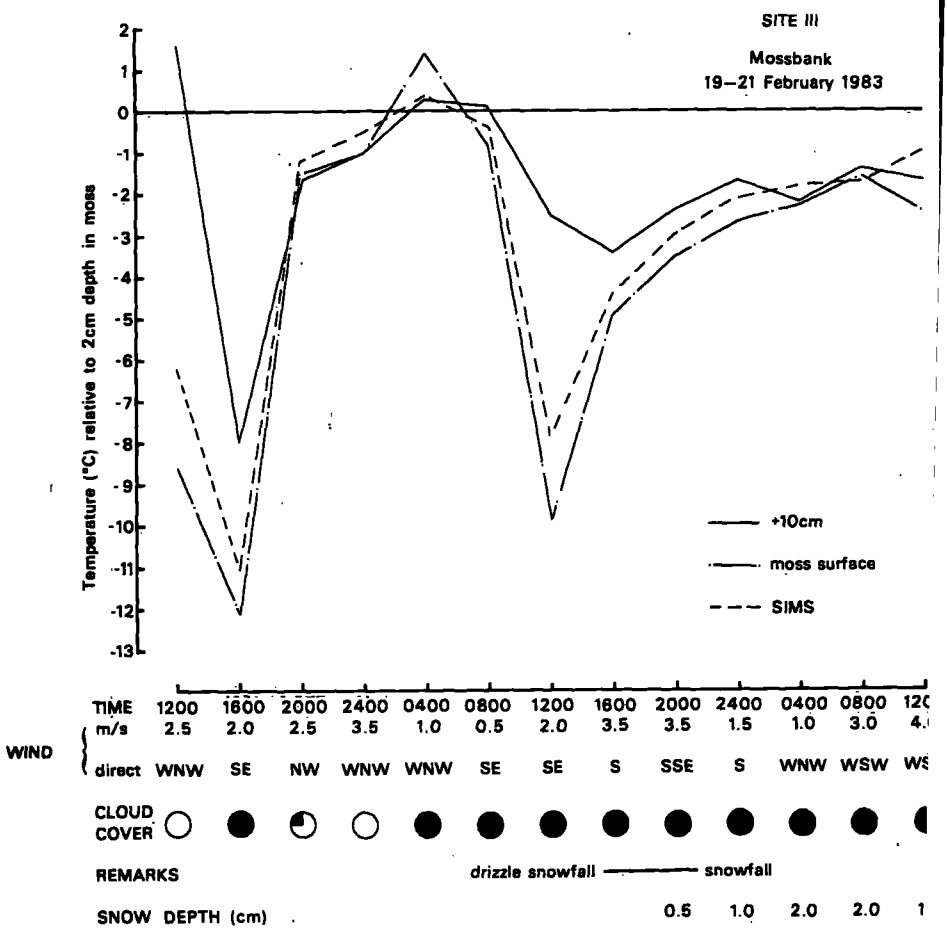


Fig. 2c. Relative temperatures at the mossbank site (site III).

Table I. Comparison of air temperatures and atmospheric humidity for each of the three study sites v SIMS (Signy Island Meteorological Station). All measurements at screen height except air temperat (at +10 cm above the surface) at the study sites. $n = 13$ in all cases except * where $n = 10$.

		Air temperatures (°C)		*Relative humidity* (%)	
Study period	*Site*	*mean ± SD*	*range*	*mean ± SD*	*range*
27–29 December 1982	Fellfield (I)	2.4 ± 2.9	−2.5 to 6.0	83.1 ± 9.5	69–95
	SIMS	1.3 ± 1.7	−1.2 to 4.0	85.3 ± 7.6	74–94
28–30 January 1983	*Prasiola–Deschampsia* (II)	2.5 ± 2.1	−0.5 to 6.4	88.2 ± 16.6	43–100
	SIMS	1.1 ± 1.9	−1.0 to 5.3	74.8 ± 5.2	64–80
19–21 February 1983	Mossbank (III)	0.9 ± 1.5	−0.7 to 3.6	94.2 ± 10.8*	66–10(
	SIMS	0.3 ± 1.2	−1.3 to 2.0	84.5 ± 10.3	66–95

nperature nor RH measured at SIMS showed regular fluctuations during any of
: trapping periods. However, the relative temperatures at various micro-sites
ınged diurnally and the amplitude of individual curves varied. Air temperatures at
: fellfield (site I) were between 1.3 and 4.3 deg (10 cm above the ground) and between
and 10.7 deg (surface) higher than the SIMS data (meteorological screen at 150 cm
ɔve ground) (Table I). Wind was associated with a sharp decrease in most surface
ıperatures (except the rock surfaces as a result of the stored thermal energy). In
fellfield, over the two-day period, most of the micro-sites experienced lower
ıperatures than in the moss, especially during the second day of recording. Such
ıperature deficits approached 4 deg inside lichens and 6 deg in mineral soil. Direct
iation induced a strong temperature rise at site II, whereas cloud cover moderated
rnal fluctuations. SIMS data differed greatly from micro-site temperatures when
iation was high and easterly winds occurred (Fig. 2a). Temperature fluctuations
he *Prasiola-Deschampsia* community were fewer and not so pronounced compared
h the fellfield (Fig. 2b). The maximum deficit (8 deg) between plant material and
n grass temperature occurred early in the first day of the experiment. Thereafter,
:ro-site temperatures remained within 1 deg of the substrate temperature. At site
temperatures followed each other closely but diverged when a thin (2 cm deep)
w cover formed. As above ground and surface temperatures declined, moss
peratures, moderated by snow cover, increased slightly with direct radiation (Fig.
Large fluctuations were observed in mossbank surface temperatures relative to
n depth, which produced large relative temperature deficits.

he micro-climate characteristics of the three sites during the study periods may
ummarized as follows: at site I there were large temperature fluctuations and rapid
nges, which differed significantly from the general climatic conditions, whereas,
he other two sites, temperature fluctuations were closely related to the general
ther, and the rate of thermal change in these habitats was slow compared to the
ield. In particular, wind affected the thermal characteristics of the fellfield site more
ı the other two sites. Atmospheric RH showed no diurnal patterns or regular
ıges at any of the study sites but was strongly influenced by both wind speed and
d cover. A range of 66–100% RH was recorded.

:ies composition and abundance

x micro-arthropod species occurred on the traps and were also extracted from
habitat samples in sufficient numbers for analysis. Other species, namely small
tigmatid mites, were extracted but did not occur on the traps. This may be due
ıeir deeper distribution in the substrate and their low level of surface activity.
refore, only the abundant species are discussed further.

'icro-arthropod abundance (estimated from substrate sampling) was highest at
II (*Prasiola-Deschampsia*) and lowest at site I (fellfield) (Fig. 3). In the fellfield
:rial, no arthropods were found from extraction of the four *Usnea fasciata* samples
:hey occurred in all the *Andreaea* spp. samples. The soil and stone samples also
ained micro-arthropods. Four species were found (in order of abundance) in the
eld materials: *Parisotoma octooculata*, *Cryptopygus antarcticus* (Collembola),
:otydeus villosus* and *Gamasellus racovitzai* (Acari). More than 90% of the
:mbola were adults, only a few immature individuals being found.

ıese four species were extracted also from site II samples, but only a single
'idual of *S. villosus* was recorded. In addition, *Alaskozetes antarcticus* and small
bers of *Halozetes belgicae* (4), *Friesea woyciechowski* (3) and prostigmatid mites
)ccurred. Here, *Cryptopygus* was most abundant, followed by *Parisotoma*,

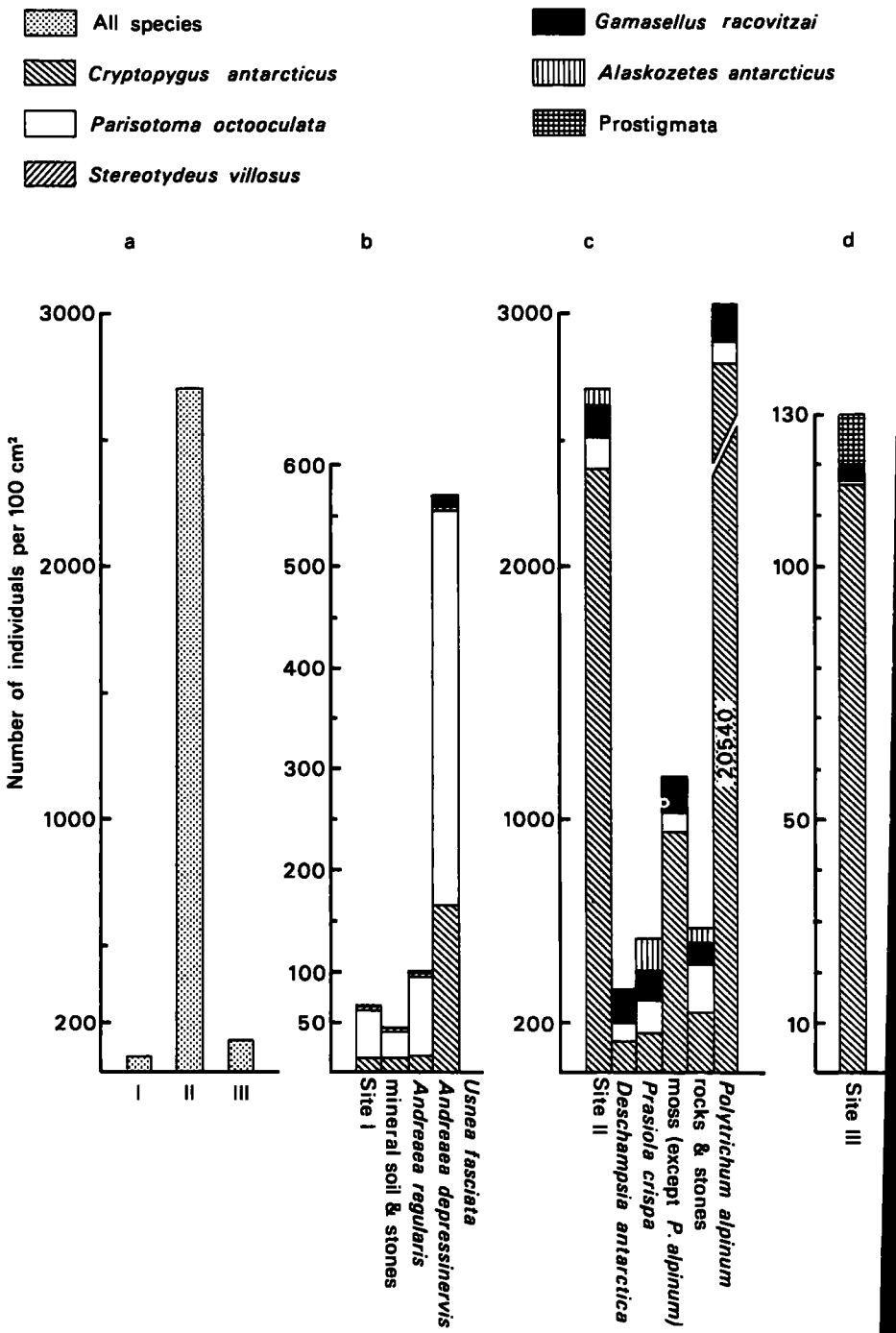


Fig. 3. Micro-arthropod abundance estimated from substrate samples at the three activity study site
total numbers of individuals of all species per 100 cm² substrate at each site (b, c, d) abun
of individual species at sites I(b), II(c) and III(d) according to micro-sites within each. It s
be noted that although the vertical scales are different, the data are standardized to 100 c
substrate.

amasellus and *Alaskozetes*. The Collembola and *Gamasellus* were distributed undantly over the whole site, but *Alaskozetes* occurred almost exclusively in *asiola* on the frost-heaved stones and on the undersides of rocks. Immature stages the four most abundant species occurred in greater numbers than adults. Of the tal of 47 600 *Cryptopygus* extracted, only *c.* 4% were adults on the basis of size (Block d Tilbrook, 1975). This was caused by a large aggregation of immature individuals the *P. alpestre* sample, which accounted for 96% of all immatures at this site. cluding these, adults made up 31% of the total for this species. The proportion of ult *Parisotoma* was estimated at 27%, 31% for *Alaskozetes* and 7% for *Gamasellus*. At the comparatively homogeneous mossbank (site III), 89% of all extracted hropods were *Cryptopygus* (of these 16% were adults). Here prostigmatid mites curred in the greatest numbers (206 individuals) for the three sites, followed by *masellus* (10 adult, 47 immature), *Parisotoma* (3 adult, 12 immature), *Stereotydeus* , *Halozetes* (1), *Friesea* (1) and one *Alaskozetes* larva.

tivity

Total activity i.e. individuals trapped on each plot during each 4-h trapping period, compared in Fig. 4. As the activity expressed in this way is related to species' ndance, an index (I_{act}), which is corrected for abundance, was used (Fig. 5). The a of the four abundant species for each site are presented using the measure of al activity obtained and the calculated activity index.

Except for single individuals of *Stereotydeus* and *Parisotoma* only *Cryptopygus* was pped in the fellfield (site I). Activity increased after midnight reaching a peak ween 0400 and 0800 h in the morning, and decreased again to a minimum towards lnight (Figs. 4 and 5). Most animals were caught on traps in the frost-heaved stones mineral soil and in the *Andreaea* spp. mosses. However, although no animals were racted from *Usnea*, some *Cryptopygus* were found on the traps in this lichen (Fig.

otal activity at site II (*Prasiola–Deschampsia*) differed for the various species. For Collembola (*Cryptopygus* and *Parisotoma*), it was relatively even over time with eak, however, in *Polytrichum* where the large aggregation of *Cryptopygus* was nd. The main characteristics of the activity pattern of *Cryptopygus* and *Parisotoma* e the divergent activity index curves (Fig. 5). Throughout the observation period *isotoma* showed high activity when *Cryptopygus* showed low activity, but a re- sion of their activity indices on each other was not significant. *Halozetes* and *eotydeus* were only active during daytime. *Gamasellus* was least active in *trichum*, whereas *Alaskozetes* was active mainly in *Prasiola* on frost-heaved stones under rocks.

t site III (mossbank), the activity index of *Cryptopygus* declined steadily through- the two day period (Fig. 5) in conjunction with a decline in the numbers trapped . 4). Few other species occurred on traps at this site.

Discussion

ie three study sites had different micro-climate characteristics, although they rienced similar climatic conditions during the three separate study periods (Table f the three sites the fellfield habitat experienced the greatest variability and the st extremes of temperature. Here, micro-arthropods were not abundant and their ity (mainly *Cryptopygus*) was confined to a few micro-sites within the community. *Prasiola-Deschampsia* site experienced more moderate temperatures during the

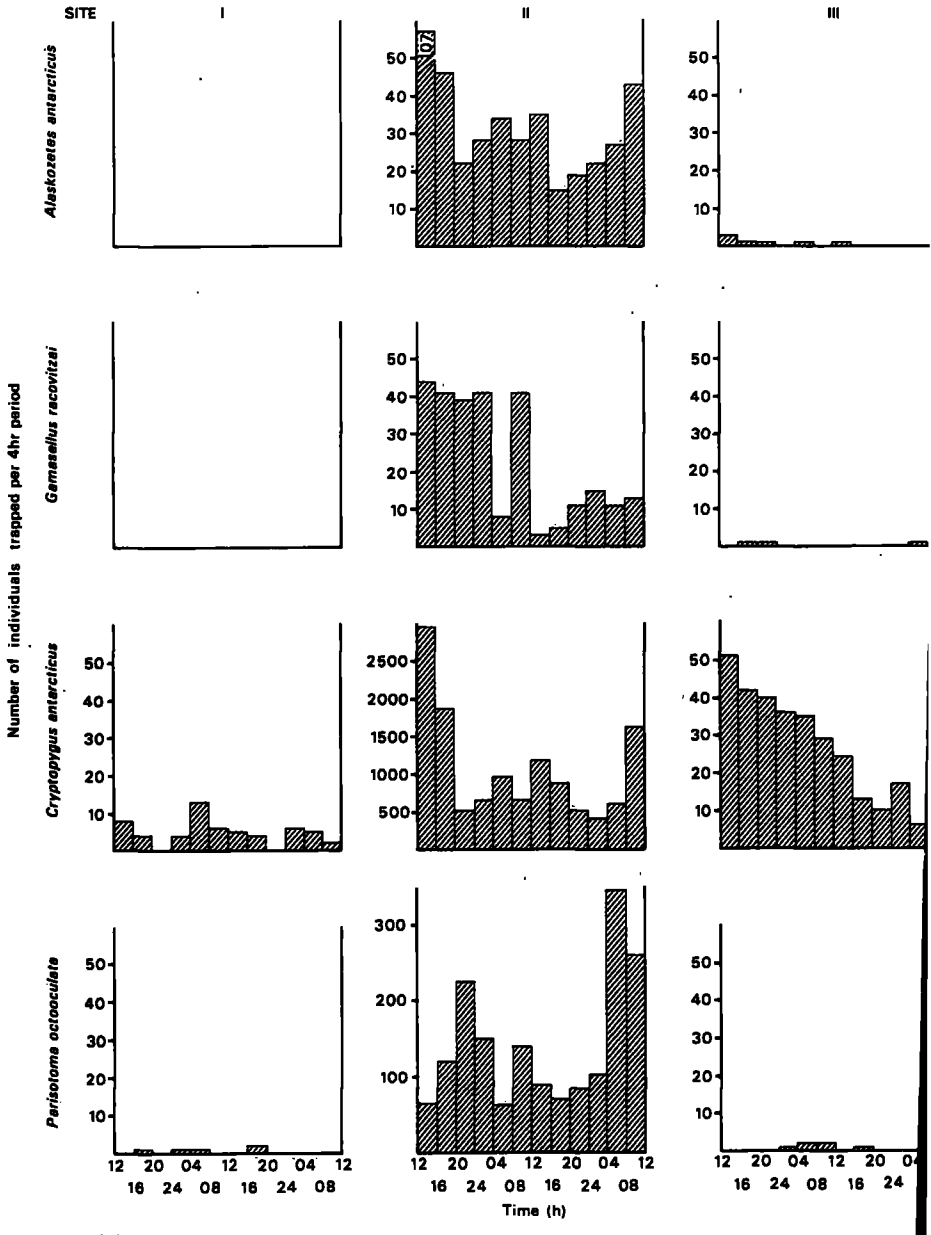
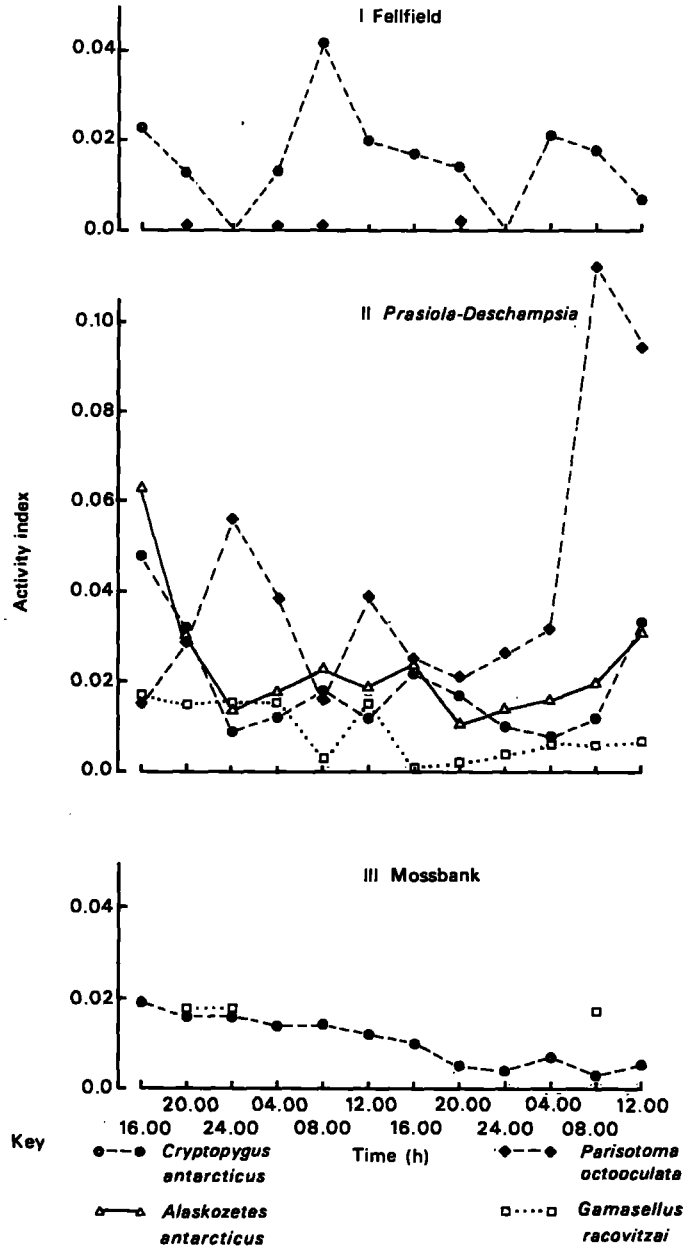


Fig. 4. Activity of six micro-arthropod species at the three sites in terms of numbers of individuals tra per 4-h periods. The scales for the two species of Collembola at site II are different from remainder.

study, and its habitat structure was substantially diverse. This resulted in arthropod abundance (the highest of the three sites), increased species diversity a high level of surface activity when environmental conditions allowed. At mossbank site, only *Cryptopygus* was abundant and showed declining num trapped (and hence reduced activity) during the two-day study. This may



. Activity indices of the four abundant micro-arthropods at the three study sites over two days. See text for details.

cted the technique of removal trapping. The single-species dominance at this site ably reflects the homogeneous nature of the habitat compared to the other two

otwithstanding the short sampling period (two days for each site) used in this , the results make it possible to suggest a relationship between arthropod activity

and air temperature at the ground surface in the habitats studied. In terms of to numbers of arthropods trapped per 4 h, only the mossbank (site III) showed significant ($P < 0.05$) regression on temperature: y (arthropod number) = 23.2+6 (mean air temperature). For the most abundant species, *Cryptopygus antarcticus* between-site comparison shows an increasing dependence of its activity index on me temperature with the sites ranked as follows: fellfield (N.S.), *Prasiola–Deschamp* ($P < 0.05$), mossbank ($P < 0.01$). A similar ranking is obtained when the number *Cryptopygus* trapped per 4 h is analysed with respect to temperature. These relati ships suggest that temperature is more limiting to arthropods inhabiting a mossba (in terms of influencing their surface activity) than those of a fellfield habitat. In mixed habitat of site II (*Prasiola–Deschampsia*), the numbers of individuals trapp per 4 h and the derived indices of activity of both *Cryptopygus* and *Alaskozetes* w significantly related to surface temperature ($P < 0.05$ in all cases). Clearly, su temperature-dependent activity will affect species differently according to th physiological and ecological requirements.

The data reported here suggest that, in addition to large-scale weather and clima conditions, the structure of Antarctic terrestrial habitats influences micro-arthrop activity by providing a variety of micro-sites in which the micro-climate is buffe to a greater or lesser degree. Therefore, a habitat comprising a series of micro-s with contrasting properties will afford a greater potential for both individual a species survival than a more homogeneous one with fewer micro-sites. The pres data are for summer conditions and in winter the observed differences in temperatu especially between the fellfield and the other two sites, may disappear with establishment of a snow cover. Temperature fluctuations will be reduced even un a shallow snow layer (Walton, 1982), and the micro-climate considerably modera It would appear that winter activity of micro-arthropods would be possible un Signy Island conditions, as their chill-coma temperatures (Schenker, 1984) are lo than soil temperatures over that period (Walton, 1977).

Temperature may be viewed as an ecological resource (Magnuson and others, 19 in the same way as food. Thus, in polar habitats, heat (or higher temperatures) be exploited by both invertebrates and plants. Activity of terrestrial micro-arthrop may be classed as thermoregulatory behaviour just as locomotion is used in the sea for food. The lower lethal temperatures have been defined for some species (Bl and Sømme, 1982; Sømme and Block, 1982), and locomotion ceases at temperat in the range −4.5 to −8.9°C. Therefore adaptation of locomotory activity persistently low environmental temperatures is of increasing survival value for s small ectotherms in relation to the demands of their life style. Ecological physiological differences between predators such as *Gamasellus* and omnivores *Alaskozetes* are already apparent. In these instances, the resources of temperature heat) and food may be of similar survival value.

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REFERENCES

CK, W. 1980. Survival strategies in polar terrestrial arthropods. *Biological Journal of the Linnean Society*, **14**, 29–38.

CK, W. *and* SØMME, L. 1982. Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. *Oikos*, **38**, 157–67.

ČK, W. *and* TILBROOK, P. J. 1975. Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos*, **26**, 15–25.

N, A. J. 1984. Life cycle strategies in two Antarctic Collembola. *Oecologia*, **64**, 223–9.

DARD, D. G. 1979. The Signy Island terrestrial reference sites: XI. Population studies on the terrestrial Acari. *British Antarctic Survey Bulletin*, No. 48, 71–92.

NUSON, J. J. CROWDER, L. B. *and* MEDVICK, P. A. 1979. Temperature as an ecological resource. *American Zoologist*, **19**, 331–43.

NKER, R. 1984. Effects of temperature acclimation on cold-hardiness of Antarctic micro-arthropods. *Revue d'Ecologie et de Biologie du Sol*, **21**, 205–20.

E, L. *and* BLOCK, W. 1982. Cold hardiness of Collembola at Signy Island, maritime Antarctic. *Oikos*, **38**, 168–76.

ROOK, P. J. 1973. Terrestrial arthropod ecology at Signy Island, South Orkney Islands. Ph.D. thesis, University of London.

R, M. B. *and* BOOTH, R. G. 1984. A portable extractor for separating micro-arthropods from soil. *Pedobiologia*, **26**, 17–23.

TON, D. W. H. 1977. Radiation and soil temperatures 1972–74: Signy Island terrestrial reference site. *British Antarctic Survey Data*, No. 1, 51 pp.

TON, D. W. H. 1982. The Signy Island terrestrial reference sites: XV. Micro-climate monitoring, 1972–74. *British Antarctic Survey Bulletin*, No. 55, 111–26.

COLD RESISTANCE AND OVERWINTERING SURVIVAL OF THE CABBAGE ROOT FLY, *Delia radicum* (ANTHOMYIIDAE), AND ITS PARASITOID, *Trybliographa rapae* (CYNIPIDAE), IN ENGLAND

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SUMMARY. Overwintering Delia radicum (L.) in a field of swedes (Brassica napus L.) near Ascot, Berks., England, were exposed to soil temperatures below 10°C on 176 days from 21 October 1983 to 22 April 1984, but no temperatures below 0°C were recorded. Collections of D. radicum taken at monthly intervals from 1 November 1983 to 30 April 1984 showed that parasitism by the cynipid Trybliographa rapae (Westw.) and by the staphylinid Aleochara bilineata Gyll. was the main source of mortality. A substantial increase in parasitism by A. bilineata occurred during November, but much of the increase was by superparasitism of pupae previously parasitized by T. rapae. Mortality from causes other than parasitism was greater in the November and December collections (c. 22%) and in the spring (c 12%) than during the winter (c. 3%) and could not be attributed to low temperatures.

In all collections, most of the adult D. radicum (c. 90%) emerged within 230°$D_{5.6}$. The mean number of °$D_{5.6}$ to eclosion did not change from 1 November to 5 March but decreased significantly by 2 April. Late-emerging adults required 259 to 992°$D_{5.6}$ to eclosion and no changes in the mean number of °D occurred among collections.

Among unparasitized D. radicum, individual supercooling points showed a strong peak at c. -23°C. A significant proportion of pupae with supercooling points above -20°C were found only in the 1 November 1983 and the 30 April 1984 collections. The 'high' supercooling points in the November collection may have comprised apparently healthy but moribund individuals, whereas in the April collection they may have included individuals that had initiated postdiapause development. The mean supercooling point of individuals in the 'low' category (supercooling points -20°C) did not vary among monthly samples.

Parasitism by T. rapae increased the variability in supercooling points, resulting in a few individuals with lower, and many more with higher supercooling points than among unparasitized individuals. The mean supercooling point increased from the collections of November and December to those of January to April.

Puparia containing unparasitized D. radicum pupae were heavier and contained more water than those with parasitized pupae, but neither group showed significant changes over winter. Supercooling points were positively correlated with puparial live weight among unparasitized but not among parasitized pupae. Supercooling points were not correlated with water content for either group.

Parasitism did not affect the occurrence or concentration of sugars and polyhydric alcohols (all $< 1\%$ of fresh weight), and trehalose, glucose and mannitol were the most abundant. D. radicum can be considered to be over-protected from lethal freezing in the pupal stage and its high supercooling capacity in England may persist because it is conferred by the structural properties of the dipteran puparium and of the pupa within it and therefore is not subject to selection pressures.

INTRODUCTION

The cabbage root fly, Delia radicum (L.) (Diptera: Anthomyiidae), and its parasitoid, Trybliographa rapae (Westw.) (Hymenoptera: Cynipidae) are Palaearctic species that have become distributed throughout the northern temperate regions of the world (Commonwealth Institute of Entomology, 1983). The larvae of D. radicum feed on the roots of Brassica crops, the puparia being formed in the soil around the roots. Overwintering normally occurs in the pupal stage within the puparium (Coaker & Wright, 1963), but the final larval instar may also overwinter (Smith, 1927). Turnock, Jones & Reader (1985) found that some overwintering puparia collected near Ascot, England, in the autumn of 1983 contained prepupae or cryptocephalic pupae rather than exarate or pharate pupae. Diapause is facultative and in southern England, where there are normally three generations per year, late-developing second generation and all of the third generation enter diapause and overwinter (Coaker & Wright, 1963). Diapause development requires, on average, 135 days at temperatures $< 10°C$ (Collier & Finch, 1983). Exposure to temperatures $< -10°C$ reduces survival and affects post-diapause development (Turnock, Jones & Reader, 1985). The threshold for postdiapause development is 5.6°C (Coaker & Wright, 1963).

Trybliographa rapae has only two generations per year in southern England but the long life span of the adults enables it to parasitize all three generations of the host. Most eggs are laid in the 1st and 2nd instar larval hosts and the parasitoid larvae remain in the host until after the puparia are formed. Subsequently, the third-instar parasitoid larvae move out of the host and feed as ectoparasites within the puparia. At this stage the parasitoid larvae and their meconium, voided in the late fourth-instar, can be seen through the host's puparium. These characteristics can be used to identify parasitized hosts. Wishart & Monteith (1954) reported that T. rapae overwinters in its 4th instar but in two classes, those that have been

in the 4th stage for some time, and those that reach it at the onset of cold weather. Finch & Collier (1983, 1984) suggest that diapause development of most T. rapae is completed by mid-winter. Both D. radicum and T. rapae are adapted to cold temperate regions and Makarenko (1968) reported high survival of both D. radicum (60-64%) and T. rapae (70-74%) over the winter of 1963-64 at Leningrad, USSR, when soil surface temperatures were -15°C for 47 days. He also found that some D. radicum survived after 24 h at -30°C.

In this paper we report on the overwintering survival, supercooling capacity and cryoprotectant levels of D. radicum and T. rapae collected at intervals during the winter of 1983-84 at Silwood Park, near Ascot, UK. The results are evaluated to show the relationship between mortality and supercooling capacity to time of collection, parasitism and potential cryoprotectants. The degree of cold hardiness in the population is related to the role of winter temperatures in the survival of the cabbage root fly in England and Wales. In this paper, the term "puparium (a)" is used to describe the pupal case and its contents.

METHODS

Field temperatures

Soil temperatures (recorded once daily at 0900 h GMT) at 5 and 10 cm depths beneath grass were available from the Meteorological Station located in the grounds of Imperial College at Silwood Park, Ascot, Berks. In a swede field, about 300 m from the Meteorological Station, soil temperatures were recorded hourly from 27 October 1983 to 27 February 1984, using a 5-channel Grant Recorder. Two sensors were placed at each of 2.5, 5.0 and 7.5 cm

depths. Daily mean, maximum and minimum soil temperatures for each depth were calculated from the 24 hourly chart records.

Materials

The experimental material was collected from a naturally occurring infestation of *D. radicum* in the field of swedes (*Brassica napus* L. cv. Acme). The density of puparia in the field in October 1983 was 48 m^{-2} (T.H. Jones & P.M. Reader, unpublished). This field population was sampled in October to determine the distribution of puparia by depth and at approximately 30-day intervals from 1 November 1983 to 30 April 1984 to obtain puparia for experiments. On each sampling occasion, about 400 kg of soil was taken from a strip *c.* 20 cm wide, 10 cm deep and 6 m long along a row of swedes. The swedes and soil were washed over a screen and the puparia removed. The puparia were examined (x10 magnification) and their contents classified as healthy, dead, or parasitized by either *T. rapae* or *Aleochara bilineata* Gyll. (Coleoptera: Staphylinidae). A sample of the healthy puparia and all of those visibly parasitized by *T. rapae* were used for determination of supercooling points and cryoprotectant assay. The dead were discarded, and the remaining healthy puparia plus those parasitized by *A. bilineata* were placed on moist vermiculite at 4°C to complete their diapause development.

Depth of Pupation

The distribution of puparia of *D. radicum* by depth in the soil was determined on 19 and 26 October 1983. On each sampling date, 10 samples (each 20 x 10 cm) were excavated in 2.5 cm layers to a depth of 10

cm. The soil from each layer was washed over a screen and the puparia removed. The puparia were classified on the basis of the condition and parasitism of their contents.

Overwintering survival

The puparia containing healthy D. radicum and those parasitized by A. bilineata were stored at 4°C from the date of collection until 2 April 1984, then at 20°C until emergence or death. Puparia from the 30 April collection were placed at 20°C immediately after examination. The dates of emergence of D. radicum and its parasitoids were recorded. The numbers of emerged, parasitized and dead individuals after incubation were combined with the dead and parasitized of the field sample to assess the survival and causes of mortality at each collection date. For the purpose of calculating the percentage emergence, the healthy puparia used for determination of supercooling points and cryoprotectants were considered to have emerged.

Determination of supercooling points and cryoprotectants

Up to 50 unparasitized puparia of D. radicum and a variable number parasitized by T. rapae were selected for these determinations. Parasitism by T. rapae was low in 1983 and it was not possible to obtain a sample of 50 parasitized D. radicum on each occasion. The sample of 5 December 1983 was augmented by parasitized puparia from collections made during the last week of November for other experiments. These were kept at 5°C (approximating the ambient soil temperatures) until 5 December.

After collection, the pupae in each sample were maintained in moist vermiculite at temperatures approximating the soil ambient (5°C for the 1 November 1983 and 30 April 1984 samples, 2°C for the other samples). They were transported to Cambridge in an insulated container, where the pupae were weighed and divided into two groups for determination of individual supercooling points and cryoprotectant assays. Supercooling points (whole body freezing points) were measured within 5 days of the date of collection. The dry weight (at 60°C) of 20 puparia of D. radicum and at least 3 parasitized puparia from each collection was determined after the supercooling point experiments.

Individual supercooling points were measured by recording the temperature of the puparium during cooling at 1 deg per minute from a starting temperature of c. 5°C. The puparium was attached to a fine (36 swg) copper-constantan thermocouple by a thin film of grease, and its temperature monitored via a 6-channel Rikadenki recorder. Cooling was achieved by a Peltier module programmed electronically to a final temperature of -35°C. The point of origin of the rapid temperature increase caused by the release of latent heat during spontaneous freezing was read as the supercooling point.

The levels of polyhydric alcohols and sugars were determined in both non-parasitized and parasitized individuals from each field collection, and for some puparia which had been supercooled and frozen. Extracts were made by macerating individuals in 70% ethanol with the addition of 10 µg of sulcitol as an internal standard, and were stored at -20°C until assayed. Derivatives were prepared using trimethylsilyl reagent with pyridine (Sigma Sil-A), and analysed using a Pye-Unicam GCD gas chromatograph with a Chrompack CP^{tm} Sil 5 non-polar, capillary column (see Block & Sømme (1982) for details).

RESULTS

Field temperatures

Comparison of the meteorological data with the soil temperature records in the swede field for 27 October to 15 November allowed soil temperatures at the 5 cm depth in the swede field to be estimated for the periods in the autumn and spring when the recorder was not available. On this basis, soil temperatures in the field were below 10°C from 21 October 1983 to 22 April 1984, with the exception of eight days in early November when the mean temperatures were between 10 and 13°C. In the swede plot, soil temperatures were below 5.6°C until 27 February, but the Silwood meteorological records indicate that soil temperatures exceeded 5.6°C on one day between 27 February and 5 March, on ten days between 5 March and 2 April, and remained above 5.6°C from 6 April onward. The mean soil temperature in the swede plot was never below 3.1°C from 27 October 1983 to 27 February 1984 (Table 1) and no soil temperatures below 0°C were recorded. The mean soil temperature at the warmest depth (7.5 cm) was only 0.3°C higher than that of the coldest depth (2.5 cm) (Table 1).

)epth of pupation

he distribution of puparia did not differ significantly between the ollections of 19 and 26 October 1983 so these data were pooled. The ercentage distribution of pupae at depths of 0 - 2.5, 2.5 - 5.0, 5.0 - 7.5 nd 7.5 - 10.0 cm were: unparasitized; 14.6, 40.4, 35.2, 9.8 (n=287); arasitized by *T. rapae*; 40.1, 22.7, 31.8, 4.5 (n=22).

Overwintering survival

In all collections except that of 30 April, 1 - 3% of all D. radicum were in the final larval instar (Table 2). It was assumed that these individuals were unable to complete their larval feeding and pupate before the onset of cold weather. The overwintering larvae appeared to suffer little mortality, since the percentage remained relatively constant from 1 November to 2 April. Samples of these larva were reared to cabbage root flies in th laboratory. Surviving field larvae probably formed puparia between 6 and 30 April.

Similar numbers of puparia were recovered from the soil samples on the various collection dates (Table 2). Differences in the proportions of emerged, dead and parasitized D. radicum in the samples over the experimental period appear to have been caused by two factors. Firstly, a marked increase in the level of parasitism by A. bilineata between 1 November and 5 December coincided with a decrease in the percentage of D. radicum and T. rapae emerging. Secondly, the percentage of dead decreased after 5 December 1983, probably because decomposition precluded their recovery from later samples. The percentage emergence for the sample of 30 April 1984 included puparia from which adult D. radicum had emerged prior to collection as well as those from which flies emerged during subsequent incubation. Mortality not attributable to parasitism but more likely to carabid and staphylinid predation occurred most frequently between puparium formation and early December, at a low level during the winter, and at a somewhat higher level after 5 March (Table 2).

Development

The D. radicum in all samples were exposed to more than 135 days at temperatures 10°C, either in the field or at the post-collection temperature of 4°C. This exposure is regarded as sufficient to break pupal diapause (Collier & Finch, 1983a, b) and a high proportion (0.86 to 0.94) of the adults emerged within the period ($< 230°D_{5.6}$) described by these authors as typical for individuals that have broken diapause prior to incubation (Table 3).

The mean number of $°D_{5.6}$ to eclosion of these early-emerging flies were not significantly different for the samples collected from 1 November 1983 to 5 March 1984, but decreased significantly between 5 March and the collection of 2 April ($P < 0.001$, 't' tests, Table 3). Therefore, some D. radicum began postdiapause development in the field during the 10 days in March when soil temperatures exceeded 5.6°C. In the 30 April collection, only late-emerging adults were recorded, the early-emerging adults being represented by emerged puparia found in the soil. After 6 April 1984 soil temperatures were consistently above the threshold for postdiapause development. Late-emerging adults required from 259 to 992° D before eclosion. The number of degree days required was highly variable (Table 3). The mean for the pooled November-January collections (557 ± 177, n=22) did not differ significantly from that of the pooled March-April collections (588 ± 114, n=13) ($P > 0.1$, 't' test).

Live weight and water content

In all the field samples, unparasitized D. radicum were heavier than parasitized ones with live weights ranging from c. 11 to 17 mg and from c. 5 to 7 mg, respectively (Fig. 1a). These differences were reflected in the water contents, which varied from 57 to 64% (unparasitized) and from c. 53 to 60% (parasitized) over the 1983-84 winter (Fig. 1b). There were no clear seasonal changes in either live weight or water content. Water content was positively correlated with live weight (r = 0.366, P = 0.007, n = 47) among parasitized but not for unparasitized pupae (r = -0.084, P = 0.652, n = 114).

Supercooling potential

Sub-samples of healthy and parasitized pupae from three collections (1 November, 30 January, 30 April), which were maintained at 10°C in the laboratory after supercooling tests until May 1984, showed no adult emergence. It was concluded that freezing and subsequent cooling to -35°C was lethal to both D. radicum and its parasitoid, T. rapae.

The frequency distribution of supercooling points for unparasitized pupae from all sampling occasions except 30 April 1984 had a strong peak at about -23°C (Fig. 2). The distribution for November 1983 showed a "tail" of supercooling points ($>$ -20°C), which comprised 28% of the total. This high group was reduced to only 6% for all the supercooling points from 5 December to 2 April, then it increased to 81% in the 30 April collection. The mean supercooling point for unparasitized pupae decreased from -19.6°C on 1 November to -22.7°C on 5 March (Fig. 3). The low group of supercooling points ($<$ -20°C) showed little variation among collections (means of -22.4

to -23.5°C) and no trends over winter. The lowest supercooling point for an individual unparasitized pupa was -25.4°C.

Mean supercooling points ranged from -12.7 to -23.5°C for parasitized pupae. The distribution of supercooling points for parasitized pupae was not strongly peaked in the low group compared with that of the unparasitized pupae (Fig. 2). The low group of parasitized pupae had mean supercooling points of -23.3 to -25.3°C and 23% of the pupae in this group had a lower supercooling point ($>$ -29.8°C) than the minimum recorded for the unparasitized pupae. In contrast to the unparasitized pupae, the proportion of parasitized pupae in the low group decreased from 1 November and 5 December (0.79) to those of 1 January to 2 April (0.54). The mean supercooling point for parasitized pupae increased as the proportion in the low group decreased (Fig. 3). For both unparasitized and parasitized pupae the proportion in the low group decreased and the mean supercooling point increased in the 30 April collection. Supercooling points were positively correlated with live weight in unparasitized pupae (r = 0.138, P = 0.043, n = 160), but not among parasitized pupae (r = 0.045, P = 0.352, n = 78). Supercooling points were not correlated with water content for either group.

Cryoprotectants

As the water content of the puparia did not alter significantly during the study, the concentrations of potential cryoprotectants are expressed on a fresh weight basis. No differences were seen in the composition of polyhydric alcohols and sugars in unparasitized and parasitized pupae. Four sugars (fructose, glucose, trehalose and sucrose) were detected together with four sugar alcohols (glycerol, erythritol, mannitol and myo-inositol) in both types. The concentrations of all polyols were low ($<$ 1% of fresh

weight, i.e. < 10 μg mg^{-1} fresh weight), and only three compounds (trehalose, glucose, mannitol) had average concentrations $>$ 0.1% of live weight overwinter (Table 4). The concentrations of glucose and trehalose were higher than those of mannitol in both categories of pupae, and parasitized pupae tended to have higher concentrations of all three compounds than those unparasitized. Even at these low concentrations some seasonal trends were observed, but the variation about their mean values was high. The peak concentration of glucose was in January for unparasitized pupae (c. 8 μg mg^{-1} fresh weight) and in March for unparasitized pupae (c. 9 μg mg^{-1}). Trehalose reached a maximum (11.6 μg mg^{-1}) in March among parasitized pupae but tended to decline with time among unparasitized ones.

It was clear from a comparison of the sugars extracted from unparasitized pupae on six sampling occasions that supercooling followed by freezing and thawing altered the relative concentrations of glucose and trehalose. Freezing caused an increase in glucose relative to trehalose, which had a lowered concentration after freezing in all cases.

DISCUSSION

During the winter of 1983-84 a small percentage (1-3%) of the population of D. radicum overwintered as larvae (3rd instar) with little mortality. Larvae of D. radicum do not normally overwinter (Smith 1927) and their presence at Silwood in 1983-84 (Table 3) may have been caused by the delayed development of the 1983 population. Emergence of spring adults in 1983 was prolonged by cool weather, and, despite a warm summer, the third generation of D. radicum was later than usual and pupation did not occur

until mid-October (P.M. Reader & T.H. Jones, unpublished). These larvae formed puparia in the spring, as Smith (1927) reported that exposure to low temperatures did not prevent larvae from continuing development when conditions improved.

Most of the population overwintered as pupae, and parasitism was the major mortality factor. The decrease in the percentage parasitism attributable to T. rapae that occurred following the collection of 1 November 1983, which was coincident with an increase in parasitism by A. bilineata, could have been caused by the latter species being more active in the soil near the surface. At depths of 0–2.5 cm, only 15% of the unparasitized hosts but 40% of those parasitized by T. rapae occurred. Mortality from causes other than parasitism (eg. predation) was greater for the November and December collections (c. 22%) and in the spring (c. 12%) than during the winter (c. 3%). High survival overwinter was probably due to the mild weather and lack of sub-zero soil temperatures.

Exposure of D. radicum from all collections to at least 156 days at < 10°C, either in the field or the post-collection temperature of 4°C, was sufficient to break pupal diapause (Collier & Finch, 1983a, b). Nevertheless, a proportion of the flies (0.06 to 0.14) from every collection required more time (259 - 992°$D_{5.6}$) to eclosion than expected for pupae that had completed diapause development before incubation. Finch & Collier (1983) suggested that such late-emerging flies were genetically different from early-emerging flies, possibly because the late-emergers have a second phase of diapause development at temperatures > 4°C. However, the collection of 30 April 1984, taken after the eclosion of the early-emergers, had the same proportion of late-emergers as the other monthly samples, even

though these pupae had been exposed to temperatures > 5.6°C for 31 days prior to their collection on 30 April. Alternatively, Turnock, Jones & Reader (1985) suggest that the late-emergers are individuals that were caught in the prepupal or cryptocephalic pupal stages by the onset of winter. Such individuals, which have completed their larval development and formed puparia at temperatures near the threshold for development, may enter a more intense diapause than those in puparia formed earlier in the autumn. At present, it can only be concluded that a portion of the overwintering populations of D. radicum in southern England have different °D requirements for postdiapause development than the bulk of the populations.

Host and parasitoid are freezing susceptible, both dying when frozen after extensive supercooling. The only published supercooling point for D. radicum is -25.2°C for a winter sample in Estonia (Merivee, 1978). The weak bimodality shown by unparasitized pupae in the 1 November 1983 sample (Fig. 3) cannot be attributed to feeding and non-feeding groups as found in some arthropod populations (Block & Sømme, 1982) because all individuals were non-feeding. Further, it cannot be linked to the synthesis of cryoprotectants in any significant quantity by D. radicum. This bimodality disappeared in subsequent collections, where very few individuals had high supercooling points. The occurrence of the high group in the 1 November collection may be related to a stage in the structural re-organisation of larval and pupal elements, which could be important in freezing initiation. Alternatively, this high group may have included moribund individuals that were not distinguishable from healthy pupae. By the time of the next collection, 5 December 1983, dead individuals would have been more easily seen and, as indicated above, little additional mortality occurred during the winter. The bimodality observed in the collection of 30 April 1984 can be attributed to the loss of supercooling ability by those members of the population that had begun postdiapause development.

Parasitism by T. rapae affected its host by increasing the variability in the supercooling points, resulting in a few individuals with lower and many more with higher supercooling points. The effect of the parasitoid on the nucleating properties of the cabbage root fly pupa is complex. The increased variability between individual supercooling points may be related to the amount of feeding or meconium voided by the final instar larva before the onset of winter, thus influencing the nucleation temperature of the puparial structure. Several larvae within a single puparium may lead to a multinucleation process, but this is very rare for T. rapae. In addition, there was no evidence of multiple freezing events on the host freezing curves as reported by Humble & Ring (1985).

The extensive powers of supercooling in over 91% of the unparasitized pupae and in 47% of the parasitized pupae that were observed early in the winter and which persisted until April seem excessive in relation to winter soil temperatures in England and Wales. Since the lowest temperature recorded at the 10 cm depth in soil is -2.8°C (Davies, 1974; Finch & Skinner, 1980), freezing cannot be considered to be a mortality factor in these species. The persistence of this high degree of cold hardiness in the absence of selection pressure may occur because it is conferred by the structural properties of the dipteran puparium and the pupa within it. Furthermore, specific compounds for the enhancement of cryoprotection and not synthesized. The trends in the three polyols suggested by the present study probably reflect metabolic changes which occur during the development of the cabbage root fly pupa to adult, and by the feeding and growth of its cynipid parasitoid. Both D. radicum and T. rapae appear capable of surviving soil temperatures more severe than those normally prevalent overwinter in England and Wales. This suggests a degree of pre-adaptation in both species. The main factor influencing survival of cabbage root fly pupae in a normal winter is not freezing, but parasitism or cultural practices (Finch &

Skinner, 1980). Survival is reduced and post-diapause development affected only when soil temperatures $< -10°C$ occur (Turnock, Jones & Reader, 1985).

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REFERENCES

Block W, Sømme L (1982) Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. Oikos 38: 157-167

Coaker T H, Wright D W (1963) The influence of temperature on the emergence of the cabbage root fly Erioischia brassicae (Bouche) from overwintering pupae. Ann appl Biol 52: 337-343

Collier R H, Finch S (1983a) Completion of diapause in field populations of the cabbage root fly (Delia radicum). Entomologia exp appl 34: 186-192

Collier R H, Finch S (1983b) Effects of intensity and duration of low temperatures in regulating diapause development of the cabbage root fly (Delia radicum). Entomologia exp appl 34: 193-200

Commonwealth Institute of Entomology (1983) Distribution maps of pests. Delia radicum (L.). Map No. 83 (revised).

Davies J W (1974) Averages in soil temperatures at 10 and 20 cm depth 1959-1968. London Meteorological Office, Agriculture Memorandum No. 646. (Unpublished; available from National Meteorological Library, Bracknell, Berks, UK)

Finch S, Collier R H (1983) Emergence of flies from overwintering populations of cabbage root fly pupae. Ecol Ent 8: 29-36

Finch S, Collier R H (1984) Parasitism of overwintering pupae of cabbage root fly, Delia radicum (L.) (Diptera: Anthomyiidae), in England and Wales. Bull ent Res 74: 79-86

Finch S, Skinner G (1980) Mortality of overwintering pupae of the cabbage root fly (Delia brassicae). J Appl Ecol 17: 657-665

Humble L M, Ring R A (1985) Inoculative freezing of a larval parasitoid within its host. Cryo-Letters 6: 59-66

Makarenko G N (1968) Resistance to cold in Trybliographa rapae West (Cynipidae) and its host, the spring and summer cabbage flies. Trudy Vsesoyuznogo Inst Zashchity Rastenii, 31: 276-288 [In Russian, English summary]

Merivee E (1978) Cold-hardiness in insects. Academy of Sciences of the Estonian S.S.R., Tallinn [In Russian, English summary]

Smith K M (1927) A study of Hylemyia (Chortophila) brassicae Bouche, the cabbage root fly, and its parasites, with notes on some other dipterous pests of cruciferous plants. Ann appl Biology, 14: 312-329

Turnock W J, Jones T H, Reader P M (1985) Effects of cold stress during diapause on the survival and development of Delia radicum (Diptera: Anthomyiidae) in England. Oecologia (Berlin) 67: 506-510

Wishart G, Monteith E (1954) Trybliographa rapae (Westw.) (Hymenoptera: Cynipidae), a parasite of Hylemyia spp. (Diptera: Anthomyiidae). Can Ent 86: 145-154

TABLE 1. Mean soil temperatures (°C) at three depths in a field of swedes (*Brassica napus*) at Silwood Park during the winter of 1983-84

Period	n (days)	Depth (cm) 2.5	5.0	7.5
27 October - 6 November	11	8.9	9.0	9.2
11 - 30 November	20	5.7	5.9	6.2
1-20 December	20	3.0	3.1	3.3
21 December - 9 January	20	5.9	6.0	6.2
10-29 January	20	3.1	3.1	3.3
30 January - 18 February	20	4.3	4.4	4.5
19 - 27 February	9	3.2	3.3	3.4
Total	120	4.7	4.8	5.0

TABLE 2. Percentage emergence, parasitism and mortality among puparia of *Delia radicum* collected on seven occasions over the 1983-84 winter at Silwood Park and incubated at 20°C after the completion of diapause development

Collection date	n	Larvae	*D. radicum* puparia			
			Emerged	Dead	Parasitized	
					T. rapae	*A. bilineata*
1983						
1 November	316	2.2	45.6	22.1	21.2	8.9
5 December	248	1.2	31.8	21.4	7.3	38.3
1984						
2 January	269	2.6	33.1	8.5	11.9	43.9
30 January	300	2.9	47.9	3.6	6.5	39.1
5 March	302	1.3	37.1	2.7	12.2	46.7
2 April	307	1.3	37.1	12.1	7.8	41.7
30 April	290	0.0	36.2	12.1	14.8	36.9

TABLE 3. Proportion (P) of the total emergence of adult Delia radicum that were early-emerging ($< 230°D_{5.6}$), the number of $°D_{5.6}$ at 20°C to mean emergence for early emerging adults, and the range of $°D_{5.6}$ to emergence (°D) for late-emerging adults overwinter 1983-84. See text for details

Collection date	n	Early-emergers (P)	Time of emergence (°D) Early-emergers (x ± SD)	Late-emergers (range)
1983				
1 November	120	0.941	148 ± 0.8	317 - 992
5 December	57	0.912	147 ± 1.0	547 - 648
1984				
2 January	44	0.931	145 ± 0.7	403 - 739
30 January	77	0.911	147 ± 0.9	288 - 634
4 March	76	0.947	138 ± 1.3	317 - 662
1 April	66	0.859	121 ± 1.3	490 - 778
10 April	54*	0.944	⊛	374 - 432

51 puparia from which the adult had emerged were found in the soil at the time of collection.

⊛ Early emerging flies had emerged by this date.

Concentrations ($\mu g\ mg^{-1}$ fresh weight) of two sugars and one polyhydric alcohol in healthy and parasitized puparia of Delia radicum at Silwood Park during the 1983-84 winter. Average values for the total of the seven monthly samples are also given. All values are mean (±SD) with the number of samples in parentheses

Unparasitized				Parasitized			
n	Glucose	Mannitol	Trehalose	n	Glucose	Mannitol	Trehalose
(10)	1.10±0.58	2.69±2.71	7.46±2.39	(9)	5.30±4.53	6.07±6.95	3.66±2.69
(10)	2.10±1.70	1.20±1.67	6.90±2.53	(10)	3.35±1.69	2.66±3.45	8.15±2.33
(15)	7.96±5.28	1.04±0.65	5.55±3.61	(5)	6.73±5.93	2.14±1.49	7.23±6.51
(10)	5.43±5.32	1.23±2.21	6.62±1.78	(3)	5.13±4.23	0.64±0.14	7.55±4.34
(10)	1.63±2.08	0.32±0.18	5.67±2.34	(3)	8.83±4.51	2.54±1.93	11.56±2.00
(7)	1.89±1.63	0.33±0.12	5.80±2.23	(5)	1.98±1.34	2.46±1.76	7.23±3.68
(9)	3.41±4.38	0.70±0.39	3.71±2.46	(4)	6.28±5.12	0.49±0.35	1.36±1.66
(71)	3.81±4.39	1.11±1.60	5.97±2.76	(39)	4.93±4.08	2.97±4.16	6.54±4.09

FIGURE CAPTIONS

Fig. 1. (a) Live weight (mg) and (b) water content (% of live weight) of unparasitized (●) and parasitized (▲) pupae of Delia radicum during the winter of 1983-84 at Silwood Park. Values are mean ± SD, and the numbers of observations (n) are given

Fig. 2. Frequency distributions (%) of the supercooling points of (a) unparasitized pupae of Delia radicum and (b) those parasitized by Trybliographa rapae over the 1983-84 winter at Silwood Park. The data for the period 5 December 1983 to 2 April 1984 are pooled

Fig. 3. Mean (±SD) supercooling points for pupae of Delia radicum during winter 1983-84 at Silwood Park. Unparasitized pupae (●) are compared with those parasitized by Trybliographa rapae (▲). R = total with supercooling points $< -20°C$ divided by total number in sample

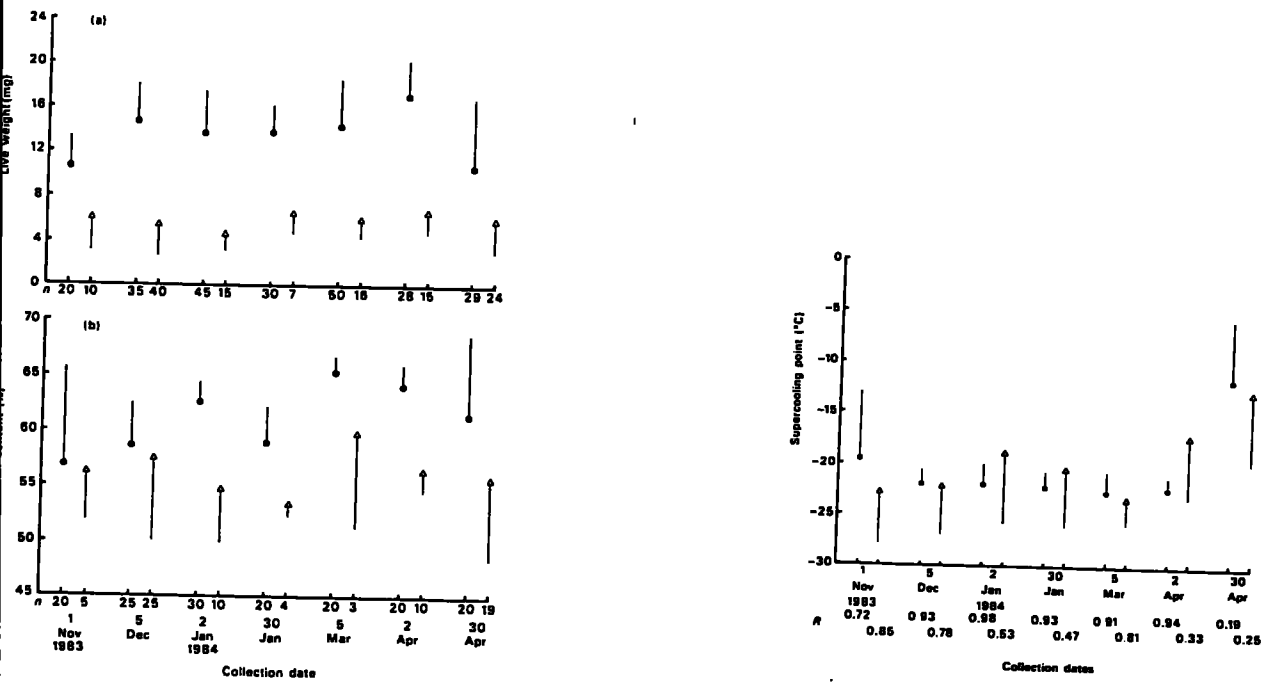

FIG. 3. W. BLOCK ET AL.

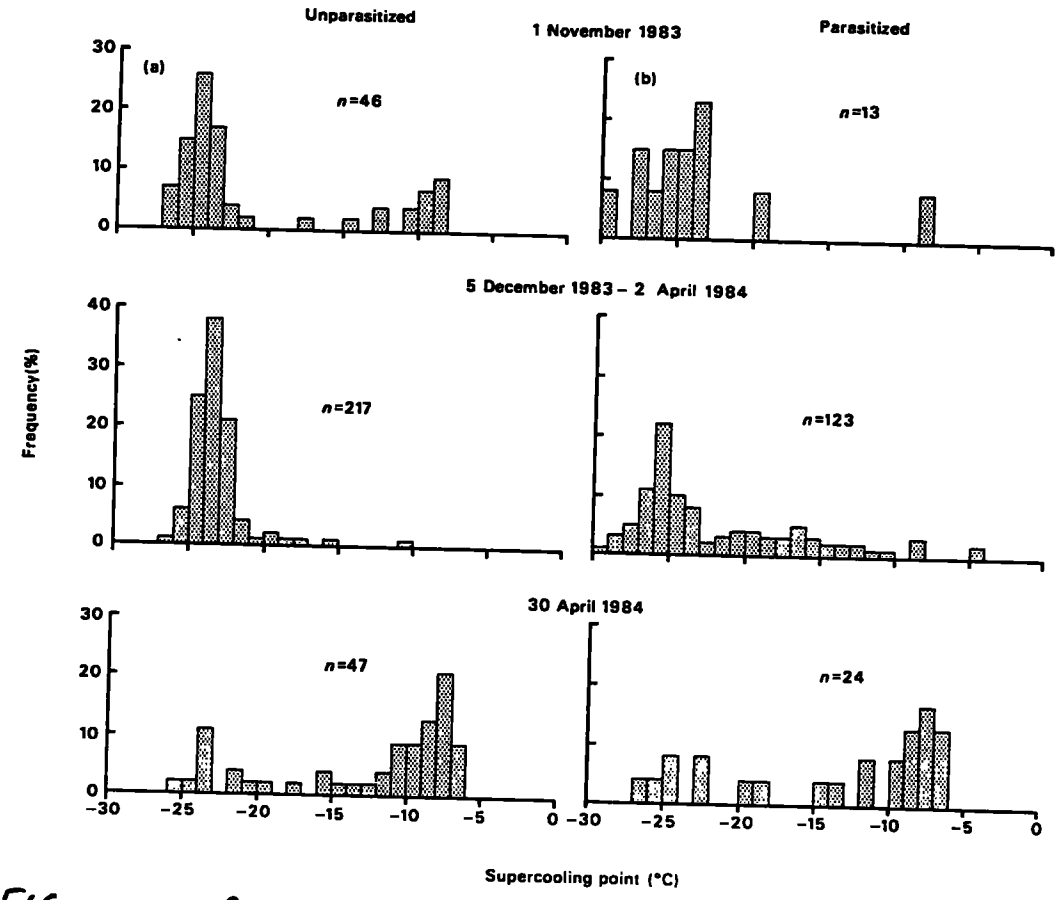

FIG. 2. W. BLOCK ET AL.

SOIL BIOLOGICAL PROCESSES IN THE NORTH - AND SOUTH

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ABSTRACT

Soil biological processes which have been studied in the north are extended and compared with those of the south polar region. Much can be learned from exploiting the biological similarities and differences of the Arctic and the Antarctic. Firstly, the environmental conditions which control these biological processes are identified, and secondly, the ecology and physiology of the soil organisms are examined as a basis for understanding the functional processes. Soil processes can then be placed in the natural context of the terrestrial ecosystem from their interaction with other components of the system.

1. INTRODUCTION

The traditional fascination of the North has led many biologists to examine the flora and fauna of tundra and polar deserts, but they have rarely strayed below ground. That has been the province of the pedologists and glaciologists who have provided considerable insight into the physical processes which determine the present wide variation in soil conditions. Soil biology in the North is a relatively young area of research and, of necessity, has tended to concentrate in the initial stages on description, particularly on the composition of the soil fauna and microflora. Functional aspects of soil organisms have received relatively little attention despite their importance to the understanding of soil development, plant growth and vertebrate populations; for example, through organic matter decomposition which influences soil temperature and moisture regimes, nutrient supply to the vegetation and is the basis for food chains to many birds.

The nature of soil biological research forces attention on a very limited area in the context of the vast expanses of the North and particularly on places, such as Abisko, where the foresight of the scientific community has provided the essential facilities which encourage good soil biological research. The focus on specific sites, whilst having certain limitations, was the approach adopted during the International Biological Programme (IBP) and which stimulated soil biological research, with the important benefit of association between disciplines - the organisms do not function in isolation, neither should the scientists. We draw heavily and unashamedly from those IBP efforts.

We also extend our view of soil biological processes from the North to the South. The reason is that the fundamental controls of soil biology, ie. climate and geology (lithology) are similar, therefore results from one are applicable to the other - with due precautions, but with the benefit of increasing the value of research results. Further, there is a major difference between the two polar regions in that the flora, fauna and, to a lesser extent, the microflora in the South, have a much smaller range of species, probably through geographic isolation. Thus, a natural bio-polar experiment has been established through which it is possible to explore the effect of species diversity on soil and ecosystem processes.

In considering soil biological processes, we first identify the environmental conditions which control these processes, and secondlly examine the ecology of soil organisms as a basis for understanding the processes. Following discussion of soil processes, we place these in the natural context of the ecosystem because of their interaction with other components of that system.

2. THE PHYSICO-CHEMICAL ENVIRONMENT

Although there is wide variation between individual areas in age since exposure from the sea or ice within the Arctic and Antarctic, the soils all tend to be young compared with many temperate and tropical latitudes. Carbon dating of organic deposits indicates that it is unlikely that the oldest soils pre-date the last 12,000 years (Everett et al., 1981). Many soils are obviously younger where there is recent glacial retreat and this provides opportunity for analysis of chronosequences to distinguish successional changes in processes as in the classic studies of Crocker and Major (1955), the raised beach

sequences on Devon Island (Bliss, 1975), the deglaciated headland on Anvers Island off the Antarctic Peninsula (Smith, R.I.L., 1982) and the fellfield studies in the maritime Antarctic (Block et al. 1980). An alternative approach to analysis of the effects of changing environments, uses the accumulated peats (pergelic cryofibrists) of the Stordalen mire in Abisko (Sonesson, 1980), at Signy Island in the South Orkney Islands (Davis, 1981) and the "temperate tundra" at Moor House, UK and Glenamoy, Ireland (Rosswall and Heal, 1975). This evidence within a system of the changes in vegetation and environment since initiation of the peat-forming process, usually 5-10,000 years ago, is of great value to the soil ecologist. A further opportunity for the study of terrestrial ecological processes such as colonisation and succession lies in areas which have been subject to recent volcanic activity; e.g. Surtsey in the Arctic (Brock, 1972), Deception Island in the South Shetland Islands, Antarctica (Smith, R.I.L. 1984; Smith, H.G. 1985).

A wide variety of soils have developed in the tundra - or rather, are developing. Pedogenesis is still in progress and many soils are subject to short term cryoturbation and longer term cyclical processes such as the thaw lake cycle (Brown et al. 1980). Detailed descriptions and classifications are available for soils and for climate, but to bring these together to provide a definition of the environmental conditions of relevance to soil biological processes, French (1981) used selected climatic and soil variables in a multivariate classification of the IBP sites (Fig. 1). This overrides the boundaries of geography, pedantry/scientific disciplines and politics to provide an ecological description of the environment without involving arguments on classification of soils or tundra - although it raises other arguments. It identifies that the main axes of variation include both climate and

soil factors, implying their functional relationship. The analysis indicates that whilst in some cases the environmental conditions from a number of sites within a small geographic area are distinctive, e.g. Moor House (MHC, MHE, MHJ, MHS) and Glenamoy (CB, CF, GG), in other cases the conditions in adjacent habitats are similar not to one another, but to geographically distant areas. For example, the wet depressions of the Stordalen (AP) mire are most similar to the oceanic peat bogs whilst the drier elevated parts at Stordalen (AH) are most closely related, in terms of climate and soil, to sites at Kevo, Finland and Hardangervidda, Norway. Further, the grassland and marble moraine soils of the Antarctic Signy Island (SG, SOM) are most closely related to sites at Disko Island, Greenland (DKSB, DKF) and the Alpine Niwot Ridge, Colorado (NK, ND).

Thus, the soil climatic and physico-chemical environments, North and South, show ecological gradients which, whilst partly related to latitude and altitude, show considerable variation within short distances, often over centimetres or metres. These gradients relate as much to variations in soil moisture, nutrients and acidity as to the more obvious temperature parameters. This implies that soil biological processes may be constrained by other factors as much as by temperature.

One feature which is inadequately expressed in Fig. 1 is the microclimate variation within a soil. Seasonal air temperature variations are considerably modified with depth in the soil (Fig. 2); surface temperatures can fluctuate greatly and attain 30°C for short periods as a result of aspect and reflectance; short term surface desiccation of litters occurs on wet sites as well as in polar deserts; severely reducing conditions can occur within a profile where local drainage is impeded. These variations highlight the importance of

microhabitat definition and the potential for using microhabitat gradients in biological research. They also emphasise that biological processes respond to an extreme range of conditions, with the added possibility that the more mobile (arthropods) or extensive organisms (fungi) have the potential to operate over that range of conditions.

3. PHYSIOLOGY AND AUTECOLOGY

To what extent have the soil fauna and microflora adapted to or been selected by the prevailing polar environments? This information provides the mechanistic basis for understanding soil processes.

On present evidence there is no reason to believe that Northern and Southern fauna and microflora have any significant differences in their physiology, other than those attributable to specific taxonomic differences. There is no obvious dominance of psychrophiles in either Arctic or Antarctic soil communities. Fundamental processes such as protein synthesis proceed in a similar fashion in cold adapted organisms from North and South, although different enzymes may be at work. In all organisms which experience freezing temperatures, the maintenance of membrane fluidity appears to be crucial in their survival and this we know little about in any of the polar soil biota.

Metabolic adaptations to low temperatures in soils are similar in temperate and polar species. Cold adaptation has been documented by Block and Young (1978) in soil micro-arthropods, where the metabolism - temperature curve is shifted to a lower temperature range but with no alteration of its slope compared to temperate species (Fig. 3). Such micro-arthropods have Q_{10}s varying from 1.3 to 3.4 over an environmental temperature range of 0 to 10°C. Higher insects in the Arctic (e.g. the

tipulids Pedicia hannai and Tipula carinifrons) have a Q_{10} of 2.3 over 0.5 to 20°C, but the adults show a faster response to increasing temperature than the larvae (MacLean, 1980). The soil microflora, on the other hand, tend to exhibit an elevated Q_{10} (average c. 3.6) for different fungi and substrates with higher values in surface litters. This is reflected in a more responsive microbial respiration in the litter compared to plants below ground. Bacteria utilise lower molecular weight substrates at cold temperatures whereas fungi metabolise complex substances down to -5°C. In general, the soil microbial components seem to have a faster reaction to small temperature increments, whereas the soil fauna response is not so pronounced. This is considered to be a reflection of the life styles and strategies adopted by these functionally different members of the soil community.

Freezing resistance is widespread in polar soil communities, and is achieved in two ways: organisms either tolerate the formation of extra-cellular ice or avoid nucleation by extensive supercooling (the maintenance of body fluids in the liquid phase below their normal freezing point) (Block, 1982). The latter, supercooling, strategy is by far the most common in the soil fauna of both Northern and Southern tundra systems, whereas freezing tolerance is restricted to a relatively few higher insects (e.g. beetles, dipterans, etc.) and some plants. Supercooling may be more efficient energetically and metabolically in cold environments with a high frequency of freeze-thaw cycles. Almost nothing is known about freezing resistance in soil micro-flora. The extent of supercooling is determined largely by the absence or masking of potential ice nucleating agents and the action of low molecular weight compounds such as sugar alcohols and sugars. In invertebrates ice nucleators may occur in the gut contents or in the haemolymph. High body water content may encourage lethal freezing. In plant sap, polysaccharides may initiate nucleation at high temperatures and thereby

protect freeze tolerant species (Krog et al., 1979). Survival of freezing temperatures, especially in overwintering sites, appears to be mainly by the freeze avoidance strategy in a wide range of soil organisms. Again, such a phenomenon is not restricted merely to cold adapted species, but is known to occur in temperate and sub-tropical soil biota.

The dependence of all soil organisms on moisture is considerably exaggerated in drier areas of the polar regions, where liquid water may not be biologically available, being locked up as ice, at least for part of the year. Therefore, much of the biological activity and, in turn, life cycles may be largely regulated by the supply of moisture (e.g. areas of continental Antarctica such as Ross Island and south Victoria Land). In such habitats, dehydration stress is as important as low temperature in the survival of soil organisms (especially invertebrates). The result may be a trade-off between water requirement for growth, etc. and the increased potential for ice nucleation in the animal's body during short periods of sub-zero temperatures.

Many soil invertebrates exhibit maximum growth in summer at temperatures around 3-5°C, provided moisture and other environmental conditions are optimal. Antarctic springtails have their highest energy assimilation efficiency around 0°C, and their young stages maintain a positive net production at similar temperatures (Burn, 1984). Some Arctic tipulids exhibit similar features, and these species are clearly facultative as distinct from obligate polar forms. Growth rates, although adapted to cold, are necessarily slow in such soil animals, and hence the period of exposure to potentially lethal conditions is prolonged in many species. Life cycles of between 7 and 13 years have been postulated for particular species.

Overwinter survival, therefore, becomes a key factor in the success or failure of the inhabitants of polar and tundra soils. In mites and springtails most life stages overwinter, whereas in the higher insects, larvae and pupae are more important. The advantages to soil invertebrates of asexual reproduction are clear; the enchytraeids being a good example. Such features, which may be considered to be pre-adaptive, may be typical for colonists of soils in tundra regions. On the other hand, most soil arthropods employ sexual reproduction, and several establish 'pools' of immature stages in the soil with maturation occurring as the environment and the climate allow. In this way, the constraints of sexual reproduction on the life cycle may be negated.

The now traditional ideas of r-k selection are too limiting for application to tundra soil organisms. A more useful concept is that of adversity or A-selection (Fig. 4), which favours the species' conservation of adaptations to environments which are consistently and predictably severe (Greenslade, 1983). It can be applied equally to Arctic and Antarctic species, and forms an excellent conceptual framework for attempting to understand why particular organisms - plant, microbe, invertebrate - live in tundra soils.

4. POPULATIONS AND COMMUNITIES

Polar soil communities show a general reduction in numbers of species and in their taxonomic range compared with other soils. Such reduction in diversty is more pronounced due to the geographical isolation of the Antarctic, where many of the higher insect groups are absent from the soil invertebrate fauna (Block, 1984). The striking difference with the Arctic is in the almost complete absence of Diptera in the south polar region (only the apterous midge Belgica antarctica existing in sheltered

localities along the Antarctic Peninsula). However, some invertebrates introduced into the Antarctic by human agency have survived and established small populations (e.g. Block, Burn and Richard, 1984). The general lack of large decomposers in polar terrestrial communities leads to reduced comminution of litter and organic material, which may be partly overcome by the effects of cryoturbation. In the microbial component, yeasts often dominate and exhibit substantial population growth during spring melt. The patchy information on populations of polar soil organisms show that densities are variable (by season and site), but nevertheless they are broadly similar to those of comparable temperate soils. The fauna is often restricted to the top 5-6 cm of the soil profile by anaerobic conditions below this zone. Of the population dynamics and their causes, we are largely ignorant. Microbial groups exhibit growth pulses in spring and autumn, but why? Is microfloral predation restricted only to the surface layers, and what levels of overwintering mortality are sustained by microbes and invertebrates alike? Predation mortality of invertebrates may be considerable in the Arctic, e.g. 20-25% of adult tipulid production is consumed by insectivorous birds which may constitute the entire diet of same species (MacLean, 1980). However, it is not known whether such predation pressure on invertebrates is opportunistic or not, and whether the population densities of predation and prey are controlled by such interaction (i.e. predation) or by the environment. By way of contrast, in the relatively simple terrestrial communities of the maritime Antarctic, often the only arthropod predator - a mesostigmatid mite (Gamasellus racovitzai) - largely feeds opportunistically with its population level being controlled by the physical environment (Fig. 5). It may be that obligate polar species may be mainly density dependent, whilst populations of facultative species are density dependent (e.g. Coulson and Whittaker, 1978), but firm evidence is lacking.

In the absence of terrestrial vertebrates and above-ground herbivores of any kind in Antarctica proper, the importance of a below-ground invertebrate-microbial grazing chain is increased compared with Northern soil communities. The role of the various microflora is enhanced. The full range of metabolic capabilities is possessed by most microbial groups in both North and South polar soil communities, there being no evidence of loss of particular functions such as enzymic activity. Whilst there is no obvious dominance of psychrophiles in polar soil microbes, the functional capabilities of the Antarctic fauna appear to be rather more restricted. These features probably emphasise the greater age and depauperate nature of the South polar terrestrial biota, compared with the Northern situation. However, the functional structure of the simpler communities in the South polar soils suggests fewer biological interactions, where predation and inter-specific competition are at very low levels and processes such as grazing are regulated entirely by invertebrates. Niche breadth, especially of free-living forms, maybe larger than for comparable Arctic forms. In turn, Antarctic land invertebrates, appear less sensitive to variations in primary production due to their catholic diets, and hence more efficient exploiters of cold environments. However, further and more detailed research on both Northern and Southern soil communities is required to substantiate these theories.

PROCESSES

The combined activities of the microflora and fauna are integrated in the processes of organic matter decomposition and mobilisation of nutrients. The importance of the overall temperature regime and of the more localised variations in moisture in the physiology and population characteristics of soil organisms are clearly reflected in the rates of

decomposition, analysed under both field and controlled laboratory conditions. In the field, weight loss from confined litter is usually of the order of 5-25% in the first year although much higher rates are recorded from sub-Antarctic sites. Whilst these loss rates are broadly related to site temperature and moisture conditions (Heal et al., 1981; Davis, 1986), a more detailed understanding comes from laboratory studies, using respiration as a measure of decomposition, especially when combined with mathematical models (Bunnell et al., 1977 a, b; Flanagan and Bunnell, 1980).

Developed to express the decomposition relationships in the tundra of the north slope of Alaska, the model of Bunnell et al. (1977 a, b) is summarised as:

$$R(T,M) = \frac{M}{a_1 + M} \times \frac{a_2}{a_2 + M} \times a_3 \times a_4^{\frac{T-10}{10}}$$

Where R(T,M) is the respiration rate in μl O_2 g^{-1} hr^{-1} of a resource at temperature T (°C) and moisture M (% dry weight), a_1 is the percentage moisture content at which the resource is half saturated with water; a_2 is the percentage moisture content at which half the pores are saturated or blocked with water; a_3 is the respiration rate at 10°C when neither oxygen nor moisture is limiting; a_4 is the Q_{10} coefficient.

The model represents the hump shaped surface of respiration response to temperature and moisture in which shortage of moisture limits respiration (a_1), high moisture contents inhibit oxygen diffusion and

hence aerobic respiration (a_2). The increased respiration with temperature (a_4) causes oxygen depletion to occur at lower moisture contents as temperature increases, giving an asymmetrical hump. The rate of respiration is also influenced by the quality of the resource, e.g. the concentration of soluble carbohydrates and nutrients. The resource quality influences the overall height of the response surface and is represented by the respiration rate under optimal conditions (a_4).

The model, whilst not unique in general principles, has been developed from laboratory and field data and used to explore the relative importance of environmental factors and quality (Fig. 6). In examining the respiration of a number of resources from different microhabitats and sites Flanagan and Bunnell (1980) concluded that microbial respiration was most sensitive to temperature, then to resource chemistry and least sensitive to moisture, particularly at higher moisture contents. However, low moisture contents may markedly reduce respiration rates in certain microhabitats such as standing dead plant material. Whilst recognising the contribution of many chemical components, Bunnell et al. (1977b) showed that definition of the proportions of ethanol-soluble fractions allowed distinction of the decay rates for different resources.

In the present context, the importance of the decomposition study centred on Point Barrow, Alaska (Flanagan and Bunnell, 1980) is that a detailed and rigorous analysis of the basic factors controlling the process there have much more general application. With limited information on the respiration rates of a number of litters and of the site environmental conditions, Bunnell et al. (1977b) predicted the rate of decomposition of litters at Abisko (Sweden) and at Moor House (UK).

The predicted annual loss rates were 70-90% weight loss measured in independent field studies (Table 1). The basic form of the decomposition (respiration) response to temperature, moisture and chemical composition is derived from physiological information and shows how the wide variety of individual species responses are combined with, for example varying Q_{10} responses by the populations of different microhabitats and resources. There is no general temperature response curve characteristic of the tundra microbial community, rather there are a variety of responses which are adapted to or selected by the environmental conditions (Fig. 7). The same principle applies to microbial responses to moisture and quality, i.e. a general form within which there are variations related to habitat.

Thus the rates of organic matter decomposition shown from physiological and field studies reflect the flexibility of the microbial community, and activity is maintained under the severe environmental conditions by the ability of its constituents to respond even at sub-zero temperatures, under a variety of moisture conditions, utilising short periods when temperatures rise. Further, there is no evidence that any restrictions in the species composition of the microflora of the Arctic, or more particularly the Antarctic, have a significant effect in modifying the rates of decomposition.

Nutrient limitation may retard soil community development under certain polar conditions. Freeze-thaw cycling (and other cryoturbic processes) are important in facilitating the release of soluble organic compounds especially at snow melt in spring (Fig. 8). This is often followed by a period of relatively constant soil temperatures, when microbial, invertebrate and cryptogamic activity is high. With excessive moisture and waterlogging, anaerobic conditions commonly develop, and methane

production may be up to 50% of the carbon loss. Levels of nutrient mobilisation are much as expected from the climatic conditions with nitrogen and phosphorus limiting plant growth. Rates of nitrification are generally low in polar soils. The active or seasonally-thawed zone is of importance as nutrients are released into it from the permafrost interface. Many nutrients are locked out of the biological active system in such permafrost areas.

It is concluded, therefore, that in general the rates of soil processes appear to be controlled primarily by the environment, particularly the prevailing microclimate. The spectrum of adaptations so far documented for the range of soil organisms found in polar soils, indicates that these biological characteristics only partly overcome the environmental constraints. On current knowledge, there is no reason to think that the restricted community structure of such soils alters the pattern of biological processes. The main processes occur but often at slower rates and possibly via different factors. For example, the distinctive absence of Antarctic macrofauna may reduce comminution of organic matter and microbial stimulation, but this is compensated by the effects of cryoturbation.

5. ECOSYSTEMS

North and South polar ecosystems have three common features: (1) low temperature limitation of the rates of most physical and biological processes; (2) relatively short annual period for biological activity; (3) frequent occurrence of freeze-thaw cycles and permafrost. By contrast, there are also important differences: (a) the proportion of primary production contributed by cryptogams is low in the Arctic and high in the Antarctic; (b) the detritus input into the soil community is

utilized in different ways in the North compared with the South; (c) the composition and trophic structure of the invertebrate component varies; (d) levels of herbivory and carnivory are well developed in the Arctic and restricted in the Antarctic. French and Smith (1985) detail further similarities and differences.

In the south polar ecosystems which have been analysed, very little of the primary production from mosses (and lichens) is directly eaten by invertebrate consumers. The main energy flux is via the microflora, which assimilate dead organic matter thereby converting it to a form more readily metabolized by invertebrates. The micro-algae play a crucial role in such microfloral energy and nutrient cycling, which does not seem to have an Arctic functional counterpart. Davis (1981) calculated that an amount equivalent to c. 58% of the annual net primary production was consumed by the soil fungi in a mossbank in the maritime Antarctic. Comparable Arctic tundra exploitation efficiencies have been estimated at < 1.5% (Whitfield, 1977). On the other hand, carnivore efficiencies are high (15-33%) in Arctic systems and low (< 1.0%) in the Antarctic. These functional differences between Northern and Southern terrestrial systems were postulated by Holdgate (1977) from the Heal and MacLean (1975) model on the basis that observed invertebrate production was much less than predicted in the maritime Antarctic environment.

It is instructive to compare land with aquatic systems and their functioning in both the North and South. In the Antarctic, the terresrial animals appear to be functionally analogous to the marine benthic fauna, which is largely composed of suspension feeders of various types. They are similar in that both are unspecialised opportunists with broad ecological niches. The marine benthos, however, is primarily regulated by food supply, whereas the land fauna appears to be controlled more by physical conditions. The marine and terrestrial

fauna experience totally different microclimates in which temperature ranges, both seasonally and diurnally, are in marked constrast. As the temperature of the marine inshore environment is stable throughout the year (0 $\pm$ 2°C), so that of land habitats fluctuates widely (-28 to 30°C). Such thermally different conditions may explain why the physiological phenomena of cold adaptation has been recognised in certain elements of the terrestrial fauna (Block and Young, 1978) but not in the benthic forms which have been studied (Clarke, 1980).

It may be concluded that although there are large differences in species composition between Northern and Southern ecosystems, these have not resulted in significant functional changes. The functioning of tundra ecosystems appears to be a scaled-down version of that operating in temperate ecosystems with environmental temperature as a major constraint. Finally, within particular tundra ecosystems there are many possible variations brought about by microhabitat differences.

7. CONCLUSIONS AND FUTURE

Many research opportunities are provided in terrestrial ecology by the natural North-South polar comparison. The importance of the study of soil biological processes is undisputed, and once the broad patterns and controls have been understood for organic matter decomposition, the way is open for studies of the dynamics of nutrient release and transformation in tundra systems. Detailed research is also needed in organism physiology and ecology including population dynamics. As many of the key environmental variables are now understood, and close simulation of the field situation is now possible in environmental chambers, there is considerable potential for laboratory investigations of ecological processes at the individual, community and perhaps

ecosystem level. Results from controlled fluctuating environments in such simulations may be used to develop models and then to be applied to field manipulations. Thus, such tundra studies would be of much wider application, far beyond the limits of polar ecology. In no way could such developments in research support the view of Remmert (1980) when writing of Antarctic terrestrial ecosystems:

"Such systems are mainly of interest to physiologists, since they provide valuable examples of organisms clearly indicating the cold limits to existence. The systems are of no significance for the Antarctic ecosystem as a whole...."

The International Biological Programme generated a major surge in soil biology, which was valuably linked to other disciplines. That initiative has now been assimilated, and the time is ripe for another step forward. The next step is an important phase for the polar regions, but particularly so for the Antarctic, where an understanding of the soil biological processes will underpin any management and terrestrial conservation plans which are developed. It is vitally important that the exploitation of both renewable and non-renewable natural resources, at either end of the earth, is conducted on a sustainable basis and that all developments proceed with minimal disturbance to the terrestrial environment (Holdgate, 1984). Polar research should also continue to draw on, and make a major contribution to, the wider field of ecology.

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9. REFERENCES

Bliss, L.C. 1975. Devon Island, Canada - In: Rosswall, T. & Heal, O.W. (eds.) Structure and function of tundra ecosystems. Ecological Bulletins 20: 17-60. Swedish Natural Science Research Council, Stockholm.

Block, W. 1982. Cold hardiness in invertebrate poikilotherms. - Comparative Biochemistry & Physiology 73A: 581-593.

Block, W. 1984. Terrestrial microbiology, invertebrates and ecosystems. - In: Laws, R.M. (ed.) Antarctic Ecology, vol. 1: 163-236. Academic Press, London & New York.

Block, W., Burn, A.J. & Richard, K.J. 1984. An insect introduction to the maritime Antarctic. - Biological Journal of the Linnean Society 23: 33-39.

Block, W., Smith, R.I.L., Walton, D.W.H. & Wynn-williams, D.D. 1980. British Antarctic Survey: Fellfield Ecology Research Programme. - Unpublished Report. British Antarctic Survey, Cambridge.

Block, W. & Young, S.R. 1978. Metabolic adaptations of Antarctic terrestrial micro-arthropods. - Comparative Biochemistry & Physiology 61A: 363-368.

Brock, T.D. 1972. Microbiological observations on Surtsey, 1970. - Surtsey Research Progress Reports 6: 11-13. The Surtsey Research Society, Reykjavik.

Brown, J., Miller, P.C., Tieszen, L.L. & Bunnell, F.L. (eds.) 1980. An Arctic Ecosystem, the coastal tundra at Barrow, Alaska. Dowden, Hutchinson & Ross, Inc., Pennsylvania, U.S.A. US/IBP Synthesis Series 12.

Bunnell, F.L., Tait, D.E.N., Flanagan, P.W. & Van Cleve, K. 1977a. Microbial respiration and substrate weight loss. I. A general model of the influence of abiotic variables. - Soil Biology & Biochemistry 9: 33-40.

Bunnell, F.L., Tait, D.E.N., Flanagan, P.W. & Van Cleve, K. 1977b. Microbial respiration and substrate weight loss. II. A model of the influence of chemical composition. - Soil biology & Biochemistry 9: 41-47.

Burn, A.J. 1984. Energy partitioning in the Antarctic collembolan Cryptopygus antarcticus. - Ecological Entomology 9: 11-21.

Clarke, A. 1980. A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. - Biological Journal of the Linnean Society 14: 77-92.

Crocker, R.L. & Major, J. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. - Journal of Ecology 43: 427-448.

Coulson, J.C. & Whittaker, J.B. 1978. Ecology of moorland animals. - In: Heal, O.W. & Perkins, D.F. (eds.) Production ecology of British moors and montane grasslands: 52-93. Springer-Verlag, Berlin.

Davis, R.C. 1981. Structure and function of two Antarctic terrestrial moss communities. - Ecological Monographs 51: 125-143.

Davis, R.C. 1986. Environmental factors influencing decomposition rates in two Antarctic moss communities. Polar Biology 5: 95-103.

Ellis-Evans, J.C. & Wynn-Williams, D.D. 1985. The interaction of soil and lake microflora at Signy Island. - In: Siegfried , W.R., Condy, P.R. & Laws, R.M. (eds.) Antarctic nutrient cycles and food webs: 662-668. Springer-Verlag, Berlin.

Everett, K.R., Vassiljevskaya, V.D., Brown, J. & Walker, B.D. 1981. Tundra and analogous soils. - In: Bliss, L.C., Heal, O.W. & Moore, J.J. (eds.) Tundra ecosystems: a comparative analysis: 139-179. Cambridge University Press, Cambridge. International Biological Programme 25.

Flanagan, P.W. & Bunnell, F.L. 1980. Microflora activities and decomposition. - In: Brown, J., Miller, P.C., Tieszen, L.L. & Bunnell, F.L. (eds.). An Arctic ecosystem, the coastal tundra at Barrow, Alaska: 291-334. Dowden, Hutchinson & Ross, Inc., Pennsylvania, U.S.A. US/IBP Synthesis Series 12.

Flanagan, P.W. & Veum, A.K. 1974. Relationships between respiration, weight loss, temperature and moisture in organic residues on tundra. - In: Holding, A.J., Heal, O.W., MacLean, S.F. & Flanagan, P.W. (eds.). Soil organisms and decomposition in tundra: 249-277. Tundra Biome Steering Committee, Stockholm.

French, D.D. 1981. Multivariate comparisons of IBP Tundra Biome site characteristics. - In: Bliss, L.C., Heal, O.W. & Moore, J.J. (eds.) Tundra ecosystems: a comparative analysis: 47-75. Cambridge University Press, Cambridge.

French, D.D. & Smith, V.R. 1985. A comparison between northern and southern hemisphere tundras and related ecosystems. - Polar Biology 5: 5-21.

Greenslade, P.J.M. 1983. Adversity selection and the habitat templet. - American Naturalist 122: 352-365.

Heal, O.W., Flanagan, P.W., French, D.D. & MacLean, S.F. 1981. Decomposition and accumulation of organic matter. - In: Bliss, L.C., Heal, O.W. & Moore, J.J. (eds.) Tundra ecosystems: a comparative analysis: 587-633. Cambridge University Press, Cambridge.

Heal, O.W. & MacLean, S.F. 1975. Comparative productivity in ecosystems - secondary productivity. - In: van Dobben, W.H. & Lowe-McConnell, P.H. (eds.) Unifying concepts in ecology: 89-108. Dr W. Junk, The Hague.

Holdgate, M.W. 1977. Terrestrial ecosystems in the Antarctic. - Philosophical Transactions of the Royal Society of London B 279: 5-25.

Holdgate, M.W. 1984. The use and abuse of polar environmental resources. - Polar Record 22: 25-48.

Krog, J.O., Zachariassen, K.E., Larsen, B. & Smidsrød, O. 1979. Thermal buffering in Afro-alpine plants due to nucleating agent-induced water freezing. - Nature, London 282: 300-301.

MacLean, S.F. 1980. The detritus-based trophic system. - In: Brown, J., Miller, P.C., Tieszen, L.L. & Bunnell, F.L. (eds.) An Arctic ecosystem, the coastal tundra at Barrow, Alaska: 411-457. Dowden, Hutchinson & Ross, Inc., Pennsylvania, U.S.A. US/IBP Synthesis Series 12.

Remmert, H. 1980. Arctic Animal Ecology. Springer-Verlag, Berlin.

Rosswall, T., Flower-Ellis, J.G.K., Johansson, L.G., Jonsson, S., Rydén, B.E. & Sonesson, M. 1975. Stordalen (Abisko), Sweden. - In: Rosswall, T. & Heal, O.W. (eds.) Structure and function of tundra ecosystems. Ecological Bulletins 20: 265-294. Swedish Natural Science Research Council, Stockholm.

Rosswall, T. & Heal, O.W. (eds.) 1975. Structure and function of tundra ecosystems. - Ecological Bulletins 20: 1-450. Swedish Natural Science Research Council, Stockholm.

Smith, R.I.L. 1982. Plant succession and re-exposed moss banks on a deglaciated headland in Arthur Harbour, Anvers Island. - British Antarctic Survey Bulletin No. 51: 193-199.

Smith, R.I.L. 1984. Colonisation and recovery by cryptogams following recent volcanic activity on Deception Island, South Shetland Islands. - British Antarctic Survey Bulletin No. 62: 25-51.

Smith, H.G. 1985. The colonisation of volcanic tephra on Deception Island by Protozoa: long-term trends. - British Antarctic Survey Bulletin No. 66: 19-33.

Sonesson, M. (ed.) 1980. Ecology of a subarctic mire. - Ecological Bulletins 30: 1-313. Swedish Natural Science Research Council, Stockholm.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? - Journal of Animal Ecology 46: 377-365.

Walton, D.W.H. 1982. The Signy Island terrestrial reference sites: XV. Micro-climate monitoring, 1972-74. - British Antarctic Survey Bulletin. No. 55: 111-126.

Whitfield, D.W.A. 1977. Energy budgets and ecological efficiencies on Truelove Lowland. - In: Bliss, L.C. (ed.) Truelove Lowland, Devon Island, Canada: a high Arctic ecosystem: 607-620. University of Alberta Press, Edmonton.

Table 1. Annual weight losses of various litters measured and predicted from the simulated microbial respiration (from Flanagan & Bunnell, 1980)

Research area	Substrate	Weight loss (% of initial weight)		Simulated as a percentage of measured
		Measured	Simulated	
Abisko, Sweden	Rubus chamaemorus leaves	32	23.3	73
Barrow, Alaska	Dupontia fisheri leaves	15	13.4	89
	Carex aquatilis leaves	14.6	13.4	
Moor House, United Kingdom	Calluna vulgaris shoots	15-20		
	Calluna vulgaris stems	8	7.1	92
	Rubus chamaemorus leaves	36-38	20.1	81

FIGURE LEGENDS

Figure 1. Abiotic analysis of tundra sites (from French, 1981), showing the distribution of sites along components I and II, indicating primary clusters. Arrows show the nearest linkages of 'outlier' sites. Codes:- G: Glenamoy, Ireland; MH: Moor House, U.K.; H: Hardangervidda, Norway; K: Kevo, Finland; A: Abisko, Sweden; D: Devon Island, Canada; B: Point Barrow, Alaska, U.S.A.; T. Tareya, Taimyr, U.S.S.R.; M: Macquarie Island, Australia; SG: South Georgia, Antarctica; S: Signy Island, Antarctica; DK: Disko Island, Greenland; N: Niwot Ridge, Colorado, U.S.A.

Figure 2. Typical temperature gradients in air, snow, vegetation and soil - at Stordalen, Abisko, Sweden (after Rosswall, et al., 1975). Key: ● : 1320 h, 14 May 1972, snow-free; Δ : 1320 h, 15 May 1972, partly snow-covered; □ : 1320 h, 23 June 1973; o : 1320 h, 16 October 1972, partly snow-covered; + : 0100 h, 23 January 1973, snow.

Figure 3. Metabolic activity of cryptostigmatid mites from Antarctic and temperate systems in relation to temperature (from Block and Young, 1978).

Figure 4. Habitat characteristics and organism response (after Southwood, 1977).

Figure 5. Field diet and potential prey of a mite predator (Gamasellus racovitzai) in an Antarctic terrestrial community (from Block, 1985).

Figure 6. Respiration rate of litter from Point Barrow, Alaska in relation to temperature and moisture (from Flanagan and Veum, 1974).

Figure 7. Arrhenius plots of log specific growth rate versus absolute temperature for two aquatic (♦ , Cytophaga and ● , Chromobacterium fluviatile) and two terrestrial (▼ , Corynebacterium and ■ , Candida sp.) micro-organisms (from Ellis-Evans and Wynn-Williams, 1985.

Figure 8. Maximum diurnal surface temperature range (°C) (within five-day blocks) in a moss bank at Signy Island over three years (from Walton, 1982).

FIG. 1

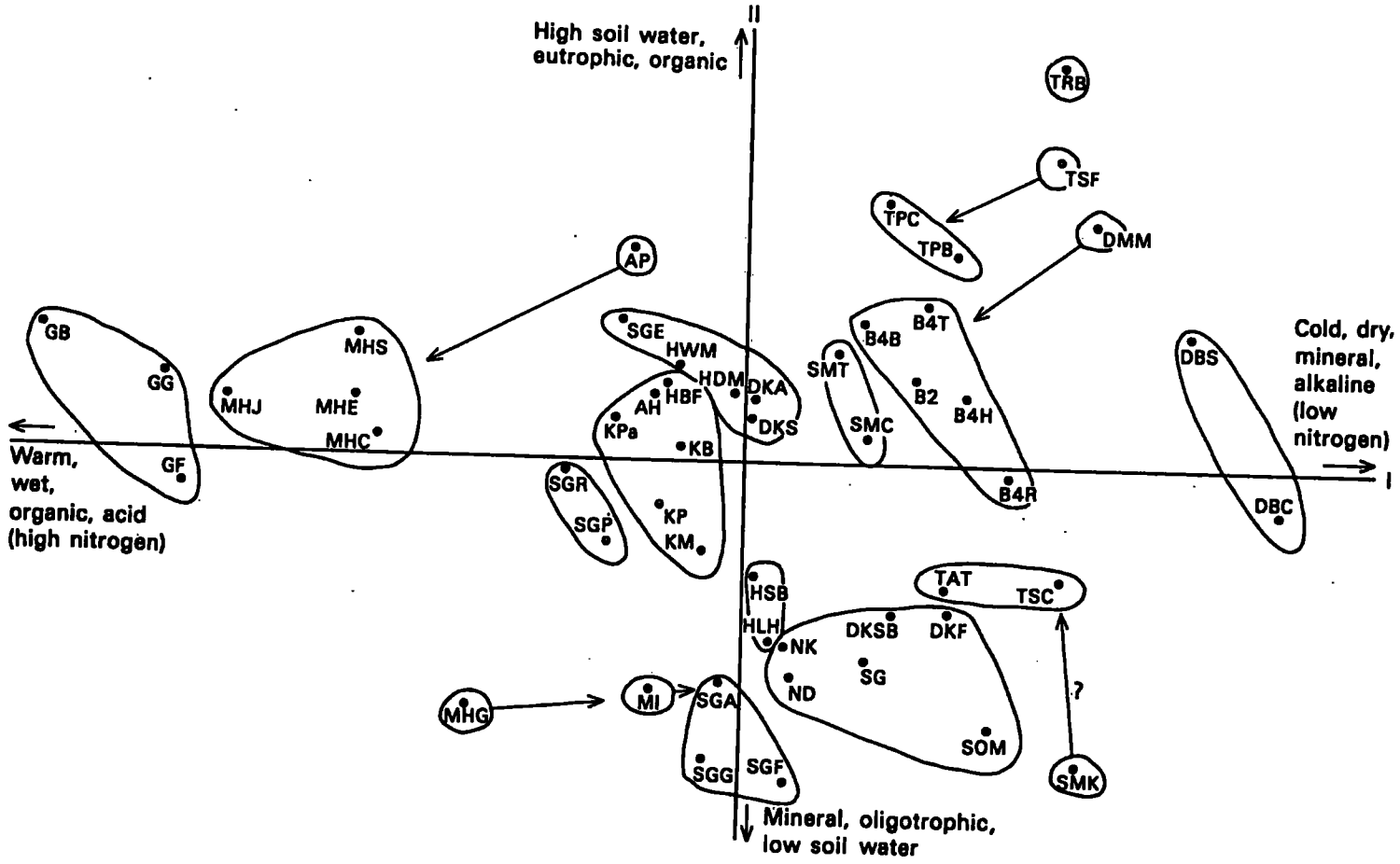

II
High soil water,
eutrophic, organic
TRB
TSF
TPC
TPB
DMM
AP
GB
GG
GF
MHS
MHJ
MHE
MHC
SGE
HWM
HDM
DKA
AH
HBF
KPa
KB
DKS
SMT
SMC
B4B
B4T
B2
B4H
B4R
DBS
DBC
Cold, dry,
mineral,
alkaline
(low
nitrogen)
I
Warm,
wet,
organic, acid
(high nitrogen)
SGR
SGP
KP
KM
HSB
HLH
NK
TAT
TSC
DKSB
DKF
SG
ND
SOM
?
SMK
MHG
MI
SGA
SGG
SGF
Mineral, oligotrophic,
low soil water

FIG. 2

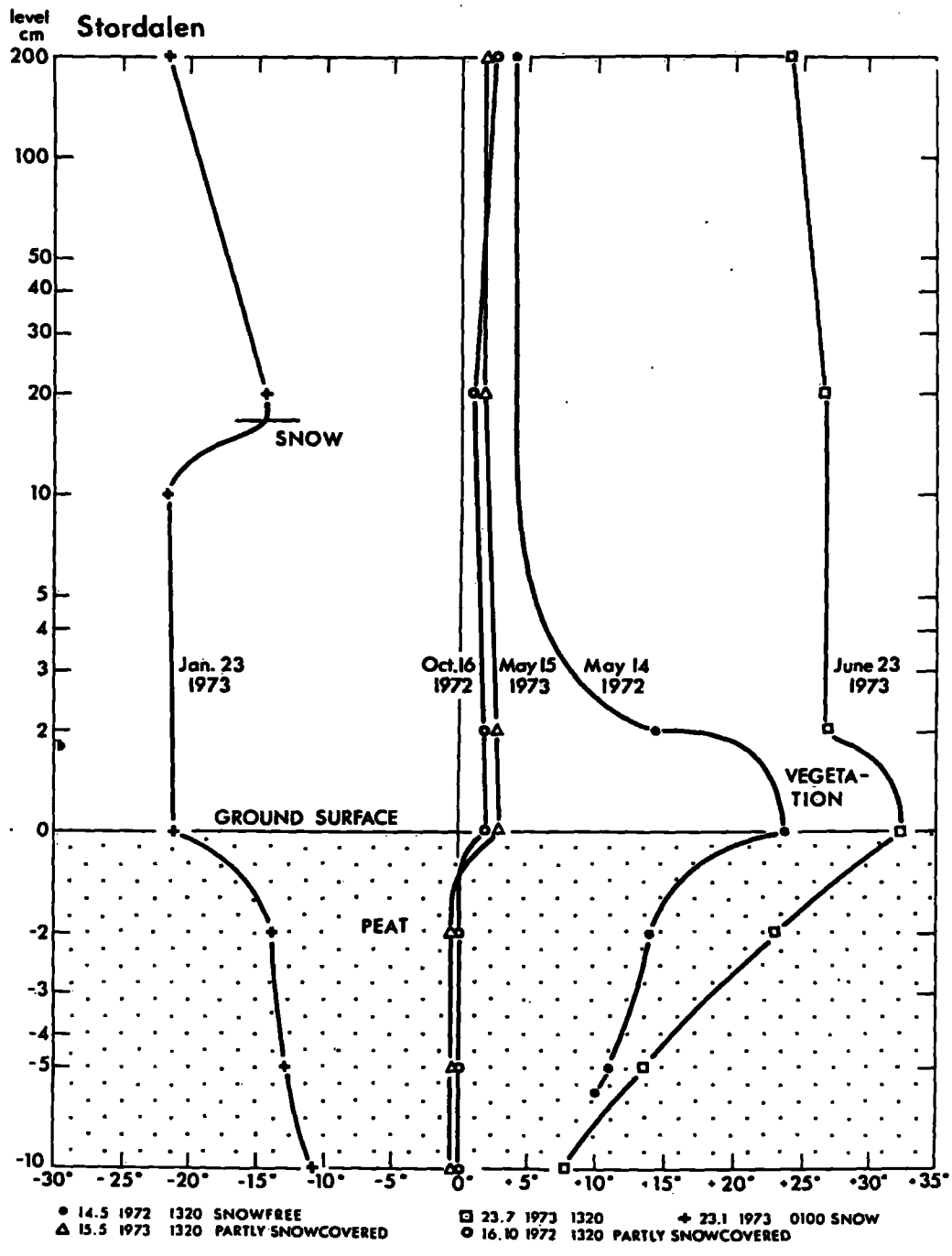

level cm
Stordalen
200
100
50
40
30
20
10
5
4
3
2
0
-2
-3
-4
-5
-10
SNOW
Jan. 23 1973
Oct.16 1972
May15 1973
May 14 1972
June 23 1973
VEGETA-TION
GROUND SURFACE
PEAT
-30° -25° -20° -15° -10° -5° 0° +5° +10° +15° +20° +25° +30° +35°
● 14.5 1972 1320 SNOWFREE
△ 15.5 1973 1320 PARTLY SNOWCOVERED
□ 23.7 1973 1320
○ 16.10 1972 1320 PARTLY SNOWCOVERED
+ 23.1 1973 0100 SNOW

FIG. 3

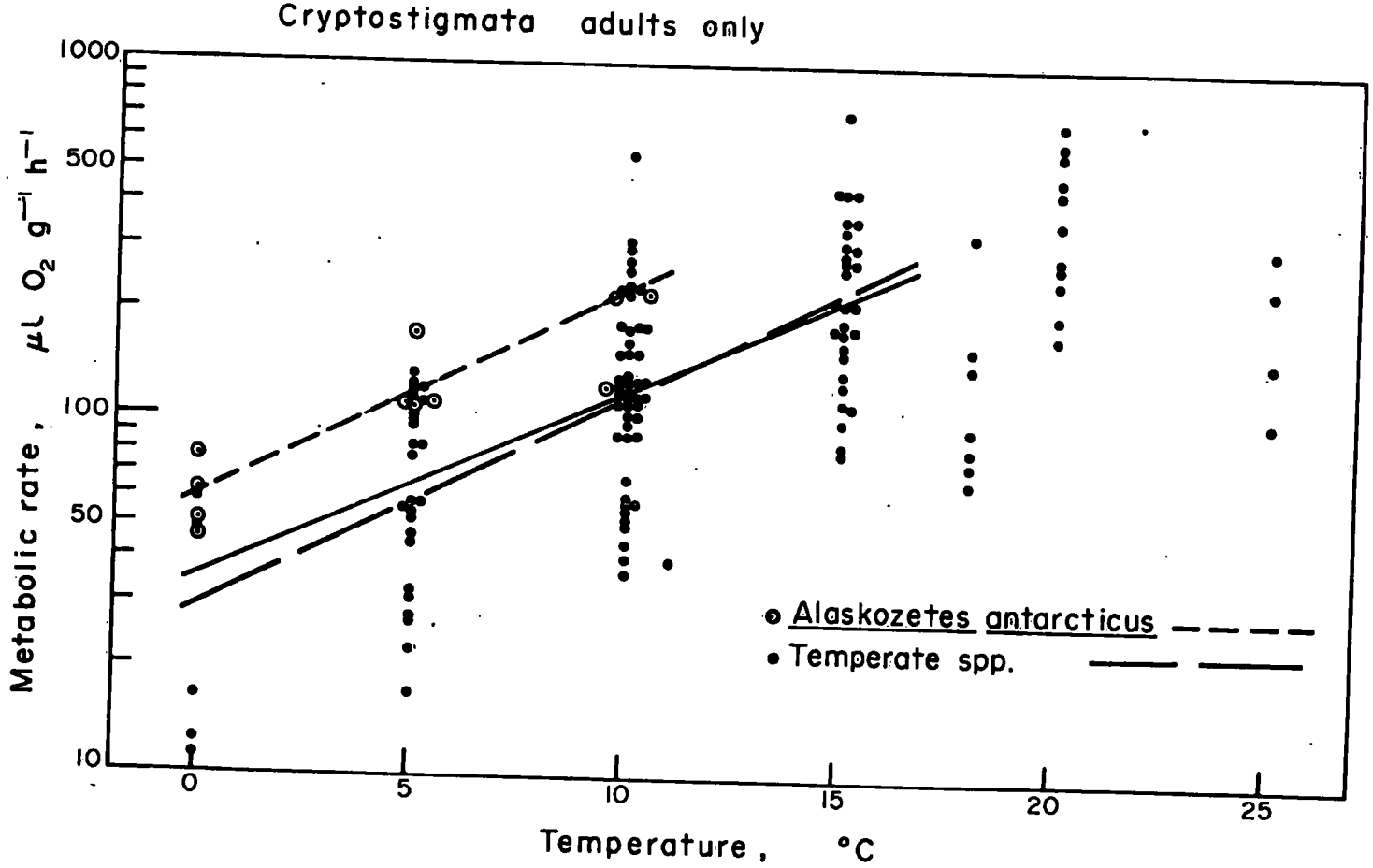

Cryptostigmata adults only
1000
500
100
50
10
Metabolic rate, µl O_2 g^{-1} h^{-1}
0
5
10
15
20
25
Temperature, °C
Alaskozetes antarcticus
Temperate spp.

FIG. 4

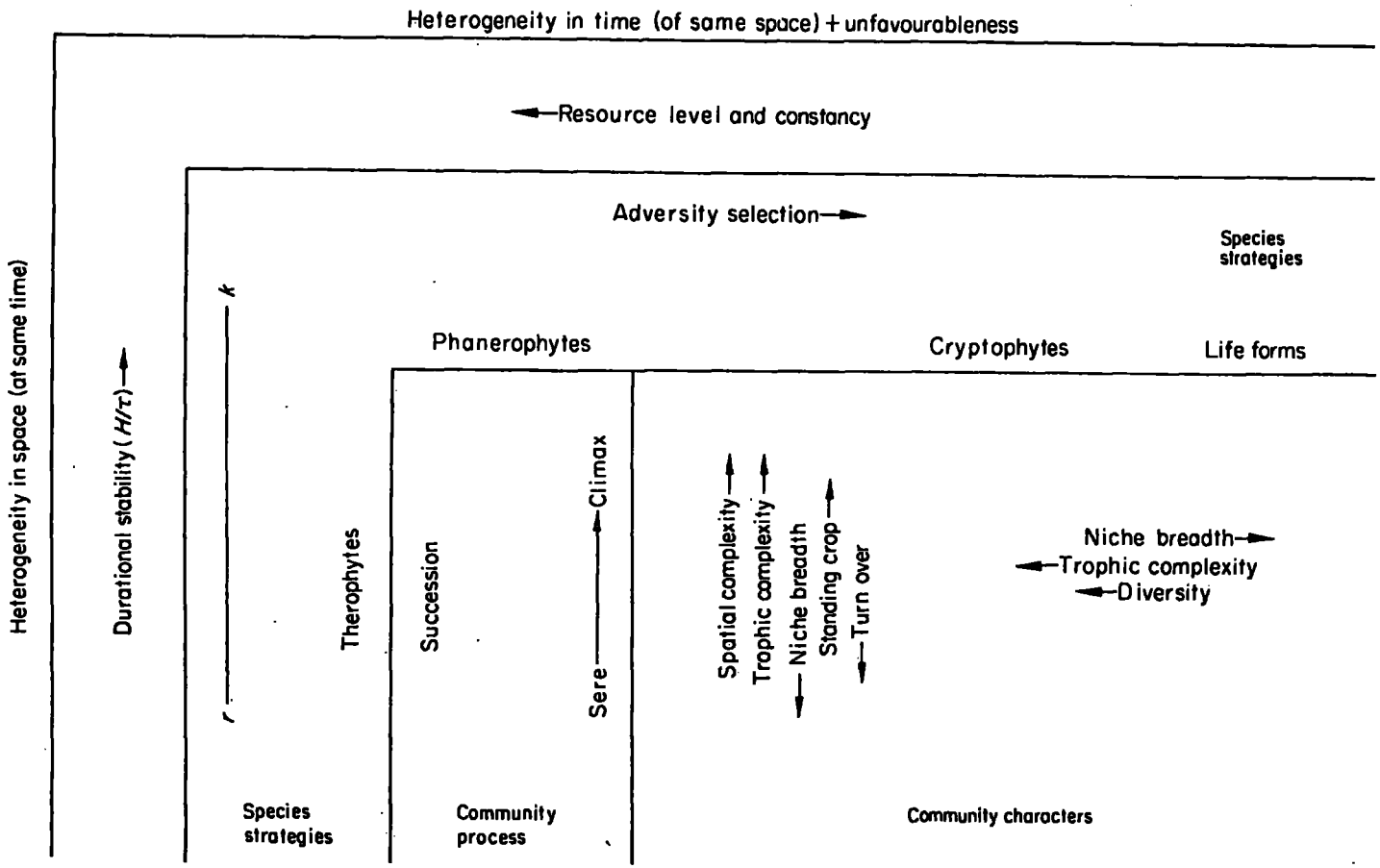

Heterogeneity in time (of same space) + unfavourableness
Resource level and constancy
Adversity selection
Species strategies
Heterogeneity in space (at same time)
Durational stability (H/τ)
k
r
Therophytes
Phanerophytes
Cryptophytes
Life forms
Succession
Sere
Climax
Spatial complexity
Trophic complexity
Niche breadth
Standing crop
Turn over
Niche breadth
Trophic complexity
Diversity
Species strategies
Community process
Community characters

FIG. 5

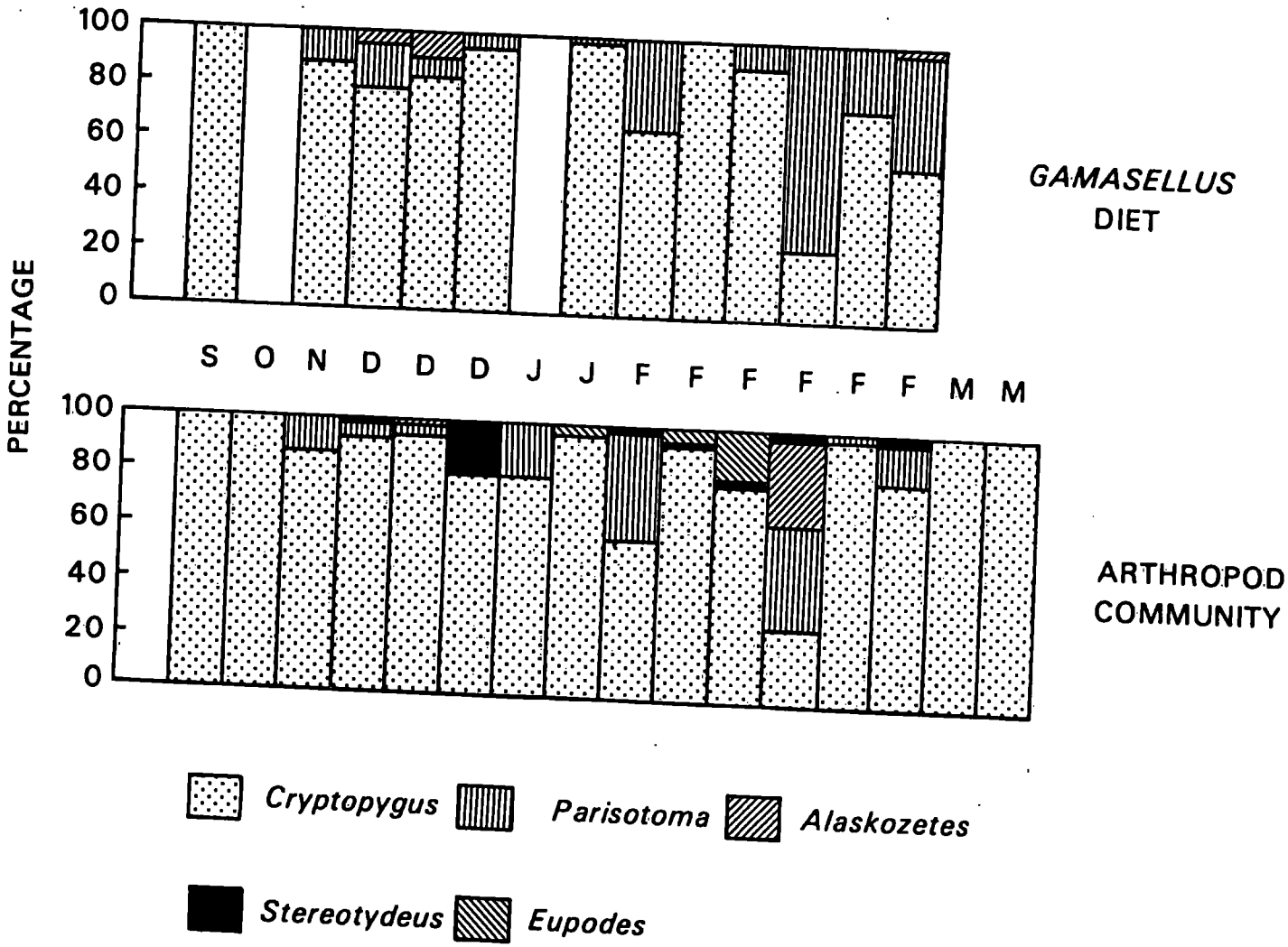
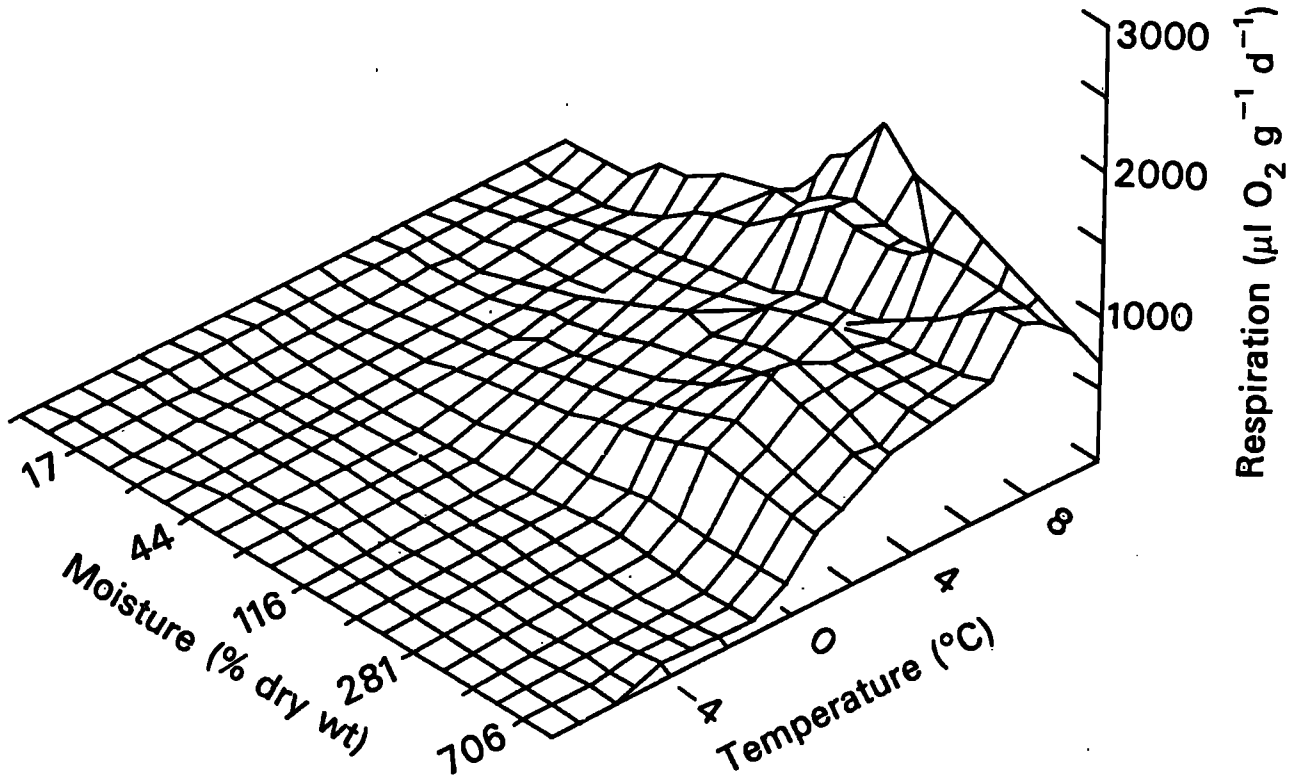

PERCENTAGE
100
80
60
40
20
0
S O N D D D J J F F F F F F M M
GAMASELLUS DIET
ARTHROPOD COMMUNITY
Cryptopygus
Parisotoma
Alaskozetes
Stereotydeus
Eupodes

FIG. 6


3000
2000
1000
Respiration (µl O_2 g^{-1} d^{-1})
17
44
116
281
706
Moisture (% dry wt)
-4
0
4
8
Temperature (°C)

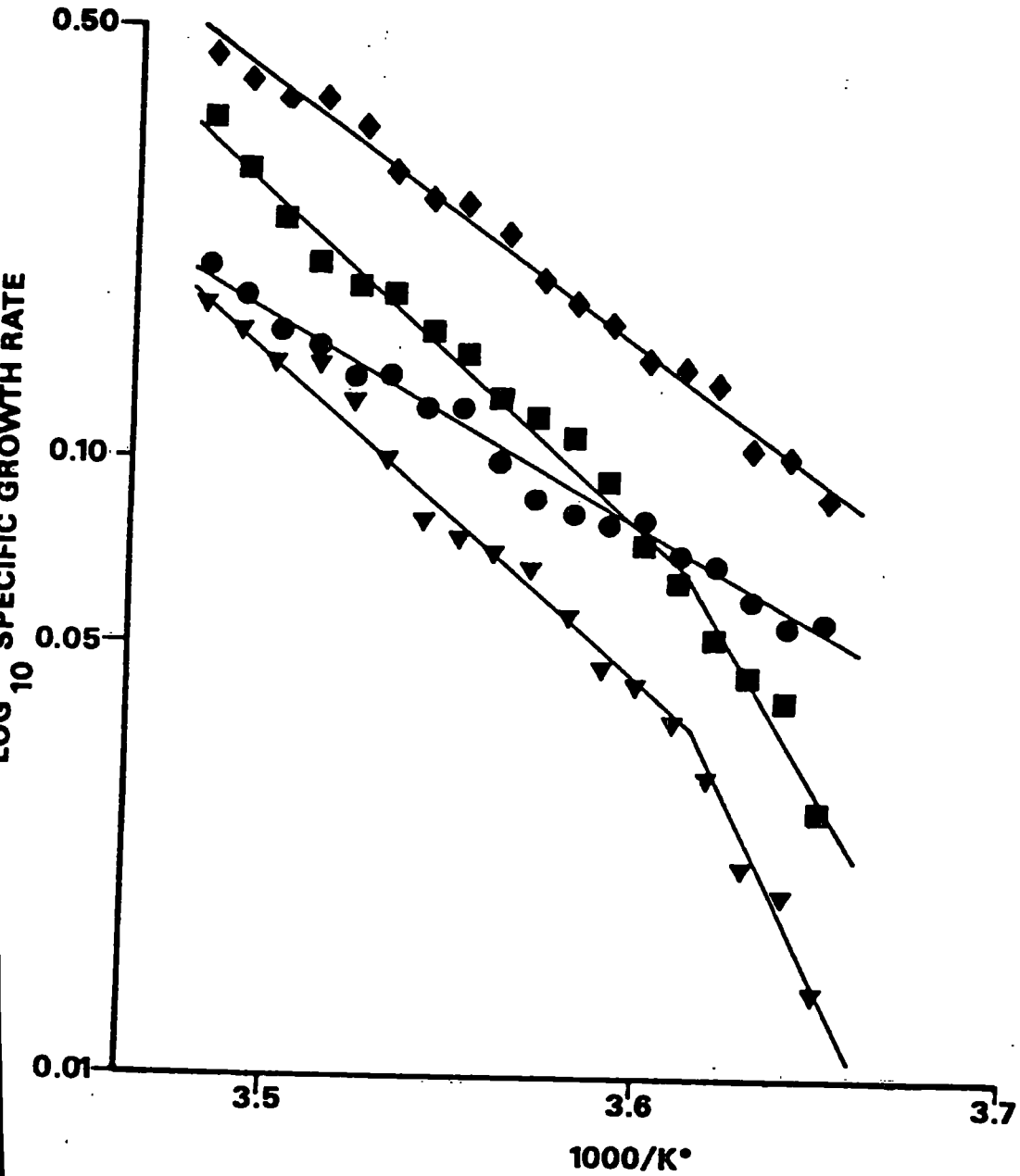
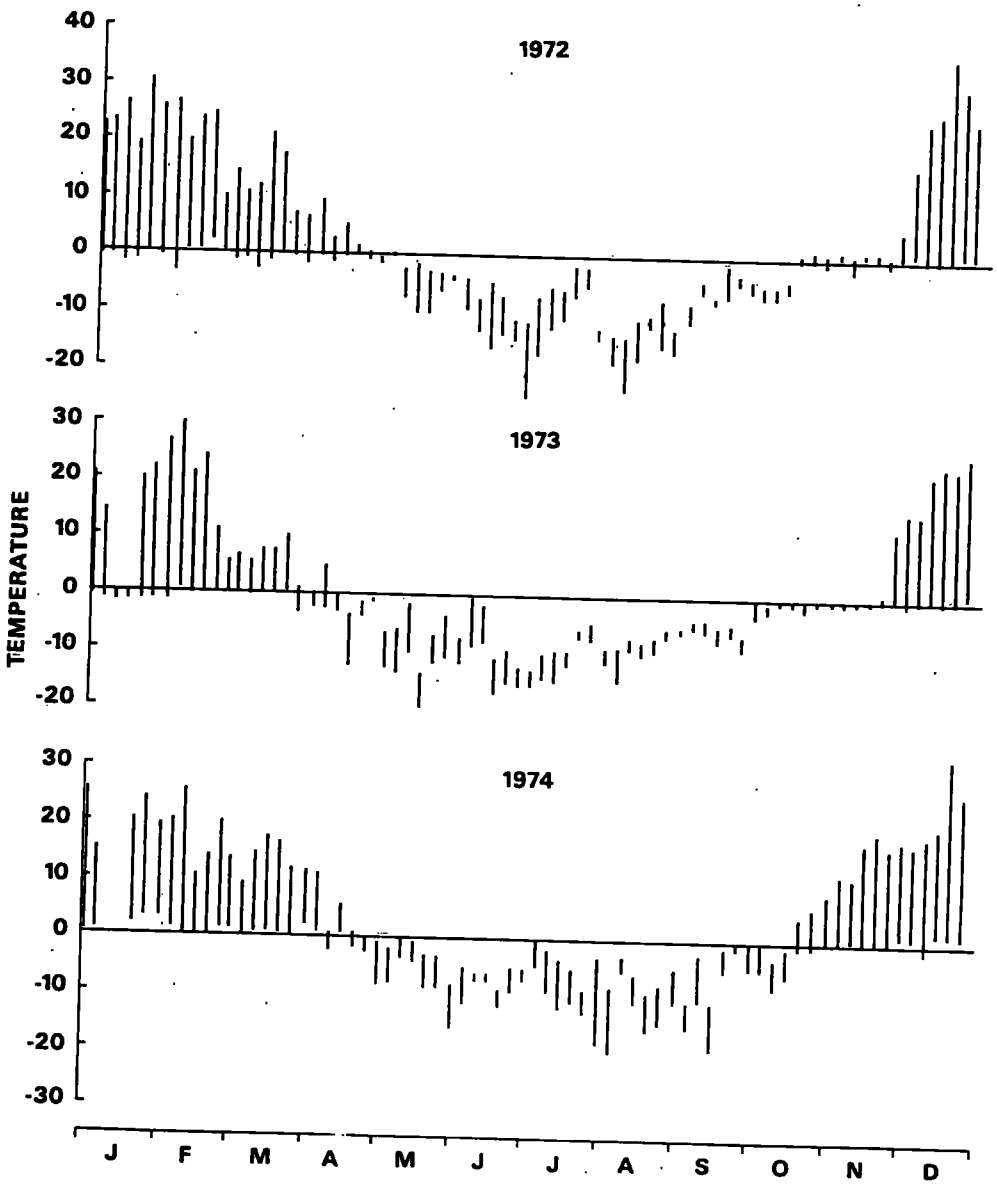

0.50
0.10
0.05
0.01
LOG 10 SPECIFIC GROWTH RATE
3.5
3.6
3.7
1000/K°

FIG. 8


1972
1973
1974
TEMPERATURE
40
30
20
10
0
-10
-20
-30
J
F
M
A
M
J
J
A
S
O
N
D

ADAPTATIONS OF POLAR ARTHROPODS TO COLD

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Running title: POLAR ARTHROPODS AND COLD

(Based on a paper presented at TEMP'85: Symposium on "Adaptations of invertebrates to extreme temperatures", University of Victoria, British Columbia, Canada; 5-10 August 1985).

(Submitted to Biological Reviews)

ABSTRACT

The paper reviews information on the ecophysiology of polar terrestrial arthropods both at low temperatures (0 to 10°C) and at sub-zero temperatures (<0°C). The review is restricted to freezing susceptible species (mainly micro-arthropods) of the maritime Antarctic.

Adaptations to low environmental temperatures in such invertebrates include the extension of locomotory activity to below 0°C with a concomitant lowering of the chill-coma temperature, the enhancement of metabolic rate (compared to temperate species over their normal temperature range), and the maintenance of feeding and assimilation below 5°C to produce a positive energy balance. These features, together with the short polar growing seasons, lead to prolonged development times and extended life cycles (up to 7 years in some instances).

Adaptations to potentially freezing temperatures result mainly from the requirement of individuals to overwinter several times. Avoidance of freezing by extensive supercooling is the main strategy. The degree of supercooling is influenced by several factors including food type and gut content of potential nucleators, possible cryo-protectants such as glycerol and body water composition.

Growth points for fundamental studies include (i) the relationship between melting point and supercooling point depression of a variety of solutions; (ii) the characterisation of the supercooling process itself for different species; (iii) the relative roles of moisture and temperature in cold hardiness, and (iv) the part played by dehydration and cold resistance mechanisms in survival. We also need to know more about organism recovery and resumption of metabolic and ecological activity after exposure to freezing conditions.

Finally, a plea is made for such cold adaptations to be viewed against a background of the life history strategy of the species, the evolution of successful options and the habitat templet, where A-(adversity) selected species appear to dominate in polar land communities.

KEYWORDS: Polar arthropods, low temperatures, sub-zero temperatures, adaptations.

LONG-TERM FLUCTUATIONS IN COLD HARDINESS OF TERRESTRIAL ARTHROPODS AT SIGNY ISLAND, ANTARCTICA

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ABSTRACT

Six species (two Collembola and four Acari) were studied at Signy Island in the maritime Antarctic over six years (1979-85). Monthly field samples were used to test individual supercooling ability (using a cooling rate of *c.* 1°C min^{-1}), and to monitor potential cryoprotectants by gas chromatography. All the species are freezing susceptible and utilize varying, and often expensive, supercooling to survive sub-zero temperatures.

Supercooling point distributions were bimodal in at least one monthly sample per year of each species. High group (HG) and low group (LG) individuals were separated at either -15° or -20°C. Mean supercooling points for HGs ranged from -4° to -19°C over the six species. The lowest mean LG supercooling points (together with the lowest individual supercooling point recorded) per species were:- *Cryptopygus antarcticus*: -27° (-38°C); *Parisotoma octooculata*: -19° (-22°C); *Gamasellus rocovitzai*: -30° (-32°C); *Alaskozetes antarcticus*: -34° (-38°C); *Stereotydeus villosus*: -25° (-31°C); *Nanorchestes antarcticus*: -24° (-37°C). The largest numbers of LG animals occurred in early winter samples (May and June) concomitant with a decline in mean LG supercooling points. This was followed by a rise in LG (and HG in some species) supercooling points during spring and early summer associated with an increased proportion of the monthly sample in the HG. Large shifts in the distribution of individual supercooling points within the samples accompanied these seasonal changes in cold resistance. *G. racovitzai*, which did not form a LG in summer, became bimodal in winter, and this was especially evident in its deutonymphal stage.

Assays of the polyols and sugars contained in the haemolymph extracts showed that glycerol and glucose were present in all six species, whilst fructose, ribitol, inositol and mannitol were also detected. Seasonal variations were found in the concentrations of some of these compounds. In general, higher concentrations of polyols (in particular glycerol, but also mannitol) occurred in winter compared with summer animals, whereas a trend towards the reverse was observed for the sugars especially glucose. In *A. antarcticus*, the concentrations of glucose and glycerol were negatively correlated indicating a direct link in synthesis between them. In the field, LG individuals of this species (adult and nymphs) may supercool to *c.* -25°C without significant quantities of glycerol being present. Below this temperature, there is a positive correlation between the lowering of the LG supercooling point

(y) and increasing glycerol concentration (x) as $y = -24.30 - 0.55x$ (r^2: 0.88; n: 12) up to *c.* 20 µg glycerol mg^{-1} f.w. Although concentrations in excess of this value are found in winter samples, they do not result in further depression of the LG supercooling point. This suggests that glycerol accumulation may proceed beyond the requirements for supercooling point depression in this species under such environmental conditions.

The annual temperature cycle for a typical soil surface habitat at Signy Island shows that weekly mean temperatures were not below -16°C, and that -27°C was the extreme minimum in the months of May and June in some years. It may be concluded that all the species investigated are sufficiently cold hardy (in terms of their LG supercooling points) to survive such sub-zero conditions, and on occasions, lower temperatures. However, the fauna must also be able to survive high summer temperature extremes of around 20°C with weekly mean temperatures of *c.* 5°C.

ARTHROPOD COLD HARDINESS: THE EVIDENCE FROM ANTARCTICA

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Running title: ARTHROPOD COLD HARDINESS: THE EVIDENCE FROM ANTARCTICA

(In preparation for submission to Cryobiology)

ABSTRACT

Cold hardiness studies on species of micro-arthropods from the maritime Antarctic have concentrated on the determination of their supercooling ability, and the environmental factors which influence it, with the implicit assumption that the extent of undercooling largely determines their survival in a polar environment. A synthesis of field and laboratory studies is presented, with the aim of evaluating the relationship between supercooling capacity and survival in two principal species: the cryptostigmatid mite Alaskozetes antarcticus and the collembolan Cryptopygus antarcticus.

The results of experiments which investigate long-term survival under constant sub-zero conditions are presented. They show that survival is highly correlated with supercooling capacity. Summer animals exhibited short-term modulations in survival corresponding to field temperature conditions. Two-step survivorship curves reflect inherent bimodality in supercooling point distributions. Winter samples (Alaskozetes) showed extensive survival ability in such experiments, with little variation arising from collection date. Samples with median supercooling points of c. -30°C, showed 81% (-10°C) and 52% (-15°C) survival after 250 days. At -20°C, 73% of the adults of this species survived for 100 days.

By comparison, Cryptopygus shows a more labile response to field temperature changes, with changes in supercooling capacity corresponding to observed activity in the field, during transient winter thaws.

It is concluded that the measured supercooling point is a meaningful determinant of cold hardiness in such polar species, as it represents the lower lethal temperature under the experimental conditions. Their survival ability appears to exceed that demanded by average winter temperatures in their habitats. Discussion explores the factors affecting nucleation and places these results in a wider context.

Fauna

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and
W. C. BLOCK

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Chapter 6

Fauna

INTRODUCTION

The account of the Leicestershire fauna in the Scientific Survey of Leicester a District published by the British Association in 1933 refers to the incompleteness the two previous accounts, that in *The Victoria County History* (1907) and that Horwood in the British Association's handbook for the same year. It later apologiz for its own disconnected and incomplete nature. The intervening four decades ha witnessed a dramatic increase in popular interest in natural history and a comme surate increase in our knowledge of some aspects of the fauna of the county. Howev most effort has been concentrated on the more popular groups, such as mamma birds, beetles and butterflies, and until recently little has been published on grou other than these. In the notes that follow we have had to rely heavily on the knowled and experience of a number of Leicestershire naturalists, to whom acknowledgme is made at the end of this chapter.

The present state of knowledge of the Rutland fauna is such that we have ha regretfully, to omit any reference to it in this account. MacQueen (1970) contai a good up-to-date list of Lepidoptera found in the vicinity of Uppingham, and t publications of the Rutland Natural History Society, which is engaged in acti fieldwork and recording, are a useful source of information on vertebrates.

URBAN AND SUBURBAN AREAS, SEWAGE FARMS AND DISUSED RAILWAYS

The fauna of urban areas is a widely neglected topic but enough is known about th of Leicester to indicate its interest. Even the city centre has characteristic speci the feral pigeon for instance, restricted to areas where public and commercial buil ings provide suitable nesting sites, and accompanied by its host-specific flea *Cera phyllus columbae*. Swifts nest in the older hosiery factories and kestrels on the cathed

igure 33. Leicestershire: built-up areas, canals, reservoirs and disused railway lines.

spire, the tower of St Peter's, Highfields, and, further out, at the Aylestone gaswork Kestrels, like tawny owls in the inner suburbs, rely much more heavily than rur representatives of the species on small birds, particularly house sparrows, for foo From time to time large roosts of pied wagtails occur in the city centre and in 19 the black redstart was discovered to be breeding at Aylestone power station.

Of the mammals in the city centre little is known except that brown rats and hou mice certainly occur. Bats may be seen hawking for prey in parks and squares le than a mile from the Clock Tower and amongst those identified are pipistrelle, con mon long-eared and noctule.

The city no doubt houses a large and varied invertebrate fauna but only tho species of unusual appearance or supposed economic importance come to the noti of the naturalist. In the first category are wood-wasps from timber yards, pa ticularly *Sirex gigas* and *S. noctilio*, and immigrant species of hawkmoths such as t two silver-striped hawkmoths *Hippotion celerio* found by small boys in Septemb and October 1963 not far from the centre. There is also the exotic fauna associate with imported fruit and particularly with bananas. The warming rooms of the banar importers harbour a wide range of species including the cosmopolitan cockroach *Periplaneta americana* and *P. australasiae*, *Nyctibora laevigata* and *Pelmatosilpha larifu* from the West Indies and *Leucophaea maderae*, *Henschoutedenia tectidoma* and *flexivitta* from tropical Africa. Altogether over 14 species have been recorded. Al represented is the awesome tropical African tettigoniid *Cosmoderus maculatus*, a five other species of tettigoniids of more conventional appearance, includi *Nesonotus tricornis*, *N. denticulatus* and *N. superbus*. Amongst spiders frequently import are the tropical crab spider *Heteropoda venatoria* and a number of mygalomorp including *Psalmopaeus cambridgii*. In addition the warming rooms have at tim supported a flourishing population of the theridiid spider *Theridion tepidariorum* a both our largest British spider *Tegenaria parietina* and its relative *T. pagana* ha been found. Vertebrates imported alive with fruit have included the West Afric dormouse *Graphiurus crassicaudatus* and the geckos *Sphaerodactylus argus* and *Tarento mauretanica*.

In the second category are pest species such as the mealworms *Tenebrio molitor* a *T. fuscus*, the source of whose regular occurrences is probably the nests of hou sparrows. Other native species of interest found in the city are the churchyard bee *Blaps mucronata*, and its predator *Sphodrus leucophthalmus* and two uncomm spiders, *Zelotes rusticus*, found in the Museum basement and only once elsewhere Leicestershire, on a rubbish tip at Shepshed, and the agelenid *Tegenaria agrest* a colony of which was found in a back garden at West Humberstone in 1960.

Parks are a feature of Leicester and recent bird censuses give some idea of how mportant they are as habitats, as also are suburban areas with large, mature gardens. Spinney Hill Park, which is 13.8ha (34 acres) in extent and situated in a densely ɔopulated part of the city, was found by H. Bradshaw in 1960–8 (Bradshaw, 1969) o have 17 breeding species including carrion crow, wood pigeon and spotted lycatcher. A count of cock blackbirds in Abbey Park on 4 March 1966 totalled :19 individuals, and 49 bird species have been noted in Knighton Park on the outhern outskirts of the city. A request made by Leicester Museum in 1966 for nformation about birds visiting gardens within the built-up area yielded records of 55 species including wintering blackcaps and breeding goldcrest, linnet and nut- ıatch. Collared doves were first recorded as breeding in Leicestershire in a suburban ;arden at Stoneygate in 1965. Finally, an intensive survey of the breeding species of ı small area of Birstall on the northern outskirts of Leicester which is being under- aken by M. D. Kirkman has revealed 21 species at densities considerably in excess ıf those previously recorded for suburban areas.

Although there is insufficient space here to discuss many other aspects of the fauna ıf built-up areas of the county it is perhaps worth mentioning that melanic forms ıave been recorded in over 30 species of moths and that in the classic example of ndustrial melanism, the peppered moth *Biston betularia*, the melanic form *carbon- ria* occurs ten times more often than the normal form. The large elephant hawkmoth s exceedingly numerous in some years and poplar, lime and eyed hawkmoths occur egularly in the suburbs. Amongst the curiosities recorded are the large amphibious eech *Trocheta subviridis* of which there are nearly a dozen records, mainly from ;ardens, and the land planarian *Microplana terrestris*, a specimen of which was found n a garden at Rothley in November 1963.

Outside the built-up areas of Leicester and towns and villages in the county the ctivities of man still dominate the landscape and even the most unprepossessing- ɔoking areas have their interest. The old-fashioned sewage farm at Beaumont Leys, n the outskirts of Leicester, was for many years a mecca for birdwatchers. Breeding pecies recorded by Mason and Pickering (1968) between 1944 and 1964 included nallard, lapwing, redshank, snipe, tawny, barn and little owls, jay and whinchat, nd in the years following the closure of the farm in 1965 the densely vegetated lter beds were a favourite hunting ground for kestrels, of which up to 14 were seen t one time. Rubbish tips are also of interest. During the day they are a favourite eeding ground for the many thousands of gulls that are now resident in Leicester- hire throughout the year, and at dusk the populations of the house cricket *Acheta omestica* which many of them support attract several species of bats.

Disused railway lines, particularly those in the east of the county, have proved fruitful hunting ground for the lepidopterist. Buckler (1954) recorded the hedg brown from a cutting at Medbourne and the chequered skipper at Marefield an more recently H. Bradshaw has listed 18 species of butterflies in the deep cutting a Thorpe Satchville, including ringlet, green hairstreak, duke of burgundy and ding and grizzled skippers. These cuttings are also notable for large populations of burne moths, and Davey (1967) recorded in the early 1960s the aberrations *flava* an *cytisi* of the six-spot burnet in the cutting at East Norton which is now, alas, a rubbis tip. The rose chafer *Cetonia aurata* has been found on a number of occasions on railwa banks and one of the two known localities in the county for the tiger beetle *Cicinde campestris* is a railway cutting in the north-east. The cuttings are also good places t see grass snakes.

FRESHWATER

There are five main freshwater habitats in Leicestershire: springs, streams and river canals; ponds; flooded pits and quarries; and reservoirs. In addition there are th spring-fed and river valley marshes, in some ways intermediate between this habita category and farmland. Together these habitats have a rich and varied freshwat fauna. The streams are of two main types, those that drain the hard rocks of Charn wood Forest and those of the rest of the county. The former tend to be fast-flowin with a stony bottom, the latter more sluggish and muddier. There is little differen between the slower stretches of the rivers and the canals except that the latter tend t be less polluted, either by agricultural or industrial effluent. The commonest type o standing water body in many parts of Leicestershire is the field pond, but the coun is well endowed with ornamental lakes, flooded gravel pits and quarries. The on natural water body of any size is Groby Pool, on the edge of Charnwood Forest, b there are nine reservoirs, of which the Eye Brook Reservoir, straddling the coun boundary in the south-east, is the largest.

The fauna of springs has been little studied but there is a record of the planaria *Crenobia alpina* from a spring-fed village pump at Bushby, and the water crick *Velia caprai* is commonly found on the water surface at springs and downstream them.

The water shrew is found throughout the county in the neighbourhood of strear and occasionally in marshy areas. There are isolated sightings of otters every ye from rivers, canals and reservoirs, and they have bred sporadically until recently o

ributaries of the River Wreake in east Leicestershire. A single specimen of the American mink shot on the River Wreake at Thrussington in 1959 was almost certainly a recent escape from a fur farm, and the species has not established itself n the wild as it has done in parts of neighbouring counties. The kingfisher population as now recovered from the drastic effects of the severe winter of 1962–3, but the improvement' of streams, by straightening and removal of waterside trees and other egetation, must be restricting its choice of feeding and nesting sites and it is likely hat the species will become less common in the future. Of the kingfisher's potential rey the three-spined stickleback is ubiquitous, and there are a dozen or so recent ecords of the ten-spined stickleback from streams and pools, but minnows are now urprisingly patchy in occurrence. Water voles occur along most of the larger water ourses and around fishponds and lakes. They do not tolerate continual disturbance nd are therefore generally absent from built-up areas, with the result that there are number of isolated populations on the larger streams flowing into Leicester.

The water rail is much commoner than its skulking habits lead one to suppose, and has been seen occasionally on the River Soar near to the centre of Leicester. The River Soar, though polluted in places, does support good numbers of fish, mainly yprinids such as roach, rudd, tench and carp. Perch also occur and local heating of ne water by power stations keeps some species active throughout the winter. Cooling ater from Leicester Power Station also has marked effects on the invertebrate una (Markowski, 1959).

The canals of Leicestershire and Rutland provide slow-moving or in some cases lmost static water subject to very different patterns of use and maintenance. The ldest, the Charnwood Canal, is dry throughout most of its length. The Oakham anal, purchased and put out of action by a railway company over a century ago, ill has several stretches containing water, in most cases invaded by dense reedswamp. he Grantham Canal, closed to traffic in the 1930s, contains water throughout, and ne Ashby and Grand Union canals still carry traffic and are subject to regular redging. Between them they provide a wide range of conditions. Extensive beds of mmon reed on the Grantham Canal support one of the largest populations of reed arblers in the county, and sedge warblers nest along the banks of all the canals. At ylestone, Kilby and Foxton in the south of the county the Grand Union Canal is e major local spawning site for the common toad, and grass-snakes may be seen ar any of the canals. Pike are often numerous, standing guard in the deeper water, nd bream and chub also occur. There is a rich invertebrate fauna associated with e water, towpaths and boundary hedges. At a field meeting of the Conchological ciety on the Ashby Canal at Higham-on-the-Hill in 1967, for example, a prolific

freshwater fauna was recorded including *Viviparus viviparus, Valvata cristata, Limnae auricularia, Unio pictorum, U. tumidus, Anodonta cygnea, A. anatina, Sphaerium rivicol* and *Dreissena polymorpha.* Together with land species from the adjacent banl which included *Carychium minimum* and *Retinella radiatula,* and a marsh fauna in silted-up winding hole, which yielded *Vertigo antivertigo, Planorbis leucostoma, Succine pfeifferi* and three species of *Pisidium,* an area of less than 50m² (538ft²) produce 56 species of molluscs (Kerney, 1967). Few aspects of the insect fauna have bee studied in depth, but the canals are the best places in Leicestershire to see dragonflie Males of *Aeschna cyanea* and *A. grandis* patrolling their territories are a common sigl in late summer and the emperor dragonfly *Anax imperator* was proved to breed, f the first time in the county, on the Ashby Canal in the early 1960s. Martin (197 recorded the corixid water bugs *Callicorixa praeusta, Sigara falleni* and *S. fossaru* in abundance in canals, and the water measurer *Hydrometra stagnorum* is widespre at the outer edge of the reedswamp.

Sponges are common on lock walls, bridges and revetments throughout the can system and amongst the freshwater crustaceans are two invasive species of particul interest. One, *Crangonyx pseudogracilis,* is a North American species recently introduc and now widespread in a variety of aquatic habitats in Leicestershire and elsewhe in the Midlands. The second, *Corophium curvispinum* var. *devium,* was known previous in this country only from a single record on the River Avon at Tewkesbury un recorded by Moon (1970) in considerable numbers along the Grand Union Can throughout south Leicestershire. The invasion of freshwater by this one representati of a genus otherwise confined to brackish or marine waters may in time come parallel that of the snail *Potamopyrgus jenkinsi,* a brackish water species first record inland in 1893 and now found throughout the river systems of the Midlands, inclu ing Leicestershire, from sources to the sea. The occurrence of the water hog-lou *Asellus meridianus* in isolated parts of the Oakham Canal, while *A. aquaticus* is t typical canal species, may be evidence for the invasion of the Midlands by the lat species along the canal system a century or more ago. There are three canal tunn in Leicestershire and two of these, at Saddington and Husbands Bosworth, harbo colonies of Daubenton's bats with their characteristic nycteribiid fly ecto-parasit Natterer's bats also occur at Saddington. In all the tunnels the pear-shaped e masses of the cave spider *Meta merianae* can be seen in considerable numbers.

A recent survey of field ponds in north-east Leicestershire by Jones (1971) e phasizes the rapid disappearance of this habitat with changes in agricultural pr tices. Most of the ponds were excavated at the time of the enclosures to prov water for stock, and as stock farming becomes uneconomic, or water is piped

roughs, the ponds become obsolete and are being allowed to dry out or are filled in. Some aspects of their fauna have recently been studied in some detail in Leicestershire. The life cycle of the mayfly *Cloeon dipterum* in farm ponds in the south-east of the county was described by Brown (1961), and Martin (1970) recorded 13 species of corixid water bugs from ponds, the commonest being *Corixa punctata*, and discussed factors reducing competition between species sharing the same pond. Ponds are of paramount importance to the amphibians found in the county. Bell (1970) lists 93 spawn sites for the common frog and of these, 63 are ponds. Ponds similarly account for 11 out of the 23 spawn sites listed for the common toad, 37 out of the 57 spawn sites listed for the smooth newt, and 15 out of the 20 spawn sites listed for the crested newt. Records of fish from field ponds are few, although crucian carp are occasionally found, as at Sileby.

Flooded mineral workings, some of considerable antiquity, occur throughout Leicestershire. The 'granite' quarries on the edge of Charnwood Forest and in the isolated outcrops of syenite in the south-west of the county are steep-sided, often very deep and they have a lifeless look about them. However, collections made recently by members of the Leicester Underwater Exploration Club in Stoney Cove showed sponges, *Potamopyrgus jenkinsi* and *Dreissena polymorpha* to be abundant at depths of 10–14m (33–46ft) and present to 30m (98ft). Perch and crayfish occur in other quarry pools.

A contrast is provided by the rich fauna of a pit in the Lower Lias Limestone at Kilby Bridge, long ago worked-out and flooded. Recorded so far are *Hydra*, flat-worms, leeches, a variety of crustaceans including *Daphnia*, ostracods, *Crangonyx pseudogracilis*, *Argulus*, *Asellus aquaticus* and crayfish, six species of freshwater molluscs, at least 13 species of dragonflies, including one, *Sympetrum sanguineum*, recorded new to Leicestershire here in 1953 and not known to occur elsewhere in the county: caddis flies, mayflies, at least six species of water beetles, and phantom and chironomid midges. The pit is particularly rich in water bugs. The water stick insect *Ranatra linearis* is known from no other locality in the county and the corixid *Cymatia bonsdorffi* from only one. There are in addition eight species of corixids, one species of notonectid, one species of pond skater and the minute water cricket *Microvelia reticulata*. Amongst the vertebrates found are toads, for which this is a spawn site, grass snakes, coot, moorhen and mute swan.

Mineral workings of a different kind are the sand and gravel pits which are now a conspicuous feature of the Soar and Wreake valleys to the north of Leicester. Their chief interest is to the ornithologist since the pits when first excavated and still dry have provided suitable nesting sites for a number of birds that did not previously

breed in the county. Examples are the little ringed plover which first bred in 195 ringed plover in 1965, and more recently common tern and oystercatcher. Olde flooded pits, especially those with long spits and good vegetation cover, provide i their turn nesting sites for great crested grebe, tufted duck and even, on one occasio at Wanlip, pochard. Elsewhere in the county the smaller sandpits provide almo the only nesting sites for colonies of sand martins.

Reservoirs are the most extensive, and in many ways the most important, ope water habitats in Leicestershire. The oldest is Blackbrook Reservoir and the mo recent that at Staunton Harold. The reservoir under construction at Empingham i Rutland will be the largest in England, with a surface area of three thousand acre but at present that of most interest to Leicestershire naturalists is the Eye Broo Reservoir, constructed in the early 1940s to supply drinking water to the steel tow of Corby in Northamptonshire. An excellent illustrated account of its birdlife i given in Otter (1965). It is notable chiefly for duck in winter and waders on passag in spring and autumn. Up to 3,000 duck of a dozen species can be seen on a col January morning, including surface-feeding mallard, teal, pintail and shovele tufted, pochard and goldeneye amongst the diving ducks, goosander and occasiona smew for the sawbills and wigeon grazing on the margins. Nearly 30 species c waders have been recorded and rarities seen have included Temminck's stint, avoce and purple sandpiper.

The Leicestershire reservoirs, like others elsewhere in Britain, now carry in winte large numbers of roosting gulls, particularly black-headed gulls. Hickling (1967 details the changes that took place between 1953–4 and 1963–4 and gives a figure c 37,500 gulls for Eye Brook Reservoir for 1963–4. Reservoirs have not attracted a much attention from other naturalists as they have from ornithologists. There i however, a useful account of the molluscs of Cropston Reservoir by Cummins an Rundle (1968) based on an examination of the sediments uncovered by drainage i 1965. They recorded 13 species of gastropods and six species of bivalves. Marti (1970) records the occurrence of seven species of corixids in reservoirs, of which on *Micronecta minutissima*, was found nowhere else. The margins have proved on occasio fruitful hunting grounds for the entomologist. The weevil *Bagous lutosus*, previousl known in Britain from only two specimens, was found in the spring of 1940 i thousands amongst reed litter on the margin of Saddington Reservoir. Similarly th carabid beetle *Bembidion obliquum*, once thought to be very rare, is now known t occur in large numbers at all the Leicestershire reservoirs. The margins of Grob Pool, the only large natural body of water in the county, have recently been inte sively studied for the first time and have yielded a beetle new to the county, th

nalachid *Anthocomus rufus* and a number of interesting spiders including *Eugnatha triata*, *Tmeticus affinis* and *Erigone vagans*.

The acreage of marshland in Leicestershire was never large and it shrinks every ear due to drainage and reclamation for arable farming. Snipe, once common in he county, have disappeared from many of their former breeding sites, as also have edshank. The invertebrate fauna has been little studied with the exception of the noths, beetles and spiders. H. A. Buckler and Dr A. A. Lisney recorded from Narborough Bog in the 1930s a number of species more typical of the East Anglian ens such as the round-winged footman *Comacla senex*, the southern wainscot *Leucania traminea* and the silver hook *Eustrotia uncula*. More recently S. R. Davey and P. H. Gamble have taken at light in the Soar valley at Barrow and Quorn respectively number of marshland moths new to the county including the stout dart *Spaelotis avida*, and the double-lobed *Apamea ophiogramma* (Davey, 1967).

ARMLAND

Eighty per cent of the land surface of Leicestershire is in agricultural use and of his, pasture forms rather more than half. The proportion of pasture to arable is onsiderably higher than the average for the east Midlands, but the figure still eflects a marked change in farming practice compared with 30 years ago (see Chapter 14, p. 326). Not only has there been a changeover from pasture to arable ith, as a result, the enlargement of fields and removal of hedges, but much of the asture is temporary and most of the remainder is 'improved' by the application f fertilizers or the use of selective herbicides. These changes have had a marked ffect on the numbers and distribution patterns of many forms of animal life.

An example is the yellow meadow ant *Lasius flavus*, whose characteristic aggrega- ons of hummock nests in rough grazing are now restricted to about half a dozen calities in the county, although they still survive in smaller numbers on railway nbankments. Similarly, undisturbed flood meadows where moles build fortresses accommodate their nests are only known today at Barrow-on-Soar, Narborough, uorn and Shepshed. The curlew still nests in rough grassland in the south-west nd north-east of the county but its status as a local breeding species is threatened by e continuing 'improvement' of such land. The barn owl has decreased in numbers suitable nesting sites in farm buildings are tidied up, and as ploughing of rough assland forces them to hunt along hedges and roadsides, sometimes with predictable d disastrous results. Where rough grassland is left undisturbed, as on reservoir

margins, field vole populations build up and kestrels, barn owls and, on occasio short-eared owls take advantage of the temporary abundance of prey. The elimina tion of scrub-covered corners and slopes is a practice that has had a drastic effect o the whinchat, once a common bird in east Leicestershire at least, but now ver sparingly distributed (Otter, 1965). Worse still is the elimination of hedgerow themselves, which has occurred on large estates in various parts of the county. Som idea of the possible effects on populations of common birds can be obtained from th results of British Trust for Ornithology census work carried out on farmland a Stoughton by members of the Leicestershire and Rutland Ornithological Societ In 1969 for example the hedgerows on 81ha (200 acres) of mainly arable land pr vided nest sites for the following number of pairs: turtle dove, 3; magpie, 3; wren, 1 mistle thrush, 1; song thrush, 16; blackbird, 42; robin, 15; whitethroat, 8; dunnoc 22; greenfinch, 3; linnet, 3; chaffinch, 8; and yellow hammer, 22. There were also i the survey area 13 pairs of skylarks and at least 69 pairs in all of 27 other species. Th most conspicuous hedgerow insects in recent years have often been the coloni larvae of small moths which strip the twigs of leaves. There has been no systemat work on the insect fauna of hedgerows in the county but casual collecting has yielde some species of interest. These include the striking cydnid bug *Sehirus bicolor*, whic feeds on white dead nettle, the leaf beetle *Cryptocephalus frontalis*, found on hawthor at Foxton, and the rare platystomid beetle *Platyrhinus resinosus*, taken from fungus o hedgerow ash trees in east Leicestershire.

Despite the generally depressing picture there are items on the credit side. Th only record of the yellow-necked mouse in Leicestershire during the last 40 yea is of one caught in a hedgerow at Queniborough in 1950, and in 1960, a dormous the first to be seen for over a century, was disturbed from its nest in a canalsi hedgerow at Dadlington. Similarly, harvest mice were found in a clover field Waltham-on-the-Wolds in 1964, the last previous record for the county being i 1889. Nests were later located in an adjacent hedgerow and the species turned u again in 1967 at Wymondham, where identifiable remains have occurred in o pellets, and in 1968 and again in 1970 in the Ulverscroft valley, in the heart Charnwood Forest, an area from which it had never before been reported.

Those hedgerows which survive support thriving populations of the common small mammals, as witnessed by the catches of domestic cats, a major predat where they occur. Other predators include weasels and stoats, both of which a widespread and relatively numerous in the county, although weasels probably ou number stoats by at least three to one. An interesting discovery made during the l decade is the surprisingly high proportion of stoats which assume a partially or alm

completely white winter coat at the autumn moult. Two almost pure white specimens were noted in the Fleckney–Saddington area in the spring of 1963, following the exceptionally cold winter, and others trapped by gamekeepers at Blaston and Rolleston in the intervening years show a complete gradation from a touch of white at the root of the tail to pure white except for tail tip and a little brown on the top of the head. The increase in arable farming may even have contributed to the apparent spread of one species, the muntjac, which can travel and lie up unnoticed in cereals. The first was seen at Lutterworth in 1954 and others have been reported on half a dozen occasions since in various parts of the county.

WOODLAND

Woodland accounts for only 2.3 per cent of the land surface of Leicestershire, only two other counties in England and Wales having less. That which exists is concentrated in three areas, Charnwood Forest, the Eye Brook valley and adjacent areas in east Leicestershire, and along the marlstone escarpment which strikes across the north-east of the county from Six Hills to Belvoir. Much of the woodland has been felled and replanted during the last 40 years, often with a marked change in character. However, the deciduous woodland that remains harbours a rich fauna and the mixed and coniferous woods which have been planted have their interest.

In a census carried out between 1960 and 1965 over 300 badger setts were located in Leicestershire, mainly in spinneys and woods, though some were in hedgerows or even out in the open in pits and quarries. Squires (1963) gives a detailed account of the dense population in Charnwood Forest, but the species is found throughout the rest of the county wherever lighter soils occur, and its presence is tolerated since badger digging is still actively carried on in some areas. The red squirrel is almost certainly now extinct in the county, the last authenticated reports being from Charnwood Forest in the late 1940s. The earliest record of the grey squirrel, spreading north from introductions in Bedfordshire and Northamptonshire, was in 1929, so the changeover has probably occurred in less than 30 years. An unexplained occurrence, however, is the persistence of the red squirrel flea *Monopsyllus sciurorum* on grey squirrels in Charnwood Forest until 1964. The dormouse, rediscovered in 1960, has been found on two occasions since in Owston and Launde Great Woods in the east of the county, but whether it will survive the forestry operations in progress at the former is doubtful.

A recent survey by the Loughborough Naturalists' Club of the plant and animal

life of Swithland Wood on the edge of Charnwood Forest gives some indication of th rich and varied breeding bird population that such deciduous woodland can suppor Nearly 40 species were found to be nesting in the wood proper with estimated popula tions for the 57ha (140 acres) of 150 pairs of starlings, 75–80 pairs of tree sparrow and robins, 50–60 pairs of blackbirds and blue tits, 46 pairs of willow warblers, an amongst the less common species, eight pairs of nuthatch, six pairs of woodcock, two three pairs of lesser spotted woodpeckers, two pairs of wood warblers and one pair c redstarts. Five species of tits, five species of warblers and all three woodpeckers ar recorded as breeding in Swithland Wood. Of the species mentioned, nuthatch an wood warbler are virtually confined to Charnwood Forest and the lesser spotte woodpecker is commoner there than elsewhere. The redstart is, however, widesprea wherever old trees provide suitable nest sites. For instance, Otter (1965) recorde singing redstart males at 90 localities in the east of the county in 1949. The sparrow hawk, once a widespread predator in wood and hedgerow, became extinct as breeding species in the late 1950s but bred again in 1969 and 1970 and now show signs of a return. Conspicuous by its absence from Charnwood Forest is the night ingale, a small population of which, not more than 20 pairs in all, breeds each summe in a group of east Leicestershire woods.

The felling and replanting of much of the county woodland has been of direc benefit to some species of birds. The nightjar, for instance, once a regular summe visitor to Charnwood, lingered on in young plantations at Benscliffe until the mid 1960s, and the grasshopper warbler can now be heard 'reeling' in scrub and re afforested areas throughout the county in the summer. Other species favoured by th growth of scrub following felling have been the redpoll, which has shown a marke increase over the last five years, and the turtle dove, which has shifted its allegianc for nest sites from hedgerows to plantations. The widespread planting of conifer has encouraged goldcrests and crossbills, with an attempted nesting by the latte species in 1960 at Eye Brook Reservoir.

Of the invertebrate fauna of the woodlands only the butterflies and moths, beetle and spiders have been studied in any detail. The Lepidoptera were intensively worked by H. A. Buckler and Dr A. A. Lisney during the period 1930–50 and mor recently by M. J. Leech and P. H. Gamble, amongst others. Two butterflies at leas the comma and white admiral, reappeared during the 1950s after many years absence, but because of felling and replanting the general trend has been one o diminishing numbers, as for example with the pearl-bordered and silver-washe fritillaries and purple hairstreak. In respect of moths the position is complicated b the extensive use of mercury vapour lamps in recent years. Species such as the luna

narbled brown *Chaonia ruficornis*, the marbled brown *Drymonia dodonaea*, swallow prominent *Pheosia tremula*, white-marked *Gypsitea leucographa*, figure of eighty *Tethea cularis* and scalloped hook-tip *Drepana lacertinaria* have all either appeared for the first ime or apparently increased markedly in numbers, as have conifer feeders such as he pine beauty *Panolis flammea*, tawny-barred angle *Semiothisa liturata* and bordered hite *Bupalus piniaria*.

C. W. Henderson, M. J. Leech and D. Tozer have studied the beetles, and wood- and species of interest discovered by them include the chrysomelid *Zeugophora avicollis* on aspens in Swithland Wood, the lymexylid *Hylecoetus dermestoides* also in Swithland Wood and the cerambycid *Molorchus minor*. Until it was almost clear-felled uring the last war, Buddon Wood near Mountsorrel, which contained the only eicestershire colonies of the wood ant *Formica rufa*, was noted for its beetles and me of these are still to be found. Amongst species collected there are the chryso- elids *Clytra quadripunctata* and *Galeruca tanaceti*, the weevils *Lasiorhynchites cavifrons* nd *L. ophthalmicus*, the carabid *Calosoma inquisitor* and once, in an old woodpecker est, the silphid *Nemadus colonoides*. The angle-striped sallow *Enargia paleacea*, a oth new to the county, was taken at light in Buddon Wood in 1968, but two bilberry eders once found there, the scallop shell *Rheumaptera undulata* and bilberry pug *hloroclystis debiliata*, seem to have disappeared. The county has been poorly served by rachnologists, but recent work by J. Crocker on woodland spiders has revealed a umber of species of interest. Examples are *Anyphaena accentuata*, *Oxyptila trux*, *achygnatha listeri* and *Tapinocyba insecta* in Swithland Wood, the salticid *Ballus pressus* on oaks in Buddon Wood and the oddly-shaped argiopid *Cyclosa conica* in oddington Reddish. There are old records of *Thyreosthenius biovatus* in wood ant ests at Buddon Wood.

In the bugs, as in the Lepidoptera, the widespread planting of conifers has added a umber of new species to the fauna of the county. Examples are *Elatophilus nigricornis* nd *Acompocoris pygmaeus* taken by H. A. B. Clements on Scots pine at Charnwood odge, and *Atractotomus magnicornis* beaten by him from spruce at Ulverscroft.

Other aspects of the invertebrate fauna of our woodlands remain virtually un- plored. The oak bush-cricket *Meconema thalassina*, discovered new to the county the early 1960s, is now known to be widespread, and the dark bush-cricket *Pholi- ptera griseoaptera* was taken in Owston Wood for the first time in 1970 (Evans, 1970). he woodland Diptera, however, have had virtually no attention for 30 years or ore and this is the state of affairs for most of the less popular fauna groups.

CHARNWOOD FOREST

The special interest of Charnwood Forest to naturalists is due to a number of factor for a detailed account of which the reader is referred to Horwood and Gainsboroug (1933). Suffice it to say that the hard Precambrian rock of the area weathers to well-drained sandy soil which suits some forms of animal life more than do th heavier and calcareous soils found throughout most of the remainder of Leiceste shire, and it supports heath and moorland vegetation which is the basis of food chai unique to this area. It was the last part of the county to be enclosed and much of it still unsuitable for intensive agricultural use. On its periphery are a number of o estates, many of them once deer parks, the most notable being Bradgate Park.

The fast-flowing streams which drain the Forest have already been mention and, although few aspects of their fauna have been properly documented, enough known to show how they differ from those of the rest of the county. The fish typical include brown trout, bullhead and stone loach. Spined loach were recorded Browne (1889) and have recently been rediscovered. Brook lamprey spawned un recently in the River Lin at Newtown Linford and they have occurred also in t Black Brook. Crayfish are plentiful in the River Lin and are known to be present Bardon and Swithland and in the Black and Wood Brooks. A county-wide survey Fawcett (1971) of stoneflies revealed that of the nine species which occur in Leiceste shire, seven are virtually restricted to Charnwood Forest.

Bradgate Park is one of only two deer parks still existing as such in the county, t other being at Castle Donington. The herd of fallow and red deer, the former bei about twice as numerous as the latter, is maintained by selective culling at about thr hundred head, since suitable grazing is limited in extent by the vigorous growth bracken. The fauna and flora of the Park are described at length in a report pu lished in 1962 by the Loughborough Naturalists' Club, but since this is now diffic to obtain it is perhaps worth mentioning some of the special features of the are Over 500 species of beetles have been recorded within its boundaries, including t tiger beetle *Cicindela campestris*, only known from one other locality in the county, t minotaur *Typhaeus typhoeus*, the colourful click beetle *Corymbites cupreus* var. *aerugino* and 16 species of the dung beetle genus *Aphodius* of which the rarest, *A. zenkeri*, specific to deer dung. Associated with the old stag-headed oaks is a distinctive bee fauna, which has its nearest parallel in Sherwood Forest, including the deathwat beetle *Xestobium rufovillosum*, *Xylophila pygmaea*, *Haplocnemus nigricornis* and *Phloiot rufipes*. Bradgate Park was one of the collecting grounds of H. St J. Donisthorpe a

ecords of its ants and the bugs, beetles and spiders associated with them may be ound in his *The Guests of British Ants* (1927). His record of the very rare agelenid pider *Tetrilus macrophthalmus* associated with old oaks was confirmed by the capture f two females by J. Crocker in 1962, and the species has since been taken by him at Bardon Hill. The Park is the only known locality in the county for the high brown ritillary, although it has not been seen there in the last decade, and the dark green ritillary has occurred in numbers. A conspicuous feature of the Park in the summer is he nest holes of solitary bees, *Andrena* spp., and the aculeate Hymenoptera are one of he few groups of insects whose distribution has been thoroughly investigated in Charnwood Forest. Spooner (1946) found wood and stem nesting species to be as well represented as anywhere in England but, surprisingly, that there was a striking learth of earth nesting species with a preference for light soils, the absence of which t is difficult to understand.

Charnwood Forest is by far the richest part of the county as far as reptiles and mphibians are concerned. The adder is still found in three or four localities and is hought to be restricted to these in the county as a whole, although there are sight ecords from the Willesley area, and recent reports of livestock deaths attributed to dder bites in the north-east of Leicestershire. The slow-worm is rather more wide- pread, favouring parkland and old quarries and occasionally males of the blue- potted form are found. Common lizards occur in similar habitats throughout the Forest and both they and slow-worms have been found from time to time in the area o the north-west of the Forest, where the Coal Measure sandstones weather to soils esembling those of Charnwood. Grass snakes may be found in some of the stream alleys but they are commoner elsewhere in the county. Frogs and toads spawn in uitable localities throughout Charnwood Forest, and smooth and crested newts ccur in the field ponds, though the latter only sparingly. The presence of the pal- nate newt was confirmed in the early sixties when a flourishing population was found n an artificial pond at Benscliffe. The species has since been shown to occur in five onds, all artificial and all but one at altitudes of more than 198m (650ft) (Bell, 1970).

The small acid ponds found on the highest parts of Charnwood have an insect auna not matched elsewhere in the county. Examples of species restricted to them re the pond-skater *Gerris gibbifer*, the greater water-boatman *Notonecta obliqua* and he corixid *Hesperocorixa castanea* (Martin, 1970). In the small Colony Reservoir on he Charnwood Lodge Nature Reserve in 1967 H. A. B. Clements discovered the urface water bug *Mesovelia furcata* for which there are no recent records so far north. The small areas of relict heath and moorland, both wet and dry, which survived the

efforts of nineteenth-century agriculturalists to bring the Forest into cultivatio support a distinctive invertebrate fauna of which the moths and spiders have bee most thoroughly worked in recent years. Amongst the 'upland' species of moths a the goldenrod pug *Eupithecia virgaureata*, glaucous shears *Hadena bombycina* ar northern rustic *Ammogrotis lucernea*, all of which have been taken recently on th Charnwood Lodge Nature Reserve. The spiders of Bardon Hill, the highest point the county at 278m (912ft), have received special attention from J. Crocker. Among the 141 species he has found so far there are a number of rarities including *Euophr erratica*, *Porrhomma egeria*, *Thyreosthenius parasiticus*, *Agyneta decora*, *Evansia merens* ar *Oreonetides firmus*.

Work on other groups has been confined mainly to a few localities in the Fore but the records give some idea of the potential interest of this area to the entomologis Recent discoveries by H. A. B. Clements include the carabid beetle *Pterostich angustatus* at High Sharpley, and amongst the bugs, *Stalia boops*, *Asciodema obsoletu* and *Orthotylus ericetorum* on heathland at Ulverscroft, and *Trigonotylus ruficornis* High Sharpley. Members of the Loughborough Naturalists' Club are at prese engaged in a general survey of the whole of Charnwood Forest and more detaile studies of Bradgate Park, Bardon Hill, Charnwood Lodge Nature Reserve an Groby Pool, and these will in time provide a much fuller picture of the fauna an ecology of this unique area.

SOURCES OF INFORMATION

In view of the fact that no comprehensive account of the fauna of the county h been published since that in *The Victoria County History* (1907), and the scattere nature of the available sources of information, it was thought worthwhile to provid a guide to these sources.

Local societies and kindred institutions (*in order of foundation*)

Natural History Section of the Leicester Literary and Philosophical Society (Honorary Secretary, Leicester Museum, New Walk, Leicester): records housed and publications available at Leicester Museum.

Leicestershire and Rutland Ornithological Society (Honorary Secretary: Mrs B. K. Pochin, White Haven, Links Road, Kirby Muxloe, Leicester): library and records, other than the current ones, housed at Leicester Museum.

Leicestershire and Rutland Trust for Nature Conservation (Honorary Secretary: M. Walpole, 68 Outwoods Road, Loughborough, Leics.): site and other scientific records, including those for all Sites of Special Scientific Interest in the two counties, housed at Leicester Museum.

Loughborough Naturalists' Club (Honorary Secretary: Mrs B. Bowler, 488 Bradgate Road, Newtown Linford, Leicester): for library and records apply to the Honorary Secretary, publications available in the library of Leicester Museum and Loughborough Library.

Systematic guide to sources, arranged according to Kerrich et al. (*1967*)

Leeches		Specimens and records at Leicester Museum.
Molluscs		Kerney (1967, 1968, 1970), Kerney and Morton (1970); specimens and records at Leicester Museum.
Crustaceans		Moon (1970); specimens and records at Leicester Museum.
Myriapods		Specimens and records at Leicester Museum.
Insects	Orthoptera	Burton (1965), Evans (1970), Kevan (1961); specimens and records at Leicester Museum.
	Plecoptera	Fawcett (1971); specimens and records at Leicester Museum.
	Odonata	Specimens and records at Leicester Museum.
	Thysanoptera	Morison (1971); MS. notes by Morison at Leicester Museum.
	Hemiptera	Martin (1970); specimens and records at Leicester Museum.
	Trichoptera	Specimens and records at Leicester Museum.
	Lepidoptera	Buckler (1954); Buckler, Lisney and Harris-Evans collections and records at Leicester Museum.
	Coleoptera	Headley, S. O. Taylor, S. A. Taylor, Tailby, Hunter and Clements collections at Leicester Museum.

	Hymenoptera	Collingwood (1961), Collingwood and Barratt (1964), Spooner (1946), Yeo (1961, 1963); Lowe and Martin collections of aculeates at Leicester Museum.
	Diptera	Lowe and Muschamp collections at Leicester Museum.
	Siphonaptera	Stansfield (1961); specimens and records at Leicester Museum.
Arachnids	Spiders	Specimens and records at Leicester Museum.
	Ticks	Thompson (1968); specimens at Leicester Museu
Amphibians	Bell (1970); records at Leicester Museum.	
Reptiles	Specimens and records at Leicester Museum.	
Birds	Otter (1965); publications of Leicestershire and Rutland Ornithological Society and Loughborough Naturalists' Club.	
Mammals	Squires (1963); specimens and records at Leicester Museum.	

Note The Biology Department, Leicester Museum, has extensive collections Leicestershire material in the following groups: molluscs, Lepidoptera, Coleopte Hymenoptera, Diptera, Siphonaptera, birds and mammals and smaller collecti as indicated above. There is also much unpublished documentary mate relating to these and other groups. These are readily available for study a reference on application to the Keeper of Biology at Leicester Museum.

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EFERENCES

ll, G. A. C., 1970. 'The distribution of amphibians in Leicestershire', *Trans. Leic. Lit. & Phil. Soc.*, *64*, 122–43.
adshaw, H., 1969. 'The birds of Spinney Hill Park, 1960–68', Report for 1968 of the Leics. & Rutland Ornithological Soc., 21–2.
own, D. S., 1961. 'The life cycle of *Chloëon dipterum* L. (Ephemeroptera: Baetidae)', *Entomologist*, *94*, 114–20.
owne, M., 1889. *The Vertebrate Animals of Leicestershire and Rutland.*
ckler, H. A., 1954. 'List of the Lepidoptera of Leicestershire'. Duplicated for private circulation; copies available from Biology Department, Leicester Museum.
rton, J. F., 1965. 'Notes on British Orthoptera in 1964, with some new vice-county records', *Entomologist's Record*, *77*, 71–8.
ements, H. A. B., 1967. '*Mesovelia furcata* (Muls. and Rey) (Hemiptera: Mesovelidae) in Leicestershire', *Entomologist's Monthly Magazine*, *102*, 76.
llingwood, C. A., 1961. 'New vice-county records for British ants', *Entomologist's Record*, *73*, 90–3.
llingwood, C. A. and Barrett, K. E. J., 1964. 'The vice-county distribution of indigenous ants in the British Isles', *Trans. Soc. for British Entomology*, *16*, 114–21.
mmins, W. A. and Rundle, A. G., 1968. 'Sedimentary and faunal facies associated with the draining of Cropston Reservoir', *Mercian Geologist*, *2*(*4*), 389–400.
vey, S. R., 1967. 'Some interesting Lepidoptera recorded for Leicestershire, Oxfordshire and Cambridgeshire', *Entomologist's Record*, *79*, 249–52.
nisthorpe, H. St J. K., 1927. *The Guests of British Ants, their habits and life histories.*
ans, I. M., 1970. '*Pholidoptera griseoaptera* (Degeer) (Orthoptera, Tettigoniidae) new to Leicestershire', *Entomologist's Monthly Magazine*, *106*, 66.
wcett, J. E., 1971. 'Leicestershire stoneflies', *Trans. Leic. Lit. & Phil. Soc.*, *65*, 33–48.
ckling, R. A. O., 1967. 'The inland wintering of gulls in England, 1963', *Bird Study*, *14*(*2*), 104–13.
rwood, A. R., 1907. 'Zoology' in *A guide to Leicester and district*, British Association for the Advancement of Science, 1907 Meeting, 346–62.
rwood, A. R., and Lord Gainsborough, 1933. *The flora of Leicestershire and Rutland.*
es, R. C., 1971. 'A survey of the flora, physical characteristics and distribution of field ponds in north-east Leicestershire', *Trans. Leic. Lit. & Phil. Soc.* (in press).
rney, M. P., 1967. 'Field meeting to Leicestershire, 6th May, 1967', *Conchologists' Newsletter*, *22*, 17–18.
rney, M. P., 1968. 'Field meeting to Leicestershire, 27th April, 1968', *Conchologists' Newsletter*, *27*, 72–3.
rney, M. P., 1970. 'Field meeting to Leicestershire, 6th June, 1970', *Conchologists' Newsletter*, *35*, 186–7.
rney, M. P. and Morton, B. S., 1970. 'The distribution of *Dreissena polymorpha* (Pallas) in Britain', *Journal of Conchology*, *27*, 97–100.
rrich, G. J., Meikle, R. D. and Tebble, N., 1967. *Bibliography of key works for the identification of the British fauna and flora* (third edn).
van, D. K. Mc. E., 1961. 'A revised summary of the known distribution of British Orthopteroids', *Trans. Soc. for British Entomology*, *14*, 187–205.
ughborough Naturalists' Club, 1962. Surveys of Leicestershire natural history, No. 1, *Bradgate Park and Cropston Reservoir margins.*

Lowe, E. E., Mayes, W. E., Wagstaff, R. and Taylor, S. O., 1933. 'The zoology of Leicestershi in *A Scientific Survey of Leicester and district*, ed. P. W. Bryan, British Association for the Advancem of Science, 33–40.

MacQueen, D. C., 1970. 'The Lepidoptera of the Uppingham area, Rutland', *Entomologist's Mon Magazine, 105*, 253–7.

Markowski, S., 1959. 'The cooling water of power stations: a new factor in the environment of mar and freshwater invertebrates', *Journal of Animal Ecology, 28*, 243–58.

Martin, N. A., 1970. 'The distribution and ecology of the Corixidae (Hemiptera, Heteroptera) Leicestershire', *Trans. Leic. Lit. & Phil. Soc. 64*, 101–21.

Mason, C. F. and Pickering, F. C., 1968. 'The birds of Leicester City Farms 1944–1964', Report 1966 of the Leics. & Rutland Ornithological Soc., 21–5.

Moon, H. P., 1970. '*Corophium curvispinium* (Amphipoda) recorded again in the British Isles', *Nat 226*, 976.

Morison, G. D., 1971. 'Observations and records for some British Thysanoptera. IX. Thripid *Thrips inopinatus* Zur Strassen, a species new to Britain', *Entomologist's Monthly Magazine, 1* 162–4.

Otter, J., 1965. 'The Birds of East Leicestershire'. Surveys of Leicestershire natural history, No (Loughborough Naturalists' Club).

Spooner, G. M., 1946. 'Hymenoptera Aculeata from Charnwood Forest, Leicestershire', *Entomologi Monthly Magazine, 82*, 25–9.

Squires, A. E., 1963. 'The badger in Charnwood Forest', Surveys of Leicestershire natural histo No. 2 (Loughborough Naturalists' Club).

Stansfield, G., 1961. 'Leicestershire fleas', *Trans. Leic. Lit. & Phil. Soc., 55*, 24–7.

Thompson, G. B., 1968. 'Records of Ticks (Ixodoidea) from Leicestershire', *Trans. Leics. Lit. & P Soc. 62*, 70–2.

The Victoria History of the County of Leicester, vol. I, 1907.

Yeo, P. F., 1961. 'Records of Hymenoptera Aculeata from Leicestershire', *Entomologist's Mon Magazine, 97*, 134.

Yeo, P. F., 1963. '*Bombus soroensis* (Hymenoptera, Apidae) in Leicestershire – a correction, *Coelocrabro ambiguus* (Hymenoptera, Sphecidae) in Cambridgeshire – a new record', *Entomologi Monthly Magazine, 99*, 81.

3

Terrestrial microbiology, invertebrates and ecosystems

W. Block

oduction

restrial microbial and invertebrate biota of the Antarctic inhabit a series of environments, ranging from cold desert, through progress- ırmer conditions of the continental coastal fringe and the maritime) the sub-Antarctic. The latter contains biological elements of the n cold temperate zone from the north. The terrestrial communities ıntarctic contain an impoverished and disharmonic flora and fauna; : relatively simple in terms of the number of component species, and ıe interactions involved are fewer than in species-rich communities, ave more complicated structures. They are, as yet, unaltered and ly unpolluted by Man and there is a need to study them before it is . These ecosystems are particularly suited to analysis, especially of ɔrs governing the rates of basic ecological processes such as biomass r, decomposition, metabolism and fluxes of energy and nutrients. ; a need for long-term monitoring of certain key functions and for elopment of environmental impact analysis for such systems. In ı, the adaptations of a range of organisms, which are exposed to a nd physiologically testing environment, can be investigated and the combined with biological information on life cycles, etc., allow nto their overall survival strategies. The physiological and bio- l mechanisms behind such adaptations provide some understanding volution and colonization processes in polar regions.

contribution reviews the microbiology and the invertebrates of al communities throughout the Antarctic region and considers ety of environmental adaptations which have evolved there. In

particular, an examination is made of the mechanisms which produc
ebrate cold hardiness, and of the information available on te
ecosystem structure and function. It is concluded that many
adaptational features observed are peculiar to low temperature org
which combined with the particular trophic organization of A
terrestrial communities, have resulted in the development of eco
which are unique on this planet.

This review is neither complete nor exhaustive, and is, of ne
selective in its approach. As far as possible, all groups of terrestri
tebrates occurring in both the sub-Antarctic and the Antarctic pro
reviewed, together with the bacteria, fungi, yeasts and micro-algae,
treatment of each group emphasizes the main features of their distr
ecology and, where available, their physiology. Initial attention h
paid to the energetics of selected invertebrate species, and the res
pathway in population energy flow has been particularly studied. T
tinental, maritime and sub-Antarctic ecological zones refe
throughout are defined by Holdgate (1964, 1977) and Lewis Sm
volume). The sub-Antarctic zone includes South Georgia, Mar
Prince Edward Islands, Îles Crozet, Archipel de Kerguelen, He
Macdonald Islands and Macquarie Island, but excludes Campbell
The maritime Antarctic zone includes Bouvetøya, the South S
Islands, South Orkney Islands, South Shetland Islands and the west
the Antarctic Peninsula and its offshore islands to *c.* 70°S. Pete
Balleny and Scott Islands are regarded as coastal continental Antar

2. Microbiology

2.1 Micro-organisms

Microbiology has been slow to develop in Antarctica, due partl
cryptic nature of microbes, and partly to the technical prob
Antarctic field microbiology (Wynn-Williams, 1979). Neverthele
information has accumulated since the pioneering Antarctic invest
into the microbiology of air, water, ice, snow, soil and animals by
(1908a,b) on Snow Hill Island, Antarctic Peninsula; Pirie (1904, 1
Laurie Island, South Orkney Islands; and Gazert (1912) in Wi
Land. The aerial microflora was found to be negligible. Ekelöf un
the first study of changes in soil microflora throughout a full yea
Antarctic, and isolated a wide range of bacteria, actinomycete
pseudomycelial yeast. Subsequently Tsiklinsky (1908) isolat
bacterial strains from ornithogenic soil from the Danco Coast, A

ıla, probably only one of which was not of animal origin. From soil ag bearing some vegetation she isolated a Streptomycete, a white otolerant coccus and a red pseudomycelial yeast. *Aspergillus*, *Peni-* and a species of *Mucor* were frequently found. Ten years later, n (1918, 1919) confirmed the near-sterility of Antarctic air at onwealth Bay, Adelie Coast, but found viable bacteria and yeasts in snow, glacier ice and melt water. These early land-based studies are rized in Sieburth (1965).

rctic terrestrial microbiology has developed from marine mammal -bird studies and from aerobiology. Microbes found in soils of the ıe Antarctic may be indigenous, of marine origin via spray or animal , or of temperate origin from high altitude air-streams (McLean, nd migrating animals, or contaminants from invading animals and , their faeces and other debris (Lipps, 1978). McLean's (1918) esis of aerial distribution at Commonwealth Bay has been supported olph (1970) at Cape Hallett, another windswept location, but con- by Meyer *et al.* (1967), who found no evidence that cyclonic or winds at the Haswell Islands, Greater Antarctica, brought ms from sub-Antarctic islands or distant continents. The aerial ora was of local origin but the soil population, dominated by *monas* and chromogenic micrococci, was considered cosmopolitan rds as important vectors. Nevertheless, Margni and Corte (1962) ted contamination of the Antarctic Peninsula by northerly ms from South America, although many air-borne fungal spores ıot grow under the Antarctic conditions prevailing at Hope Bay, Cape (Danco Coast) and Ellsworth Station (Corte and Daglio, Here too there was similarity between the aerial and terrestrial ora, dominated by Gram-negative bacilli of the genera *Pseudo-* *Ackromobacter* and *Alcaligenes* (Margni and Castrelos, 1963, 1964; os *et al.*, 1977). However, in the nutritionally and climatically environment of the coastal continental Antarctic, the soil popula- McMurdo Sound consisted mainly of *Corynebacterium*, *Arthrobac-* *Micrococcus* (Cameron *et al.*, 1972). Darling and Siple (1941) mainly *Ackromobacter*, *Flavobacterium* and *Bacillus* spp. from the lacier, Ford Range and Little America, although bacterial spore- are infrequent in Antarctic soils. The diversity of these populations that substrate is more important than climate in defining the ora (Boyd *et al.*, 1966). This was also demonstrated by Cameron and (1970) on Deception Island in the maritime Antarctic, whose vol- h-based soils support the *Arthrobacter–Corynebacterium–Micro-* opulation characteristic not only of McMurdo Sound, but also of oria Land Dry Valleys and the continental interior to Mount Howe

at 87°S (Cameron, 1972b; Cameron *et al.*, 1971; Cameron and Ford *Micrococcus* spp., often chromogenic (Flint and Stout, 1960), are ous in Antarctic soils (Cameron *et al.*, 1972) but the Actinomycetes on the continent (Boyd *et al.*, 1966) and the Antarctic Peninsula (and Castrelos, 1971).

Many bacterial strains isolated from soil and air of the Antarc tinent also have non-Antarctic habitats and may therefore have bee duced (Cameron *et al.*, 1972). The occurrence of psychrotolerant in the proximity of an occupied base such as Bahia Esperanza, whi capable of growth at 37°C (Castrelos *et al.*, 1977), and of clostridia, to be associated with Man, present near Syowa Station (Miwa, 1 1976) merits further study. The persistence of *Bacillus* spp. an thermophiles in areas of McMurdo Sound contaminated by early tions (Boyd and Boyd, 1963) emphasizes the ease with which the re small and simple indigenous microbial population may be invaded *et al.*, 1962, 1963; Cameron, 1972c).

Microbiological research has developed in three directions. Fi elucidation by the Dry Valleys Drilling Project of the microbi history of the Antarctic ice sheet and the survival of viable micr millennia in ice (Cameron and Morelli, 1974). Secondly, the demon of the survival and distribution of bacteria, yeasts and fungi in ex cold deserts such as the Dry Valleys (Cameron, 1971, 1972a) and mo of the interior (Cameron *et al.*, 1971; Cameron, 1972b; Cameron an 1974). Endolithic microbes, lichens, fungal filaments, uni cyanobacteria and unicellular eucaryotic algae were found within Beacon sandstone of the Dufek Massif (Friedmann, 1977). Thir vironmental impact studies which monitored contamination of tremely small indigenous population in soils of southern Victori (Cameron *et al.*, 1977; Parker *et al.*, 1978).

Autotrophic bacteria have also been monitored to assess their bution to energy and nutrient cycling (Boyd *et al.*, 1966). Specialize ways include nitrogen and sulphur cycling (Boyd, 1967; Bargho Nichols, 1961; Janetschek, 1963) and iron-oxidation (Cameron and 1970). Boyd and Boyd (1962, 1963) isolated *Azotobacter chromoco* the Windmill Islands, Wilkes Land, and at McMurdo Sound. Pho etic bacteria were not detected in soil at Paradise Harbour (Boy 1970), but *Chromatium minutissimum* formed blooms in a pond penguin rookery at Cape Adare (Boyd and Boyd, 1963) and in Skua Cape Evans (Boyd *et al.*, 1966). Obligately anaerobic bacteria ceived less attention than aerobes and are infrequent in superficial s from human contamination (Cameron and Benoit, 1970).

Much of the taxonomy of the bacterial flora of the oligotrophi

ic (Boyd and Boyd, 1963), the Dry Valleys and the continental inter-
meron *et al.*, 1970; Johnson *et al.*, 1978; Madden *et al.*, 1979) has
ıblished.

ts demonstrate great tolerance to nutritional and environmental
:s. *Cryptococcus albidus* occurs on Mount Howe, the most southerly
l mountain in the world at 87°S and 2800 m altitude (Cameron *et al.*,
Various strains of *Cryptococcus*, *Candida*, *Rhodotorula* and other
are widespread in the Dry Valleys (Atlas *et al.*, 1978) and coastal
ic locations (Goto *et al.*, 1969). These include McMurdo Sound,
hey may comprise as much as 10% of the total heterotrophic micro-
mass (Atlas *et al.*, 1978; di Menna, 1960, 1966a,b). In the maritime
ic, Boyd *et al.* (1970) showed large fermentative yeasts to be
n in soil at Paradise Harbour, Antarctic Peninsula, and Cameron
ıoit (1970) isolated *Cryptococcus* spp. from volcanic soil at Decep-
ınd. Figure 1 illustrates yeast colonies isolated from peat soils in the
e Antarctic.

e of the dominant strains of yeast isolated from peat under moss turf at Signy Island,
ıntarctic. The colonies are 8 mm diameter having been grown on Sabouraud Dextrose
ł days at 10°C. Photograph by D. D. Wynn-Williams.

e the yeasts, the microfungi and their spores form a major
ent of the aerial microflora of Antarctica. Air samples in the Scotia
ıl *et al.*, 1967; Baker, 1970a,b; Broady, 1979c), the Antarctic Pen-
Corte and Daglio, 1963, 1964), and the McMurdo Sound and

Victoria Land areas (Sun *et al.*, 1978), have been collected at variou
The dominant aerial spores are of *Penicillium* and *Aspergillus*
1965), and although they do not grow in the maritime Antarctic
Signy Island (Bailey and Wynn-Williams, 1982), they have been
from a wide range of other Antarctic and sub-Antarctic sites. The
other Antarctic fungal genera is large but only *Acremonium*,
sporium, *Cladosporium*, *Mucor*, *Phialophora* and *Trichoderma* ha
isolated from all the terrestrial sites examined in the Antarctic a
Antarctic. The factors governing their distribution are unclear, bu
the bacterial population, both aerial (Rudolph, 1970) and anima
tion may be involved. The human factor has been emphasized by t
tion of two fungal pathogens, *Phialophora dermatidis* and *Phia*
gougerotii, from the area of McMurdo Station (Sun *et al.*, 1978).

Although Ascomycetes such as *Arachniotus citrinum* are foun
south as McMurdo Sound (Sun *et al.*, 1978), Basidiomycetes are r
to the maritime Antarctic and offshore islands (Pegler *et al.*, 198
erina and *Omphalina* species are found there, and *Gerronem*
southernmost, at Norsel Point, Anvers Island (Singer and Cort
1964; Singer, 1967; Singer, 1972). Specialized fungal groups incl
genus *Thyronectria* which causes radial infections in mosses (Hawl
1973; Longton, 1973), and those predacious on nematodes (Duddi
al., 1973; Maslen, 1982).

The Scotia arc and northern Antarctic Peninsula are characteri
wide range of lichen and moss communities (Gimingham and Smit
see also Chapter 2) and associated peats or primitive soils (see Cha
These support a larger and more diverse microbial population tha
bearing areas in coastal regions of continental Antarctica (e.g. B
Rothenberg, 1968). Here Gram-negative rods including *Achrom*
Pseudomonas and *Flavobacterium* predominate over the coryne
harsher moss-free regions, but Baker and Smith (1972) found
coryneform bacteria in peat under *Chorisodontium* at Signy Island
the predominance of pseudomonads in nearby grassland soil (He
1967). Only chromogenic *Micrococcus* spp. were common to all A
soil-types. The variation in pH from 4 in Signy Island peat (Wy
liams, 1980) to 9 in Victoria Valley, Victoria Land (Cameron, 1972
of several potential controlling factors, possibly marked by the oc
of *Chromobacterium* spp. (Wynn-Williams, unpublished).

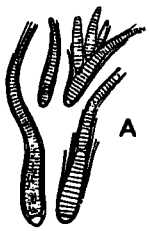
Cryptogams themselves provide a favourable habitat (Sieburt
although some lichens may have antibiotic properties. The den
population in the upper layers of Signy Island peat (Wynn-W
1982) is probably of epiphytic origin (Baker, 1970b). On
antarcticum from McMurdo Sound, di Menna (1960) found epiphyt

to temperate New Zealand strains, but different from those in non-cryptogamic soil. Flint and Stout (1960) found the same trend rial epiphytes.

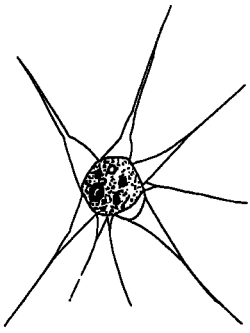
npts have been made to establish the factors determining fluctu- in soil microbial populations. Ekelöf (1908a) showed a ten-fold e in the bacterial population during the summer at Snow Hill Island. al variations were monitored by Margni and Castrelos (1971) at speranza, Deception Island and Cabo Primavera in 1960–1964 and a lag in maximum bacterial numbers commensurate with delayed eaks in both bacterial and fungal populations of comparable crypto- oil at McMurdo Sound were found in the same period (Boyd and 963) and the mesophilic bacterial peak preceded the fungal and philic bacterial peaks. The physiological characteristics of terres- chrophilic yeasts (Sinclair and Stokes, 1965), bacteria (Straka and 1960; Staley and Boyd, 1967; Baker, 1974; Inoue and Komagata, nd fungi (Latter and Heal, 1971) have largely been determined. The iles respond to thawing despite minimal rise in temperature above is temperature-independent activity and growth response has been ated at Signy Island by peat-core respirometry (Baker, 1970a; Villiams, 1980). Much of the spring-thaw activity is due to lity of soluble nutrients, as shown by amending peat with glucose *in* ynn-Williams, 1980), and with glucose and peptone *in situ* (Boyd *et* 5, 1970). The post-spring decrease is due partly to their depletion tly to predation by Protozoa (Heal, 1965) and other invertebrate vores (Holdgate, 1977; Broady, 1979c). Other regulatory factors noisture (Baker, 1970b; Cameron and Conrow, 1969), temperature 1974) and inorganic status (Boyd *et al.*, 1966).

robable that tundra decomposer fungi such as cellulolytic strains hael, 1962; Tubaki and Asano, 1965) and keratinophils (Paterson x, 1972; Caretta and Piontelli, 1977) assume increasing importance ummer as soluble nutrients are utilized. This view is supported by easing decomposition of cotton strips after the spring microbial some Signy Island peat soils (Wynn-Williams, 1980).

trial microbiological studies of Antarctica have broadened to he sub-Antarctic Islands of South Georgia (Smith and Stephenson, acquarie Island (Rountree, 1938; Bunt, 1954c; Marshall and Ohye, nkin, 1975), and Marion and Prince Edward Islands (Joubert, Iuch of this has been co-ordinated with the tundra studies of the onal Biological Programme (I.B.P.) (Flanagan and Veum, 1974). ie Island investigations have encompassed soil microbiology and sm (Bunt and Rovira, 1955a), the faecal microflora of penguins, rds and seals (Bunt, 1955), the temperature responses of soil


A


B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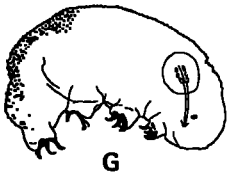
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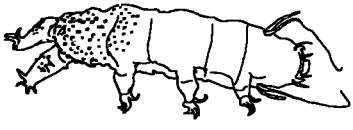
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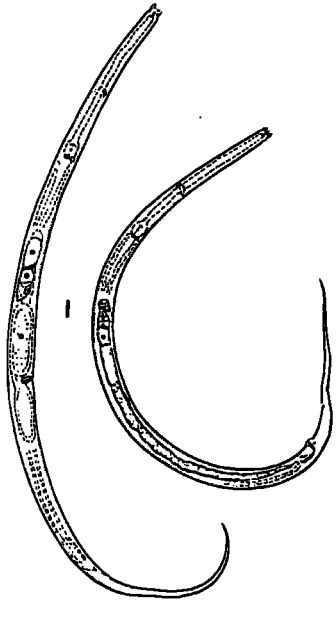
I


J


K


L

s (Bunt and Rovira, 1955b) and detailed fungal ecology of soil and nt, 1965). These have demonstrated a more complex microbial than the relative simplicity of the Antarctic region. A co-ordinated ological survey with respect to substrate, topography and latitude, andardized methodology, is now a priority.

cro-algae

dies have been made of the terrestrial algal flora of the Antarctic. t collection of a terrestrial alga (*Prasiola crispa*) was made by and Hooker (1844). Early literature on freshwater algae, including rrestrial collections, has been surveyed by Hirano (1965). Bunt gave an account of the terrestrial diatoms of Macquarie Island and tudies in the Antarctic, whilst Broady (1979f) has reviewed terres-

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B) Antarctic terrestrial algae (after Broady, 1979f).
othrix parietina (Cyanophyceae), an alga found at Signy Island, the cells of which are 0 μm wide.
niosphaera multinucleata (Euchlorophyceae), large adult cells (c. 30 μm diameter) in ptical section and surface view. The species was described from Signy Island by roady (1977a).
arctic terrestrial Protozoa (after Smith, 1978).
amoeba radiosa (Rhizopoda), a common naked amoeba found in polar soils. Cell size c. 20 μm diameter.
omonas mutabilis (Mastigophora), a flagellate restricted to acid substrates in the ntarctic where it is common. Cell size is c. 20 μm.
tricha fallax (Ciliata), one of three species of this genus found in organic habitats of rrestrial areas of the Antarctic. Length is c. 120 μm.
ela martiali (Rhizopoda), a testate amoeba with a circumpolar distribution. Length c. 50 μm.
arctic Tardigrada (after Jennings, 1976a).
sibius asper, originally described from the South Orkney Islands (Murray, 1906) it ccurs in both terrestrial and aquatic habitats. Length is typically 325 μm.
ella mollis, rare, being recorded in small numbers only at Signy Island in the Antarctic. otal length is 100 μm.
arctic terrestrial Nematoda (after Maslen, 1979a). *Teratocephalus tilbrooki*, gravid male (left), male (right). Described from moss communities at Signy Island. (By nd permission of *Nematologica*.)
arctic Collembola (after Willem, 1902).
otopygus antarcticus (Isotomidae), profile view of adult which is c. 1 mm in length. The ost abundant collembolan in the Antarctic Region.
sotoma octooculata (Isotomidae), adult (c. 1.25 mm in length). A widespread species ith a circumpolar distribution.
arctic Diptera (after Wirth and Gressitt, 1967).
lt chironomid midges: male (upper) of the wingless *Belgica antarctica* (size .5–2.5 mm) which is restricted to the islands and west coast of the Antarctic Peninsula; male (lower) of the winged *Parochlus steinenii* (size 2.8–3.00 mm), which is nly known from South Georgia and the South Shetland Islands.
a of *Belgica antarctica* (length 4.5–5.0 mm at maturity), which is often locally abunant in living and dead organic matter.

trial algal studies in Antarctica. Of particular significance were the of nitrogen fixation by *Nostoc commune* in terrestrial habitats Island and Victoria Land (Holm-Hansen, 1963), and in base rich Signy Island (Fogg and Stewart, 1968). Fogg (1967) and Kol (1968) the algae of green, red and yellow snow at Signy Island. In a detaile Broady (1975, 1979f) found 162 taxa of terrestrial algae in 122 sam at Signy Island, which included a genus and eight species new to (Broady, 1976, 1977a). Figures 2A,B show two common Antarcti Cyanophyceae (49 taxa) comprised 30% of the flora, while the E phyceae (34 taxa), Ulothricophyceae (20 taxa), Bacillariophyceae (and Xanthophyceae (17 taxa) each were between 10 and 21% of the a preliminary algal survey of ten localities on the Antarctic Penin South Georgia, 70 taxa from 47 genera were found in 37 soil and ve samples (Broady, 1979d). These included four genera and 16 spe found at Signy Island.

Ecological studies have been made of two moss communities Island (Broady, 1977b, 1979a), where the population dynamic dominant algae were followed over 21 months. Mean algal numb moss turf were 3439 (*Polytrichum alpestre*) and 1046 (*Chorisodon phyllum*) $\times 10^3$ cm^{-2}, with the majority being found in the top 1.5 c profile, and of the 11 species found, *Monodus subterraneus* was dor all seasons. In a moss carpet (*Calliergon–Calliergidium–Drepanocl* algal species were found and mean numbers varied from 136 (winte (summer) $\times 10^3$ cm^{-2}. Five green and yellow-green speci numerically dominant. Extending his quantitative survey to 50 sit senting six terrestrial habitats on Signy Island, Broady (1979b) fo mean culture counts of algal propagules ranged from 219 (fellfield 7641 (soil beneath grass and cushion plants) $\times 10^3$ cm^{-2}, and simila distribution patterns to the moss sites were observed. In an exper measure wind dispersal at Signy Island, viable algae, fungi and were recovered mainly in the summer on exposed nutrient agar The algae were all resident species and no evidence of potential from other areas was obtained (Broady, 1979e).

3. Invertebrates

3.1 Introduction

As there are no true terrestrial vertebrate animals in Antarc dominant macroscopic land fauna is composed of arthropods (principally springtails or Collembola) and arachnids (mainly

Larger invertebrates such as annelids (earthworms and enchy-
, land molluscs, the higher insects (Diptera, Hymenoptera and
era) and spiders (Araneida) are confined to warmer and
ally less severe areas, e.g. parts of the maritime Antarctic and sub-
ic. Microscopic invertebrates such as protozoans, rotifers, tardi-
nd nematodes are abundant in soil and peat which becomes free of
the austral summer. The land arthropods of the Antarctic Region
five groups of Acari (meso-, pro-, a-, crypto- and meta-stigmatids)
is Collembola, biting or feather lice on birds, sucking lice on seals,
s and two chironomid midges. The Antarctic land fauna, although
id impoverished by comparison with warmer regions, is still in-
ely known. Table I gives the number of species recorded for the
rate groups in each of the three ecological zones of the Antarctic.
h the distributions of most arthropod groups and their main species
known, a considerable amount of ecological survey and taxonomic
nains to be done for many of the microscopic groups.

istory of entomological investigations in Antarctica parallels the
exploration of the continent, but the study of non-arthropod in-
tes has lagged behind arthropod work. About one-third of the
errestrial arthropods were discovered by the early expeditions at
of the twentieth century. The first party to collect arthropods was
ian Antarctic Expedition (1897–1899) to the Antarctic Peninsula
bsequently, for approximately half a century, there was almost no
d collecting, and much of the remaining two-thirds of the fauna
me known during the past 20–25 years. Important contributions in
ect have been those of Gressitt (1967a, 1970a) of the Bishop
in Hawaii and his co-workers, but also by others, especially
s of the British Antarctic Survey (see Holdgate, 1970).

of the early invertebrate work in Antarctic terrestrial locations is
the relevant bibliographies (Gressitt and Weber, 1959; Gressitt
r, 1961; Arnaud *et al.*, 1967). These collectively provide an intro-
to the literature up to the early 1960s, and the present review
s this by listing the main publications to 1982. A general introduc-
Antarctic terrestrial animals can be found in Gressitt (1965a),
f arthropod ecology and biogeography are discussed in Gressitt
and some distributional information given in Greene *et al.*, (1967).
bitats are briefly reviewed by Gressitt and Leech (1961), and ento-
l work up to the mid-1960s south of 60°S has been drawn together
, 1967b).

Antarctic proper, soil water availability is as important as the
ects of temperature to most arthropods (Spain, 1971), and in-
1 both allow activity in high latitude habitats (Wise and Shoup,

The numbers of species in groups of terrestrial invertebrates which have been ide
the sub-, maritime and continental Antarctic zones (compiled from vario

Group	Sub-Antarctic zone	Maritime Antarctic zone	Cont Antarc
Protozoa	(124+), 83[b]		(68
Rotifera	—	—	
Tardigrada	—	17	
Nematoda	22	40	
Annelida	4	(2)	
Mollusca	3	0	
Arthropoda	358	(68), 5[a]	(78
Crustacea	1	(1)	
Copepoda	—	(1)	
Isopoda	1	0	
Insecta	210	35, 2[a]	49
Collembola	37	8	
Pscoptera	3	0	
Mallophaga	61	25	
Anoplura	6	—	
Hemiptera	4	0	
Thysanoptera	2	0	
Lepidoptera	3	0	
Diptera	44	2	
Chironomidae	9	2	
Remainder of families	35	0	
Siphonaptera	6	—	
Hymenoptera	4	0	
Coleoptera	40	2[a]	
Arachnida	144	(32), 3[a]	(29
Araneida	14	0	
Phalangida	1	0	
Pseudoscorpionida	1	0	
Acarina	128	(32), 3[a]	(
Mesostigmata	46	(4)	
Metastigmata	3	(3)	
Prostigmata	20	10	
Cryptostigmata	32	14	(
Astigmata	27	1, 3[a]	
Myriapoda	3	0	
Pauropoda	2	0	
Symphyla	1	0	
Total all groups, excluding Protozoa	387	(127), 5[a]	(10

— number unknown; ( ) number uncertain; [a] introduced species. [b] Refers to both the sub-A
maritime Antarctic zones.

1971). A detailed study of the environmental features near Hallet
was made by Pryor (1962), and during the period 1959–1966 compr
insect surveys were undertaken by teams of the U.S. Antarctic
Programme (Gressitt *et al.*, 1963, 1964; Wise *et al.*, 1964; Wise a
1967). Substantial investigations were carried out during the 196

ne Antarctic in an attempt to understand the distribution and basic
of soil arthropods (Strong, 1967; Tilbrook, 1967a) and other in-
ates (Tilbrook, 1967b, 1970a, 1973b). At the same time, the work of
acarologists and entomologists in the sub-Antarctic was published
comprehensive entomology of South Georgia and Heard Island
tt, 1970a). Terrestrial invertebrate research in the sub-Antarctic
ppears to have developed less rapidly than in the other Antarctic
primarily due to the wide dispersion and geographical isolation of
of the sub-Antarctic Islands and the greater faunal diversity. An
ant contribution was that of Watson (1967) who recorded 119 species
living arthropods on Macquarie Island; of which he considered 31%
ndigenous and 69% not well established. Of the total species list,
ere associated with plants, the remainder having animal associa-
Dreux (1965, 1966, 1970, 1971a) has provided information on the
od fauna of Îles Crozet, whilst Davies (1973) has given a
hensive account of the distribution of 46 species of surface-living
ods in three habitat types (sea-edge, moorland and bog, fellfield) on
them, Île de la Possession. Dreux (1971b) gives information on
ial invertebrates at Marion Island.

r data on the density, biomass and energy content of the terrestrial
nvertebrates (Oligochaeta, Mollusca, Araneida, Lepidoptera and
tera) in 19 vegetation types at Marion Island have been given by
(1978). Mean annual values of 1980 individuals m^{-2} (density) and
m^{-2} (dry-weight biomass) provided *c.* 27% of the resident
ills' *Chionis minor* and *c.* 13% of the kelp gulls' *Larus dominicanus*
hich was equivalent to *c.* 8% of the total standing crop of macro-
rates. Invertebrate food resources of this type were imporant for
ls' winter survival at Marion Island. Sticky traps have been tested
ully to monitor invertebrate surface movements at Marion Island
, 1979) and near Grytviken, South Georgia. The former gave rates
3 invertebrates 100 trap-h^{-1}, whilst the latter varied from 17
via bog) to 51 (*Acaena* spp.) arthropods 100 trap-h^{-1} in January
. C. West, personal communication). The numerically dominant
at South Georgia were perimylopid beetles, especially *Hydro-*
sparsutum, on *Festuca* grassland and *Acaena*, and spiders on
ia and a *Polytrichum* moss bank. There was much variation be-
ne four areas examined and between arthropod groups.

kely that in the next decade an examination of the total terrestrial
rate fauna of isolated islands or groups of islands will lead to the
y of new species and extend the known distributions of many in-
te groups. Such work in the past has been limited to short visits and
ons where biology was ancillary to other objectives. It is clear that

the land fauna of the South Sandwich Islands (Baker *et al.*, 1964; H and Baker, 1979) would repay further study, as also that of th Shetland Islands and of the Elephant Island group in particular 1979c). The discovery of enchytraeid worms and terrestrial cope Elephant Island (Block, 1979c) has gone some way towards confirm the South Shetland Islands are one of the most ecologically favour for terrestrial organisms in the Antarctic (Holdgate, 1977). Th Sandwich Islands have remained largely untouched by man and unique communities influenced by fumarole heating. Bouvetøya is island in the maritime zone which demands further investigation (H *et al.*, 1968).

The dispersal of insects and other arthropods by wind current Antarctic has been of considerable interest, primarily to determi zoogeographical relationships and the probable rates of present-da gration as an indication of past colonization patterns and processes itt, 1961; Brundin, 1970). The southernmost trappings by nets on sl on land included Acari, Collembola, Homoptera, Coleoptera, Dip Hymenoptera (Gressitt *et al.*, 1961; Clagg, 1966), some specimens o originated further north. Comparison of sub-Antarctic island inse isolated tropical island suggests a scarcity of Heteroptera (es Homoptera) on the former, whilst Hymenoptera are reduced, an notably absent, orthopteroid insects, Ephemeroptera, Plecopt Trichoptera are absent or poorly represented. Although prevailin are not favourable for dispersal of small invertebrates to the A Continent, air currents together with bird transport may be impo colonization in this region. The lack of a good fossil record (six only) makes a consideration of the origin of the Antarctic land fau cult. Aptery and flightlessness in the insects are common. Endemis in some groups possibly resulting from local evolution, island-hop extinction in source areas (Gressitt, 1965b). In respect of the sub-A islands it was thought that faunal transfer occurred after the evolved, and particularly after the Pleistocene. Gressitt (1970b) co this to be true for South Georgia, Marion, Heard and Macquarie However, evidence is accumulating to suggest that the land faun Antarctic Region may be related to those of several southern con and that the apparent endemic genera may have survived the Pleisto the Antarctic continent (Gressitt, 1971).

In what follows below, the major emphasis has been placed Arthropoda and on the micro-arthropods (Collembola and Acari) ticular. This is because they are the numerically dominant grou vertebrates in the Antarctic land fauna, and consequently, there is body of information available. Higher insects become more impo

Antarctic (see Table I), but their treatment will not be so thorough the patchiness of data. The order is systematic, and within each nformation is given on taxonomy and systematics, ecology and ogy.

otozoa

s (1907) was the earliest to record terrestrial Protozoa from the olar region, which consisted of testate amoebae from various sub- ic localities collected by the German and Swedish South Polar Ex- is (1901–1903). A concise historical review of the literature with the principal records is given in Smith (1978), which shows that a rable amount of research has been done since 1960. Sudzuki (1964) d 26 testate and five naked amoebae, 23 ciliates and nine flagellates water of Greater Antarctica. Eighteen testate species were found soil, seven of which were also present in moss peats, on Signy Island 965; Heal *et al.*, 1967). A total of 53 testates was recorded from a of habitats on Marion Island (von Grospietsch, 1971), and 24 cili- re identified from Anvers Island on the Antarctic Peninsula son, 1972). A wide diversity of flagellates, Testacida and ciliates en reported by Smith (1972, 1973a,e, 1974a, 1975) from Elephant the South Orkney Islands and Îles Crozet (Fig. 2C–F). Volcanic on Deception Island contained flagellates and ciliates (Smith, Present records of terrestrial Protozoa remain very incomplete, but lyses of 97 sub-Antarctic and maritime Antarctic island sites by 978) revealed 124 species of which 83 were considered to be estab- embers of the fauna. In the total faunal list there were 35 testate naked amoebae, 31 flagellates and 48 ciliates.

Testacida were estimated at 890×10^6 individuals m^{-2} with a of *c.* 2 g live weight m^{-2} in *Deschampsia* grassland soil at Signy Heal, 1965), and from <300 to 1170 individuals g^{-1} fresh weight of ss *Drepanocladus uncinatus* (Smith, 1974a). In contrast, on t Island, South Shetland Islands, numbers varied from 170 to 7700 weight of soil in vegetated habitats (Smith, 1972). Studies of a f and a moss carpet site at Signy Island suggested that flagellates 190 individuals cm^{-2}) and testates (11,740–34,860 individuals ere the dominant groups.

nal changes in density related to freeze–thaw conditions of the peat increase of bacterial and yeast numbers at thaw were shown by *n dubium*, which constituted on average 43% of the testate fauna oss turf. Its population dynamics were determined principally by ture and moisture content of the peat (Smith, 1973b). Work on

Protozoa inhabiting chinstrap penguin guano, by Smith (1973c), strated that when penguins left and pH was lowered, colonizatio guano by more acid tolerant Protozoa did not occur during the en months. Low moisture content of volcanic tephra was the major factor to protozoan colonization of samples from Deception following eruptions in 1967, 1969 and 1970 (Smith, 1974a). A stud bi-polar genus *Colpoda* (Ciliata) (Smith, 1973d) suggested that it i from the Antarctic because the summers are too cold and sl *Colpoda* spp. to establish and maintain themselves in terrestrial h whereas the Arctic and sub-Antarctic areas in which the genus have longer and warmer summers.

The need for qualitative and quantitative information on the and respiratory contribution to individual Protozoa energetics i Davis (1981) has suggested that in moss communities this gro critical importance to the energy flux especially under maritime A conditions.

3.3 Rotifera

The first records of Antarctic rotifers were by Murray (1910a). species of rotifers were identified from moss-water communities zuki (1964) and a single species by Matsuda (1968) in Greater An Of the 700 species of rotifers hitherto identified, only 15 species ha recorded in Antarctic samples (Sudzuki, 1979). All rotifers re water film in which to live, and they are found in greatest abun the wetter communities (Tilbrook, 1967b, 1970a). The south record is from macroscopic algae (Wise and Gressitt, 1965).

In eight sites at Signy Island rotifer numbers ranged f (moss carpet) to 931 (*Prasiola*) $\times 10^3$ m^{-2} (Jennings, 1976a,c) study of two moss communities showed that total population den high (10^5 individuals m^{-2}) and with no marked seasonal changes (J 1979). Adinetids were found in 84%, whilst other bdelloid rotife recovered from 98% of a series of samples from the Antarctic P and Scotia Ridge region by Jennings (1976b). Monogont Rotife not abundant, being found in 30% of the samples. As with tar highest densities occur in areas fertilized by birds and othe brates.

Some preliminary observations on the frost resistance of the A rotifer *Philodina* sp. have been made by Aoki and Konno (1961), (1967) and Koehler and Johnson (1969).

rdigrada

ecies lists of Antarctic tardigrades exist. The earliest were those of (1906) who described five species from Laurie Island in the South Islands, and from the collections of the British Antarctic Expedi-07–1909 (Murray, 1910b). More recently records have been given ikawa (1962), Sudzuki (1964), Matsuda (1968) and Ramazzotti Jennings (1976a,c) found 16 species in a detailed survey of 43 ranging from lichens and mosses to freshwater on Signy Island; *mollis* was reported from the Antarctic for the first time (Fig. Examination of collections from a further 70 sites in the Scotia and Antarctic Peninsula yielded 11 species or species groups gs, 1976b). The most common species in the maritime Antarctic ere *Macrobiotus furciger*, *Hypsibius* (*H.*) *dujardini*, *H.* (*Dipha-lpinus* and *H.* (*D.*) *pinguis* in a range of moss, soil and grass . A total of 28 tardigrade species in seven genera has been found whole of Antarctica to date (Sudzuki, 1979), which represents % of the species and 35% of the genera of world-wide terrestrial

a Baermann wet-funnel technique Tilbrook (1967a, 1970a, 1973b) d tardigrade densities of 88–100 $\times 10^3$ individuals m^{-2} in the moss *utans* over ten months in 1962 at Signy Island. Extracts of other revealed few tardigrades. Using a more efficient tray method for n, Jennings (1976a) found densities varied from 0.011 (*Polytri-horisodontium* moss turf) to 14.130 (*Prasiola crispa*, foliose 0^6 tardigrades m^{-2} at Signy Island. Sites affected by vertebrates er populations of tardigrades, and four species accounted for over the total biomass (26 mg live weight m^{-2} in moss turf, 1.2–19.8 g ght m^{-2} in fertilized areas). A detailed study of the population s of the tardigrades of two moss sites at Signy Island revealed of 309 (dry moss turf) and 713 (wet moss carpet) $\times 10^3$ animals ing 1971–1973 (Jennings, 1979). Using data for respiration of *otus furciger* (Jennings, 1975), which ranged from 0.18 to 1.82 nl idual^{-1} h^{-1} over 5–10°C, it was possible to calculate annual total le respiration for these sites assuming negligible oxygen uptake C. The estimates were 306 and 610 ml O_2 m^{-2} respectively for metabolism on the wet site being twice that of the dry one.

grade population densities were highest (1.92×10^6 m^{-2}) in of mosses and an alga from King George Island, South Shetland Jennings' (1976b) survey.

lerty (1964) has made observations on the culture and nutrition of rctic strain of *Hypsibius arcticus*. Apart from the preliminary

study by Jennings (1975) on oxygen uptake of *M. furciger*, no othe
logical work has been published for Antarctic species.

3.5 Nematoda

The early studies (De Man, 1904; and others) on terrestrial nemato
taxonomic, and these are reviewed by Maslen (1980). Latterly
(1972) described the new maritime species (also a new genus)
tenchus hooperi, a tylenchid, from a variety of mosses at Signy
Subsequently, 30 species of 19 genera were recorded from the san
(Spaull, 1973b), and information provided on the distribution o
todes on 15 maritime Antarctic islands (Spaull, 1973c).
Dorylaimoidea were described by Loof (1975) from collections ma
maritime zone, and three new species from each of the genera *A*
choides and *Teratocephalus* have been described (Maslen, 1979a) (
To date 40 species (34 endemic) have been recorded from the r
Antarctic, while ten species (seven endemic) and 22 species (12 e
have been reported from the continental and sub-Antarctic zones
tively (Maslen, 1980). The causes of the high endemism of the mari
continental nematode fauna are unknown and further taxonomic
tributional studies are required.

The first ecological account of nematodes was by Bunt (1954a) w
the sub-Antarctic at Macquarie Island. He examined 40 sites three
one year and found densities of $0.27–123.76 \times 10^6$ nematodes m
genera were identified. Populations of 1.2×10^6 nematodes m^{-2} we
by Tilbrook (1967a,b, 1973b) at Signy Island compared to
individuals m^{-2} in fumarole-affected areas in the South Sandwich
both of *Pohlia* moss, and Tilbrook (1970a) briefly reviewed earlier
substantial contribution to the ecology of Antarctic nematodes w
by Spaull (1972a,b,c,d,e,f) working at Signy Island. In moss
numbers declined during freeze–thaw cycles especially in the uppe
and there was evidence of vertical migration in the spring and
Microbial feeders were most abundant, nematode biomass ranged
to 8.2 g live weight m^{-2} and oxygen consumption from 54 to 2014 μl
at 5°C at Signy Island. Latterly Maslen (1979b, 1981), in a detailed
two bryophyte sites at Signy Island, identified 27 species (15 ge
which *Teratocephalus tilbrooki* (mean density 373.5×10^3 m^{-2}) and
cephalus rugosus (mean density 129.3×10^3 m^{-2}) were the most im
The total nematode population density and biomass were $766.9 \times$
150.5 mg live weight m^{-2} (dry site) and 447.0×10^3 m^{-2}, 301.8
weight m^{-2} (wet site) respectively. Over 80% of the worms occurr
0–3 cm stratum of the dry site in summer compared to 66% in the

ne of the wet site. At 5°C, population respiration was calculated at d 76.1 μl O_2 h^{-1} m^{-2} respectively, which was only 0.09 and 0.21% of al moss respiration. Caldwell (1981) gives details of the seasonal cs of the nematodes of these sites.

atode predators appear to be few; certain hyphomycete fungi are to prey mainly, though not exclusively, on these animals (Maslen, and the predatory mesostigmatid mite, *Gamasellus racovitzai* has bserved with nematodes in its chelicerae (Block, unpublished).

nt work on the energetics of the common nematodes of moss nities in the maritime Antarctic shows considerable variability in ory levels (J. R. Caldwell, personal communication). The fungal *Aphelenchoides*, ranging in live weight from 66 to 492 ng, had ion rates of 20 to 738 nl O_2 individual^{-1} h^{-1} over its normal summer ature range of 0–10°C. At similar temperatures, the predatory *Co-s gerlachei* of 0.94–29.79 μg live weight, showed oxygen consump-es of 74–5170 nl O_2 individual^{-1} h^{-1} using gradient diver techniques. l mode of life clearly influence metabolism in such animals.

igochaeta

orms have been found on many sub-Antarctic islands (Benham, ickford, 1932). Four species of oligochaete occur on Macquarie three of them being enchytraeids (*Lumbricillus macquariensis*, *ina antipodum*, *M. werthi*, and the fourth a megascolecid (*Micro-Votiodrilus*) *macquariensis*)). A single megascolecid *Microscolex us*, thought to be endemic, has been recorded for South Georgia. aeid worms have been extracted from *Acaena* humus in high s at South Georgia (Block, unpublished), and estimates of up to rms m^{-2} in grass soil have been made (Smith and Stephenson, 1975; nd Walton, 1975). Four species of enchytraeid have been identified rious lowland soil communities on South Georgia, three being holarctic forms: *Cognettia glandulosa*, *Cognettia sphagnetorum*, *perpusilla* and the fourth being a rare species related to *Marionina* (B. Christensen, personal communication).

worms (*Microscolex kerguelarum*) comprised between 73 and 89% ean monthly dry weight biomass of the macro-invertebrates of 19 on types at Marion Island (Burger, 1978). Their average density 4 worms m^{-2} and 356 cocoons m^{-2}, which produced a mean ed) biomass of 14.6 and 0.4 g dry weight m^{-2} respectively. The formed an important component of the diet of two bird species ills and kelp gulls) at Marion Island, especially during winter.

3.7 Mollusca

Gastropod land snails have been found on some sub-Antarctic Islan (1964) described *Notodiscus hookeri heardensis* from Heard Isla reported a snail (*Phrixgnathus hamiltoni*) and the Europe (*Agriolimax reticulatus*) from Macquarie Island, the latter being a duction. *Notodiscus hookeri* on Kerguelen, Possession, Marion an Islands is considered to be morphologically similar to the Austral New Zealand rather than to the South African forms (Solem, 1968)

Smith and Walton (1975) stated that "at least one mollusc inhabits moss cushions on rock faces" at South Georgia. Small fi pulmonate snails collected from rock crevices near Hope Point berland East Bay were similar to the Arionacean Family Endod but all were juveniles (Block, unpublished). Sexually mature fo required to make a specific indentification.

The land snail *N. hookeri* had a mean population density of 33 ind m^{-2} (equivalent to *c.* 0.3 g dry weight m^{-2} biomass) at Marion (Burger, 1978), which made up about 1% of the total macroscopic brate biomass in 19 plant communities. Slugs (one unidentified were also present (18 individuals m^{-2}) in the area studied.

3.8 Arthropoda

3.8.1 Crustacea

Copepoda. Several small copepods were found in terrestrial hab Elephant Island, South Shetland Islands (Block, 1979c). The site from lichen encrusted rocks to areas in chinstrap penguin rooke nests of Wilson's storm petrel. Specimens were collected up to 2 k the sea at 230 m a.s.l. from rocky outcrops. The copepods, thoug terrestrial, creeping harpacticoid forms, are being studied by speci confirmed, it will be the first record of such terrestrial Crustace Antarctic Region.

Isopoda. One species (*Antarctoniscus jeanneli*) has been found i land, bog and fellfield habitats on Île de la Possession (Davies, 1973

3.8.2 Insecta

Collembola. Springtails were first collected in Antarctica in 18 the Peninsula by the Belgian Antarctic Expedition. Three speci known as *Friesea grisea*, *Cryptopygus antarcticus* and *Parisotom*

were described from these collections by Willem (1901, 1902) (Fig. In 1899, during the British Antarctic Expedition, *Isotoma klovstadi* ınd on the north coast of Victoria Land (Carpenter, 1902). Subse-', many collections and surveys have been made of Antarctic and tarctic Collembola, (reviewed by Gressitt, 1967b, 1970a; and Wise, 970a,b, 1971). There are *c.* 17 species of Collembola in the con- l and maritime Antarctic, with 37 species in the richer sub-Antarctic The total Antarctic collembolan fauna numbers *c.* 47 species, of '0% are endemic (Wallwork, 1973). Collembola, together with the have penetrated to terrestrial habitats further south than any other ods. Two Collembola species (*Biscoia sudpolaris* and *Anurophorus ıris*) were found at 83°50'S by Tyndale-Biscoe (1960). Wise and t (1965) reported *A. subpolaris* and a *Tullbergia* sp., together with pecies of Acari, at 84°47'S; 176°W. Collembola are widespread ıout many terrestrial habitats in continental, maritime and sub- ic zones, and Rapoport (1971) has remarked on the increased of pigmentation of Antarctic forms.

' work on collembolan ecology in the continental zone concentrated ir distribution in a range of terrestrial habitats, including 'stem" and "chalikosystem" and both coastal and inland sites of ictoria Land (Janetschek, 1967a). Much of the information on field and environmental effects on the distribution patterns is summar- Janetschek (1970). Soil moisture, relative humidity and tem- e were considered to be locally the most important, whilst ion density reduced with increasing latitude and altitude. Favour- ıditions for breeding were limited to the short summer period. At allett, the distribution and numbers of three Collembola species in mmer were not clearly related to moisture levels (Wise and Shoup,

e maritime Antarctic, arthropod surveys included estimates of ɔola populations in a wide variety of habitats (Tilbrook, 1967a; , 1967c) in the Antarctic Peninsula, South Shetland Islands, South Islands, South Sandwich Islands and Bouvetøya. Tilbrook (1967b) ɔd the interrelationships of the Collembola of these areas. Highest s occurred in vegetation, both cryptogamic and phanerogamic, ıe Collembola were concentrated in the upper layers. *Cryptopygus :us* was the dominant arthropod but considerable variation in omposition existed. Localities affected by fumarolic heat possessed diverse and abundant fauna. Strong (1967) working at Palmer Antarctic Peninsula, was the first to examine the food relations of al microarthropods; the Collembola feeding primarily on fungal and dead plant material. Lippert (1971) reported on the relative

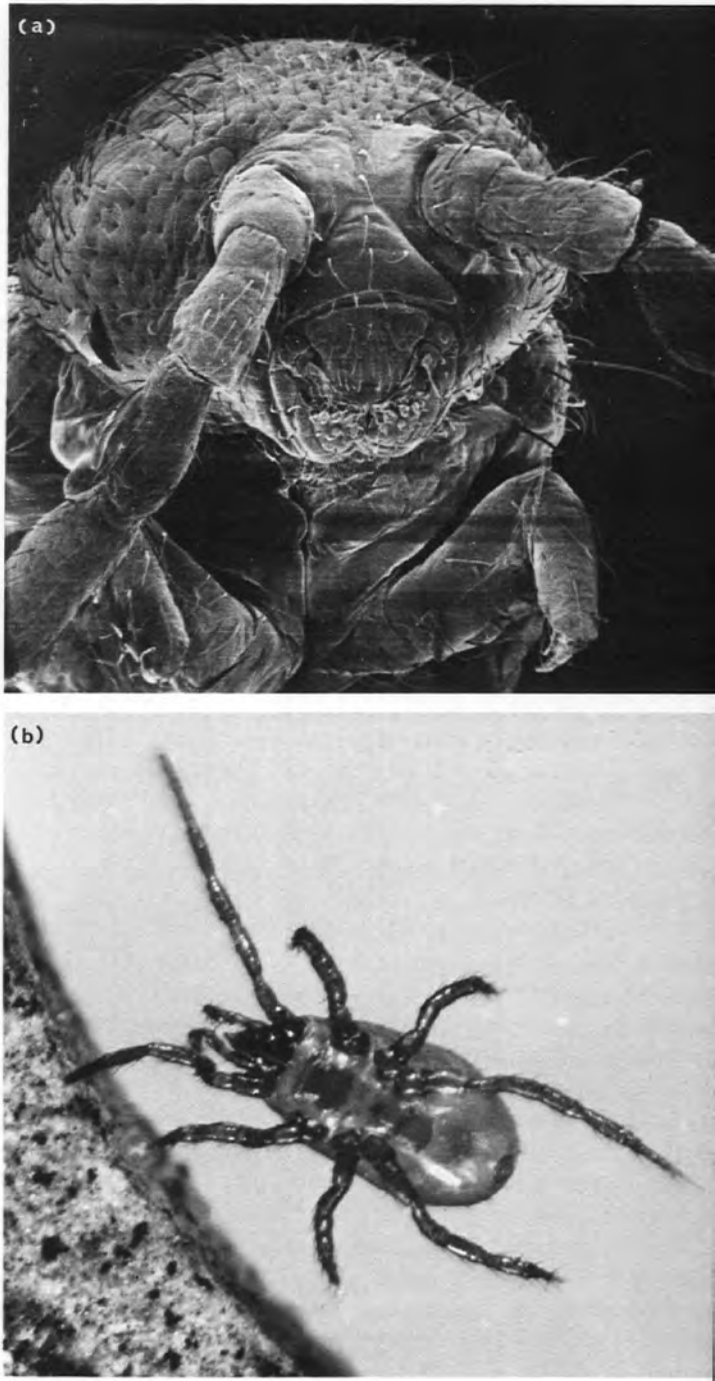
occurrence of several Collembola in mosses at Anvers Island. A
Island, four springtail species were found in a detailed study by T
(1967a, 1973b), and data on the seasonal abundance of the domi
antarcticus obtained for three moss–lichen vegetation types. N
numbers were *c.* 116×10^3 individuals m^{-2} in a stand of *Pohlia nu*
antarcticus was extracted from 68 out of 70 qualitative samples an
the highest relative abundance in 81% of these samples. At eight
along a 150 m transect from the shore inland on Robert Island
Shetland Islands (Etchegaray *et al.*, 1977), Collembola were the do
faunal group (99%) and were found in the lower, warm and wet s
whilst the Acari inhabited the higher, cold and dry stations. Colo
by Collembola of sterilized vascular plant litter introduced from
Robert Island was slow, being more restricted at the surface than
(5–10 cm) in moss (Saiz *et al.*, 1970).

A single ecological study has been made of the more diverse Col
fauna on the sub-Antarctic island of South Georgia. The populatio
mics of six species were followed over two years in two soil-litter ha
Festuca contracta grassland and a *Polytrichum–Chorisodontiu*
bank. Maximum numbers occurred at the end of summer (May
minima were observed in winter and spring (August and Novembe
total population varied from 46.5 to 106.9 (grassland) and from 20.9
(moss bank) $\times 10^3$ individuals m^{-2} (C. C. West, personal communi
The fauna was similar for both sites, with *Friesea grisea* dominan
grassland (maximum density 4620 compared to 550 individuals m
moss site), and *Setocerura georgiana* having comparable m
numbers on both sites (grassland: 1870, moss bank: 2255 individua
The species composition of Collembola was similar in two other co
ties, a dwarf shrub (*Acaena*) and a bog (*Rostkovia*).

Relatively little attention has been paid to single-species stu
Pryor (1962) investigated *Isotoma klovstadi* in relation to enviro
features at Hallett Station, north Victoria Land. Large numbers in
areas adjacent to penguin rookeries and fed on mosses and lichens i
humid conditions. Specimens tolerated low temperatures (experi
to −50°C), but desiccation at low RH was an adverse factor. Hibe
occurred particularly in the egg stage, but also in the adult stage
schek (1967b) attempted to model two populations of *Gomphio*
hodgsoni from Cape Crozier (Ross Island) and Mount England (so
toria Land coast). Instar duration ranged from 6.4–8.2 days, sexua
ity was achieved in 38.5–49.2 days, and maximum longevity was
active life or two years with hibernation periods. Some feature
biology and distribution of *Cryptopygus antarcticus* were outline
brook (1970b).

y two studies of Antarctic collembolan population dynamics have made: *Gomphiocephalus hodgsoni* by Peterson (1971) and *Crypto-antarcticus* by Tilbrook (1977) and Block (1982a). The former at Cape Ross Island, undertaken during the summer of 1967–1968, showed es of density from *c.* 1000 to 3330 individuals m^{-2} correlated with ate moisture content. The January maximum corresponded with the of Wise and Spain (1967), but the latter were generally at lower ies (47 to 188 individuals m^{-2}). The instar composition of the *G. oni* population suggested that there are two interlocking series of ations, and environmental conditions permitted either one or both to during the summer. A two-year population study of *C. antarcticus* in itime Antarctic moss turf demonstrated that mean annual density from 19.6 to 98.5×10^3 individuals m^{-2} with an average biomass of g live weight m^{-2} (Block, 1982a). Size-class analysis showed an ally consistent distribution throughout the two years, with a high rtion of young individuals which may have been due to generation >1 year, and a more rapid juvenile growth rate (Tilbrook, 1977). ations of population respiration varied from 514 to 893 ml O_2 m^{-2} oduction was estimated as 1228 mg m^{-2}, and assimilation was ated to be 8.42 Kcal m^{-2} y^{-1} with an assimilation efficiency of %. *C. antarcticus* has relatively high respiration: production ratio and imilation efficiency which corresponds to those for detritus-feeding ebrates. The annual mean density of *C. antarcticus* decreased from n 1972) to 36.2 (in 1973) $\times 10^3$ individuals m^{-2} in the moss turf, but a old decline was recorded in its annual mean population size in a moss carpet at the same time (Block, 1982a). The factors inducing hanges are unknown.

of the keys to understanding the ecology of Antarctic Collembola is eeding biology. *G. hodgsoni* in Victoria Land is reported to feed ninantly on soil fungi (three species of Phycomycetes), but *Prasiola* und in the guts of animals from one locality (Fitzsimons, 1971a). gut contents, faecal pellet analyses and microbiological techniques, y (1979c) determined that *C. antarcticus* selected its food items; ntous fungi and algae being the most important at Signy Island. Its parts are simple in structure (Fig. 3a) with grinding surfaces on the bles. *C. antarcticus* may play an important role as a consumer either ng micro-algae or of decomposer micro-organisms, and thereby their decomposition. Dissemination of viable algal cells and micro-sms in faecal pellets by such Collembola may also be significant. ling the study of *C. antarcticus*, Burn (1981) investigated the relation ling, faecal pellet production and moulting to a range of constant ratures (0–20°C) in the laboratory. He suggested that its moulting


(a)
(b)

iour is cold adapted, as both the maximum moulting frequency and inimum temperature at which moulting occurs are lower than in rate Isotomidae. Individual growth rates were measured at 10°C mandibles recovered from the shed exuviae. At a critical size (body between 1040–1134 μm) individuals either increased or decreased in subsequent moults. Such degrowth, may be due to the association of ing and excretion in Collembola. Burn hypothesized that the ium age of the largest specimens of *C. antarcticus* at Signy Island is bly 3–7 years. Field studies are in progress to test these findings.

lembolan physiology has been confined to studies of respiratory olism, lethal temperatures and preliminary cold tolerance experi- (see pp. 200–207). Measurements of individual oxygen uptake in *opygus antarcticus* were made initially on cultured animals (Tilbrook lock, 1972), and later, using a Cartesian Diver micro-respirometer for st time in the Antarctic, on field fresh animals at Signy Island (Block ilbrook, 1975). Mean oxygen uptake over the full size range varied .67 to 22.61 nl O_2 individual^{-1} h^{-1}, and from 95.66 to 469.20 μl O_2 g^{-1} er the temperature span 0–10°C. Relationships of respiration to live t and temperature were derived, and Q_{10} varied from 1.99 (juvenile) 4 (adult). Long-term storage (387 days) at 5°C decreased respiration n both an individual and a live weight basis (Block and Tilbrook, which may be adaptive in this species. Specimens of *C. antarcticus* at Georgia were smaller, lighter in weight and sexually mature at a r size than at Signy Island (Block and Tilbrook, 1978). The respir- weight and metabolism–temperature curves were not significantly nt for the two populations, however. In field-fresh *Parisotoma octo-*, mean respiration rates at 5°C were 2.14–10.75 nl O_2 individual^{-1} d 233.4–471.1 μl O_2 g^{-1} h^{-1} (Block, 1979b). Comparison of the above nd those of Strong *et al.* (1970) for *I. klovstadi*, of Dunkle and Strong and Marsh (1973) for *C. antarcticus*, and with metabolic rates of s from temperate habitats, suggests that cold adapted Collembola elevated metabolism. Using temperature gradients, Fitzsimons) found that *Gomphiocephalus hodgsoni* aggregated between 8 and , with most activity occurring between 7 and 15°C. Its upper lethal rature was 29.5°C at >90% RH, the lower limit was between −11 and

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a) Stereoscan electron micrograph of the head and mouthparts of the collembolan *gus antarcticus*. The bases of the antennae, several ocelli (simple eyes) and the first pair of also visible. The width of the head capsule is approximately 150 μm. (b) Ventral view of ostigmatid mite *Gamasellus racovitzai* (female), which is the sole predator in the d community of terrestrial areas at Signy Island, South Orkney Islands. Photograph by rt and A. Lister.

−23°C, and with prior temperature acclimation having no effect on s
at low temperatures.

Pscoptera. Psocids (three species) are confined to the sub-Ant
occurring on Marion, Crozet, Kerguelen and Macquarie Islands (G
1970a). *Antarctopsocus daviesi* has been found under stones in fellfi
Île de la Possession (Davies, 1973).

Mallophaga. Gressitt (1970a) lists 37 and 34 species of biting lic
South Georgia and Macquarie Islands respectively. Kerguelen and
Islands have 19 and 17 species respectively, whilst Marion and
Islands possess three and four species respectively. The populati
three species of *Austrogoniodes* on pygoscelid penguins were discus
Clay (1967), whilst Clay and Moreby (1967) listed 42 species of Mallo
from Antarctica. Birds occurring in the south polar region are know
hosts of at least 60 species. Infestation rates of the south polar skua
aracta skua maccormicki) at Ross Island may be high: 14–25 lice
(Schaefer and Strandtmann, 1971), whilst Spellerberg (1971) found
the skuas at Cape Royds infested with two lice species with mean i
tions varying from 3.5 to 20 lice host^{-1}. A comprehensive list of the
phaga recorded from 58 species of birds on the sub-Antarctic islan
been compiled (Clay and Moreby, 1970).

Anoplura. Restricted to the seals (Pinnipedia), there are likely t
many species of sucking lice as there are seal species in the Antarcti
species have been found (Clay and Moreby, 1967, 1970) with no r
from otariids (fur seals). It is remarkable that the Antarctic fur seal (
cephalus gazella) is devoid of ectoparasites and has very few endopa
(T. S. McCann, personal communication). Both ecological and p
logical observations have been made for the louse, *Lepidophthirius*
rhini, on the elephant seal (*Mirounga leonina*) (Murray, 1958).

Hemiptera. Two species of aphids (Family Aphididae) have
recorded from Macquarie Island and South Georgia (Eastop, 1962,
Jacksonia papillata and *Rhopalosiphum padi.* Both feed at the ba
grass stems especially *Festuca* spp. and the former is more commo
aphids and one coreid bug (*Phthirocoris antarcticus*) have been found
de la Possession (Davies, 1973).

Thysanoptera. The Family Thripidae is represented in the sub-An
by two species. At Macquarie Island, one species of a new
(*Physemothrips chrysodermus*) was reported (Stannard, 1962), w

Georgia only females and larvae of a single species (*Anaphothrips rnis*) have been found (Wilson and Stannard, 1970).

idoptera. Three species have been described: *Embryonopsis halticella* y Yponomeutidae) from Possession Island (Viette, 1952) and Heard (Common, 1970), *Eudoria mawsoni* (Family Pyralidae) which breeds icquarie Island (Common, 1962), and *Pringleophaga kerguelensis* y Tineidae) (Enderlein, 1905) from Marion, Crozet, and Kerguelen s.

era. The true flies do not penetrate the Antarctic except for two s of Chironomidae (midges): *Belgica antarctica* is wingless, occurs in tarctic Peninsula and South Shetland Islands and is the southernmost etabolous free-living insect, whilst the winged *Parochlus steinenii* is from the South Shetland Islands and South Georgia (Fig. 2L,M). and Gressitt (1967) summarize the information on both species.

sub-Antarctic dipteran fauna appears from scattered records to be nore diverse. Gressitt (1970b) lists 13 species for South Georgia, three hironomids. Taxonomic information on the various groups may be in Gressitt (1970a). About 15 species representing ten families have ound at Macquarie Island (Gressitt, 1962), where the Diptera are ant in terms of species number of all the free-living insects.

nversion polymorphism was reported in *Belgica antarctica* by Martin and chromosomal variability has been studied in the same species ey and Davis, 1979).

ham (1971) studied *B. antarctica* at Anvers Island and correlated bundance with chemical features of the soil substrate. Some physio- observations were reported, including its inability to supercool. This en further investigated in relation to the mechanism of freezing ce by Baust and Edwards (1979) and is discussed below.

structure and larval population dynamics of the cosmopolitan mid *Limnophyes pusillus*, have been discussed in relation to soil re conditions by Trehen and Delettre (1976). Recent studies on Îles len (Delettre, 1978; Delettre and Cancela da Fonseca, 1978) have that it is parthenogenetic and univoltine. Growth occurs throughout r without diapause, and adult emergence occurs when the soil tem- e becomes >5–7°C.

onaptera. Although six species of fleas are known from sea-birds in the tarctic, only one has been reported from the Antarctic continent nd Dunnet, 1962). *Glaciopsyllus antarcticus* was collected initially chick of the silver-grey petrel *Fulmarus glacialoides* and a nest of the

snow petrel *Pagodroma nivea* near Wilkes Station, and was later f Mawson and Davis Station (Murray *et al.*, 1967). The latter authors information on its habitat and biology. In the sub-Antarctic, Dunne 1962) lists five species from Macquarie Island and Smit (1970) recor species from Heard Island, one of which was found also on South G The distribution and host relations of fleas in the Antarctic regio been discussed by Dunnet (1964).

Hymenoptera. Four species have been recorded representi Families Scelionidae, Diapriidae (both at Macquarie Island (Yos 1962)), Eucoilidae (Îles Crozet (Quinlan, 1964)) and Mymaridae Georgia (Doutt and Yoshimoto, 1970)).

Coleoptera. Few collections of beetles have been made fr Antarctic, and these are considered to be wholly introduced specie lathridiid beetles, *Lathridius minutus* and *Cartodere apicalis*, hav identified from natural vegetation at Signy Island and King George (Balfour-Brown and Tilbrook, 1966). Twenty adult *Lathridius* were found in a food store at Davis Station (Rounsevell, 1978).

South Georgia has eight species of Coleoptera: Carabidae (one s Dytiscidae (one species), Lathridiidae (two species), Staphylinida species) and Perimylopidae (two species) (see pp. 234–254 in G 1970a). Of interest is the single water beetle, *Lancetes claussi*, w often taken in terrestrial samples near freshwater bodies, and two of perimylopid beetle, *Perimylops antarcticus* and *Hydro sparsutum*, the latter being more common. Remains of *H. sparsutu* been identified from a peat profile on Jason Island, South Georgia (1963). Brinck (1945) investigated the Coleoptera of Îles Crozet an Georgia, and Gressitt (1962) reported five species of Staphylinida Macquarie Island.

Over 50% of the beetle fauna of sub-Antarctic islands belong Family Curculionidae (weevils), and these insects may have an im ecological role as herbivores in such ecosystems, where arthropods diverse than in more temperate situations. Smith and Walton (1975 that Coleoptera grazed shoot apices, moss sporophytes and le *Acaena magellanica* and various grasses. Damage to the bases o shoots is sometimes considerable. High densities of beetles (up adults and 620 larvae m^{-2}) have been found in moist, sheltered *Festuca* grassland (Smith and Stephenson, 1975). These were main mylopidae which feed on plant material. The ectemnorrhine weevil important component of the Îles Crozet surface-living fauna (1973), where they are abundant in fellfields at 100–300 m altitu

Island, Smith (1977a) recorded maximum adult densities up to $^{-2}$ (biomass 1g live weight m^{-2}) of *Ectomnorrhinus similis* in -April, where captured beetles ingest *c.* 14% of body weight day^{-1} of arf shrub *Acaena magellanica* and 37% of body weight day^{-1} of the *Brachythecium rutabulum.* Adult and larval weevils (mostly *Ectemnus* spp.) were *c.* 3% of the total macroscopic invertebrate dry weight s at Marion Island (Burger, 1978), with mean (weighted) population es of 25 and 106 individuals m^{-2} respectively.

only physiological work undertaken on Coleoptera has been a pre- y study of respiration levels in adults and larvae of some South a beetles (Block, 1982b). Individual adult respiration rates from 2.11 to 8.00 (*Hydromedion sparsutum*) and from 2.29 to 5.93 *ylops antarcticus*) $\mu l\ O_2$ $individual^{-1}\ h^{-1}$ over 5–20°C. Over a similar ature range, the carabid beetle *Oopterus soledadinus* had an consumption of 1.67–2.27 $\mu l\ O_2$ $individual^{-1}\ h^{-1}$. Metabolic rates from 110.65 to 432.97 $\mu l\ O_2\ g^{-1}\ h^{-1}$ in these three species.

Arachnida

eida. Spiders are restricted entirely to the sub-Antarctic, and Gres- 70a) lists 14 species from six islands or island groups. However, two exist for the Antarctic: a portion of the cephalothorax of a member Family Micryphantidae was collected by flotation at Terra Nova Bay r, 1970), and a small spider (*Erigone autumnalis*) was captured in ets at Marble Point (Forster, 1971). The former specimen was un- able but may be related to the micryphantids of South Georgia, he latter, being native to the U.S.A., was clearly imported by ship s to McMurdo Sound.

endemic Micryphantidae have been identified from South Georgia -Lyche, 1954; Forster, 1970) of which *Notiomaso australis* is the idespread. Similarly, three species of spiders are represented at arie Island (Forster, 1962).

nformation on the biology, ecology or physiology of the sub- tic araneids has been published.

ngida. A single species, *Promecostethus unifalculatus* later termed *a" unifalculata* by Gressitt (1970b) has been recorded from Îles

doscorpionida. Austrochthonius insularis has been found on Îles (Gressitt, 1970a).

Acarina. Michael (1895) described the first species of mite from tl polar region, a cryptostigmatid, *Oribata antarctica*, collected o Georgia. Racovitza collected six species of mites, three Coll species, the wingless midge and several ectoparasitic arthropods "Belgica" Expedition of 1897–1899. The historical developn acarology in the Antarctic region has been well documented (Dale Wilson, 1958; Gressitt, 1967b; Wallwork, 1973). A bibliographic in tion has been provided by Gressitt and Weber (1959) and Gressitt an (1961). Today, over 150 species of Acari are known from the Antar sub-Antarctic (Gressitt, 1970b).

As the Acari are a large and diverse group their taxonomy and c tion will be treated initially under the five sub-orders, before tu their ecology and physiology.

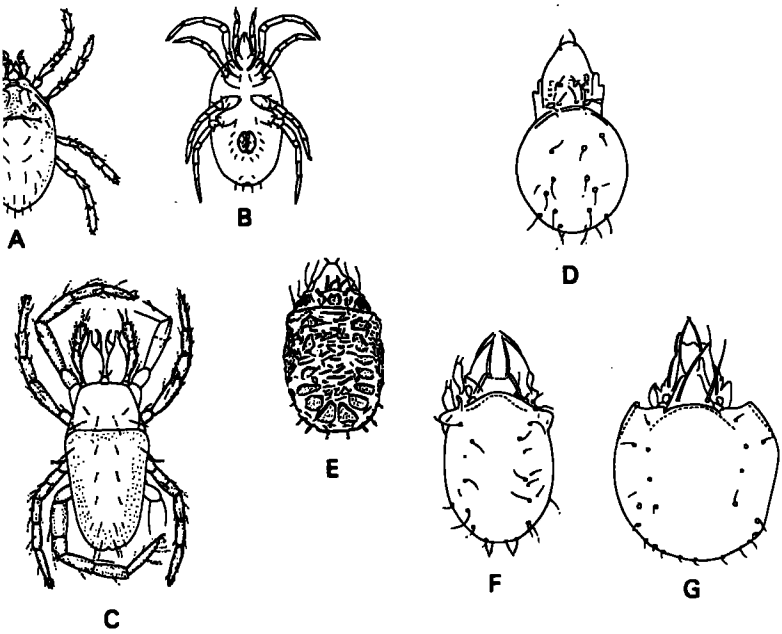
Mesostigmata. Free-living and parasitic forms probably number i of 50 species, the majority being found in the maritime and sub-A zones. Most are active, fast-moving mites. *Gamasellus racovitzai* ably the most widely distributed mesostigmatid mite in Lesser An (Fig. 3b). It is a predator of smaller, prostigmatid and cryptost mites, and Collembola. Free-living Mesostigmata collected from th arc have been described by Hunter (1967a,b), and from seve Antarctic Islands by Hunter (1964, 1970) and Lee and Hunter (1974 sitic Mesostigmata (nasal mites on Adélie penguin, South Georgia southern elephant seal) were reported in the Antarctic by Wilson and from the sub-Antarctic (Wilson, 1970a).

Haemogamasus pontiger (Family Laelapidae) has been c frequently in the vicinity of Antarctic Stations: Macquarie Island (1967), Davis Station (Rounsevell, 1978), Signy Island (Goddard, but it is considered to be introduced.

Metastigmata. Three species of ticks (Family Ixodidae) hav recorded from sea-birds and their nests in the Antarctic: *Ixodes u* host species), *Ixodes auritulus* (30 host species) and *Ixodes kergue* (hosts—South Georgia diving petrel *Pelecanoides georgicus*, sho petrel *Procellaria aequinoctialis*, and dove prion *Pachyptila d* according to Wilson (1967, 1970b).

Prostigmata. These mites are varied in habit from free-living feeding on fungi, micro-algae and plant material to predacious form consume other arthropods and soil invertebrates. Considerable tax and distributional information exists for this group, and approxim species are found in the south polar region with a high (95%) en

ork, 1973). Figure 4A–C shows some typical prostigmate mites. systematic data are given by Womersley and Strandtmann (1963), mann (1967), Strandtmann and Tilbrook (1968) and Crooker (1977) arc). For South Georgia, Strandtmann (1970), Wallace (1970) and (1970) provide information on prostigmate mites, whilst mann and Davies (1972) report on eupodiform Prostigmata from



restrial mites (Acari) of the Antarctic Region.
stigmatid mites.
reotydeus delicatus, dorsal view of adult (after Strandtmann, 1967). A small mite length c. 450 μm) recorded from the Balleny Islands and north Victoria Land.
odes angardi, venter of female (length 500–600 μm), described from specimens collected in Sverdrupfjella, Dronning Maud Land (Strandtmann and Sømme, 1977).
agidia kerguelenensis, dorsal aspect of female (length 790 μm). Collected from a variety of terrestrial vegetation on Île de la Possession (Strandtmann and Davies, 1972).
ptostigmatid mites.
pia loxilineata, adult. A small (length 358 μm) oribatid found on the South Shetland slands and Antarctic Peninsula (Wallwork, 1965).
Hacarus auberti, dorsal view of nymph with pleated integument. A robust oribatid mite rom South Georgia, which achieves an adult size of 1.1–1.4 mm.
udheimia petronia, adult (length 595–670 μm). Restricted to continental Antarctica, nd described from the Hallett Glacier (Wallwork, 1962a).
gellozetes antarcticus, adult (length: 806 μm). This species has been collected in South merica (Tierra del Fuego and Chile), South Georgia and the Antarctic Peninsula.

Îles Crozet. In Dronning Maud Land, three species were collect
Heimefrontfjella (Bowra *et al.*, 1966; Strandtmann, 1978a); f
species (two each of *Eupodes* and *Nanorchestes*) were found
drupfjella (Strandtmann and Sømme, 1977), and six species were i
by Sømme (1980) in Vestfjella. Three species have been repor
Syowa Station (Ohyama and Matsuda, 1977), and in soil fro
Charles Mountains (Rounsevell, 1979). Rounsevell (1977a) obser
ficant phenotypic variation in size of *Tydeus erebus* from several
in Greater Antarctica. Similar morphological variation occurs in
tions of *Stereotydeus mollis* in south Victoria Land (Pittard *et al*
where it is the dominant of three species (Strandtmann and Georg
The morphology and biology of *Stereotydeus villosus* is desc
Graham (1975).

Nanorchestes antarcticus is the southernmost occurring anim
world (85°32'S; 153°W) (Wise and Gressitt, 1965). It was the o
found on 19 of 32 rock exposures in Marie Byrd Land (Stran
1978b), and has the widest distribution (3–2245 m in altitude, and
Campbell Island; Gressitt and Shoup, 1967) of any Antarctic arth
has been found in large numbers in Antarctic ice (Block, 1979d).
instars have been described by Lindsay (1972). Details of body
ation and structure of the genital area and leg and pedipalp chaetot
been given for the larval and nymphal stages of four prostigmatid sp
Goddard (1979b). This is the first formal description of their i
stages, and Pittard (1971) gave comparable information for *Ster*
mollis.

Cryptostigmata. Oribatid mites total *c.* 41 species in the sub-, r
and continental Antarctic zones. There is a high degree of endemis
in the Antarctic Cryptostigmata (Wallwork, 1973). This group is
free-living, its members feeding on a variety of living and dead plan
ial (Fig. 4D–G). Early records (21 species) of the oribatid faun
Antarctic were given by Dalenius and Wilson (1958) and Dalenius
Much taxonomic work has been carried out on the group particu
Wallwork (1962a,b,c, 1965, 1967) and also in the sub-Antarctic
quarie Island (Wallwork, 1963), South Georgia (Wallwork, 1966
1972b), Heard Island and Îles Kerguelen (Wallwork, 1970b) an
Crozet (Wallwork, 1972a). In addition, Covarrubias (1968
taxonomic observations on five oribatids from the maritime zo
Travé (1976a) compiled a biogeography of the Cryptostigmata
Kerguelen (24 species), including Îles Crozet (20 species).

The cryptostigmatid faunas of the sub-Antarctic and co
Antarctic are distinctly different, whilst that of the maritime zone

being derived from the sub-Antarctic (Wallwork, 1969). The e fauna is composed of northern and southern elements, with the ry lying between the South Orkney and South Sandwich Islands. A ment, represented by the Family Podacaridae, can be identified, s consistent with a former continuous distribution incorporating reater and Lesser Antarctica (Wallwork, 1973). It is doubtful the alternative explanation of post-Pleistocene colonization can orted by sufficient long-range dispersal or rates of speciation rapid to produce the faunal divergence observed. However, a significant of the oribatid fauna of each of the sub-Antarctic islands is the very ree of species endemism (Wallwork, 1972a; Travé, 1976a), which a recent, post-Pleistocene phenomenon of dispersal from Mac- sland. Hammer and Wallwork (1979) have presented evidence to at the present-day global patterns in the distribution of oribatid n be interpreted within the context of continental drift.

nata. These mites occur free-living in soil communities, but also in ion with human activity (animal and plant materials), and are often s feather mites on birds. Systematic publications include those of and Tilbrook (1966) and Hughes (1970) for free-living forms. (1977) has erected a new family for *Glycacarus combinatus* col- om the nest of a white-chinned petrel *Procellaria aequinoctialis* on on Island. Sheathbills *Chionis minor* and skuas *Catharacta skua gi* support populations of feather mites as well as many oceanic birds and Peterson, 1967, 1970). Three astigmate mites were found at land, two in the British Antarctic Survey (B.A.S.) Station buildings third, *Neocalvolia antarctica*, in terrestrial habitats (Goddard,

derable taxonomic and morphological information has been given 18 species which comprise the acarine fauna of Signy Island (Til- 73b; Goddard, 1977c, 1979b).

ne ecology. Ecological information on the Acari is mainly con- vith the Prostigmata as this is the common soil group in the con- Antarctic. Field counts of *Stereotydeus mollis* and *Nanorchestes us* in relation to stone size and colour, were made in the McMurdo rea by Gressitt *et al.* (1964), and the former species was estimated, ation method, to have densities in the range of 20–2000 individuals several barren habitats in south Victoria Land (Strandtmann and 1973). Biological studies (Gless, 1967; Fitzsimons, 1971a) on *agidia gressitti* at Hallett Station show that it is a very active mite,

sensitive to changes of humidity and temperature, and predace
Stereotydeus sp. and other soil arthropods. Details of food ite
further three prostigmatids suggest they feed largely on soil algae
frequently, on fungi (Fitzsimons, 1971a). Life cycle data for fou
gmatid species cultured at 5–10°C and low relative humidity a
Station by Gless (1972) gave egg to adult death times of 89–135 da
comparative data exist for the populations of *Nanorchestes anta*
various continental sites lacking macrophytes (Matsuda, 1977; Ro
1977b,c; Ohyama, 1977). At Davis Station in the Vestfold Hills, i
only arthropod present in a sand substrate overlain with flat rock
foreshore (Rounsevell, 1977b,c), with mean densities ranging fro
15.86×10^4 individuals m^{-2}. Activity was from October to Mar
temperatures in the upper sand layer were >0°C and the mites g
algae. From April to September the mites were immobile in the lo
(4–6 cm), which contained <0.5% water by weight. A peak den
1500 individuals m^{-2} was found for *N. antarcticus* in exposed so
Lutzow-Holm Bay area, Greater Antarctica by Matsuda (1977), a
lation density increased in fine sand furthest away from fre
(Ohyama, 1977, 1979). All life stages of *N. antarcticus* were recove
ice cores from the Macleod Glacier, Signy Island (density 180 in
m^{-2}). The mites were probably transported by wind onto th
(Block, 1979d).

Several studies have been made of seasonal changes in mite po
in moss communities of the maritime Antarctic (Covarrubias, 1
brook, 1967a, 1973b; Goddard, 1979a). Lippert (1971) gave sc
liminary data for mites in mosses at Anvers Island, Antarctic P
Mites were numerically abundant in the *Polytrichum–Chorisodon*
lichen-encrusted zones of three moss communities studied by
(1973b) at Signy Island. Three prostigmatid species had generall
numbers (mostly juveniles) during or at the end of summer than i
In a 27-month long study of a wet moss carpet and a relatively dry m
Goddard (1979a) demonstrated within and between year density c
three prostigmatid and one mesostigmatid species in the latter si
annual numbers of Acari varied from 5977 (1973) to 10,469 (1972
overall mean of 8069 individuals m^{-2}. Higher numbers were
summer than in winter of all species, but whereas the Prostigmata
by *c.* 43% during the study, the Mesostigmata (*Gamasellus ra*
remained relatively stable in numbers. Computed population ener
via respiration for these species ranged from 4.5 (*Gamasellus raco*
82.2 (*Ereynetes macquariensis*) ml O_2 m^{-2} y^{-1}, and for the total
129.2–219.9 ml O_2 m^{-2} y^{-1} (Block, 1980a). From life stage analys
Prostigmata, Goddard (1979a) argued that the nymphal instars ma

n, resulting in a mixed nymphal population component of overlap-
stars and generations from which varying numbers mature to adults
ling upon microclimate and other factors. In the sub-Antarctic Îles
:len, Travé (1976b, 1977) found that the Acari were 66% of the
brate fauna with oribatids predominant. Mean mite density was
ıdividuals l^{-1}, with lowest numbers in degraded moss peat (572
uals l^{-1}) and highest in halophytic mosses (12,652 individuals l^{-1}).
ıth Georgia, mite populations fluctuated from 35.2 to 156.75 (moss
ınd from 51.7 to 104.5 (*Festuca* grassland) $\times 10^3$ individuals m^{-2} over
ars (C. C. West, personal communication). Maximum numbers
:d in spring and summer, with minima in mid-winter (August). The
:omprised 16 species of which six were common.
·mation is now becoming available on the field biology and life cycles
arctic mites, but the Prostigmata, due to their generally small size
gility, are poorly known in this respect. Goddard (1979b) has sum-
d the information available for the 18 acarine species of Signy Island,
ıde some preliminary observations on their feeding biology (God-
.982). Many Prostigmata feed on soil algae and, less frequently,
whilst some are predatory (Fitzsimons, 1971a). In a review of the
/ and physiology of Antarctic soil arthropods, Block (1980a) con-
that they were ultimately regulated by environmental influences
than interspecific competition. Many aspects of the life cycle, ener-
nd low temperature physiology contribute to the survival strategy of
nhabiting the Antarctic terrestrial environment. In the cryptostig-
nite *Alaskozetes antarcticus*, features of its energy balance in rela-
temperature and respiration level suggest it may be an obligate polar
, which is able to maintain a positive energy balance only at low
atures (Block, 1980b). The survival potential of this species is
ed by extended individual longevity combined with iteroparity,
:ontribute to a long life cycle (>2 years in maritime Antarctic habi-
: is difficult, at present, to suggest that *A. antarcticus* is more of an r-
rategist, and due to the predictable seasonality of its environment a
ırph between opportunism and stability may have developed. Not
it able to endure winter conditions, but also to capitalize on the
ıble summer periods for growth and reproduction. Such features
typical of the survival strategies adopted by other polar arthropods
restrial invertebrates.

ine physiology. Physiological studies of Antarctic Acari have been
first to temperature tolerances, secondly to respiration as a
ıent of the energetic balance, and thirdly, to the mechanisms of cold
:ss in several species of oribatids, mesostigmatids and prostigmatids.

The latter aspect is reviewed below and will not be considered here
sive respiration data, obtained by Cartesian Diver micro-respirom
available for field-fresh mites at Signy Island (Table II). A
individual live weights ranged from 1.37 (*N. antarcticus*) to 196.21
antarcticus), mean respiration rates varied by a factor of 450 tim
0.16 (*N. antarcticus*) to 72.05 (*G. racovitzai*) nl O_2 individual^{-1} h
0–10°C. Mean metabolic rates varied by 32 times from 50
antarcticus) to 1616.26 (*G. racovitzai*) μl O_2 g^{-1} h^{-1} over the sa
perature span. Typically, the oribatid mite, *A. antarcticus*, is the
and slowest moving of the microarthropods investigated, and it has
lowest oxygen consumption per unit live weight. In contrast, the p
mesostigmatid, *G. racovitzai*, which has a wide range of live weigh
II), possesses the highest respiration and metabolic rates. It seems
style, field habits and activity are major determinants of respirato
in such animals. In response to temperature changes within the
band, Q_{10}s vary from 1.02 (*G. racovitzai*) to 3.83 (*A. antarcticus*),
smaller Prostigmata having Q_{10}s of <2 (Block, 1977; Goddard, 197

Comparative analyses of standard respiratory metabolism for A
and temperate Acari indicated that polar Cryptostigmata and M
mata possessed elevated rates (by 2–4 times) at their normal enviro
temperatures (Block and Young, 1978). Metabolism–temperatur
of polar and temperate forms are similar for both mite groups, and
Antarctic mites correspond to the lower part of the range for te
species.

It was postulated that some Antarctic mites adapt to low tempera
elevation of standard metabolism, to levels comparable to those of
ate species at their normal environmental temperatures, thus a
active life under polar conditions. Extending the respiratory work
tured mites, it has been demonstrated that several factors af
metabolic rate of adult *A. antarcticus* (Young and Block, 1980b
vation and long culture periods reduced metabolism, various natur
influenced metabolic rates, and metabolism differed between the se
only to weight. In addition, short-term temporal variations in
uptake of individuals were found and respiration rates measured t
(9.09 nl O_2 individual^{-1} h^{-1}, 43.08 μl O_2 g^{-1} h^{-1}).

Further, it has been shown (Young, 1979a,c) that in *A. antarct*
metabolism–weight relationship changed with culture (increased
cultured animals at all weights at 0°C, and for mites <100 μg live we
and 10°C); the magnitude of the temperature response differed for
life stages and was, in general, less than that of field-fresh animals.
tion of metabolism was confirmed in the cultured mites, and it w
gested that lowering of the activation energy for certain reactions

TABLE II

Respiration and metabolic rates from field-fresh Antarctic mites over the temperature range 0–10°C

Species	Live weight (µg)	Temperature (°C)	Respiration rate (nl O_2 ind^{-1} h^{-1})	Metabolic rate (µl O_2 g^{-1} h^{-1})	Reference
Nanorchestes antarcticus	1.37(D)–3.57(♀)	5	0.16(D)–1.13(T)	161.04(D)–367.73(♀)	Block (1976)
Alaskozetes antarcticus	13.29(L)–196.21(G♀)	0–10	0.82(L)–37.28(♂)	50.87(♀)–303.78(D)	Block (1977)
Gamasellus racovitzai	4.40(L)–115.50(G♀)	0	3.23(L)–72.05(♀)	231.47(♀)–1616.26(L)	Goddard (1977a)
Stereotydeus villosus	2.80(P)–37.10(G♀)	0–10	3.53(♀) 9.23(♂)	110.91(♀)–365.64(♂)	Goddard (1977b)
Tydeus tilbrooki	1.50(T)–1.90(A)	0–10	0.24(T)–0.94(A)	111.00(T)–497.20(A)	Goddard (1977b)
Nanorchestes antarcticus	2.61(D)–8.50(A)	0–10	0.71(T)–3.79(A)	98.04(T)–363.18(A)	Goddard (1977b)
Ereynetes macquariensis	1.5[a](T)–2.0[a](A)	0–10	1.63(T) 2.70(A)	951.98(A)–1352.49(A)	Goddard (1977b)
Eupodes minutus	2.0[a](A)	0–5	1.83(A)–1.97(A)	917.01(A)–986.01(A)	Goddard (1977b)
Halotydeus signiensis	N.D.	5	3.57(G♀)	N.D.	Goddard (1977b)

L, larva; P, protonymph; D, deutonymph; T, tritonymph; A, adult; ♂, male; ♀, female; G♀, gravid female; N.D., not determined; [a], live weight estimated from mean weight of *Tydeus tilbrooki*.

part of the mechanism behind the cold adapted metabolism *antarcticus* (Young, 1979a). In temperature switching experiments 1979b), no regulation of metabolism in response to temperature within its field range was detected in adults of this species. Ab metabolic temperature compensation may be of selective adva conservation of its energy resources under Antarctic conditions.

Temperature tolerances have been scarcely studied in the Antar fauna. *Nanorchestes antarcticus* and *Stereotydeus mollis* from t Coast did not aggregate when placed in a thermal gradient of 0–2 their upper lethal temperatures at >90% RH were 37.2 and 33.2°C tively (Fitzsimons, 1971b). The lower lethal limit of *N. antarcticus* −41°C) was below that for *S. mollis* (−11 to −23°C), whose norma range was *c.* 0–23°C. *N. antarcticus* was the most tolerant to tem extremes, and was active from −23 to 31°C. The mortality of *Ster villosus* in experiments at Palmer Station increased markedly peratures <−12 and >32°C (Graham, 1974). Thus, the few availa indicate physiological adaptations that parallel temperature cond the parts of Antarctica examined, but clearly, further research is n to elucidate the mechanisms behind such adaptations.

3.8.4 Myriapoda

Pauropoda. Two specimens have been found on Îles Crozet (S 1974a).

Symphyla. Reported for the first time from the sub-Antarctic Crozet (Scheller, 1974b) from soil extractions made by L. Davies and 1973. The collection of 27 specimens belonged to a single new *Symphylella subantarctica.* It is likely that symphylids will be f other sub-Antarctic situations when critical searches are made.

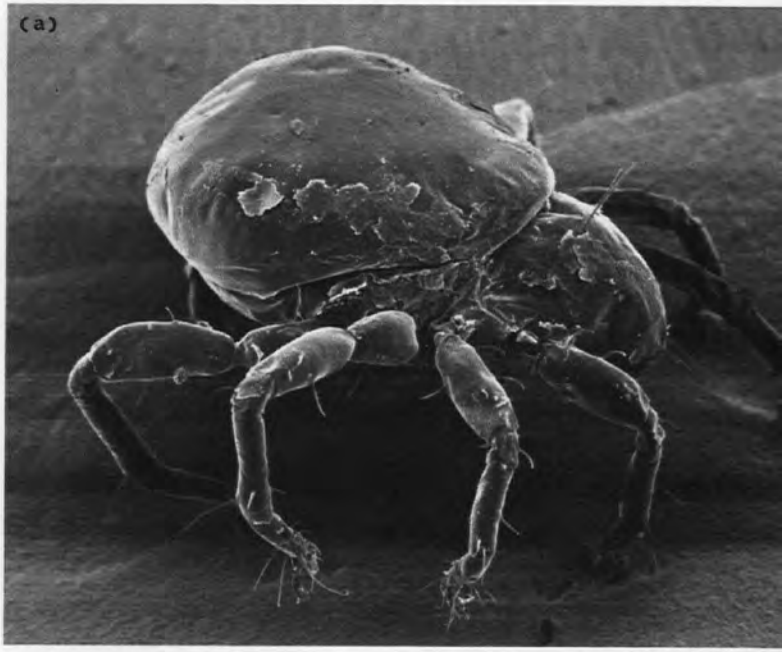
4. Invertebrate Cold-hardiness

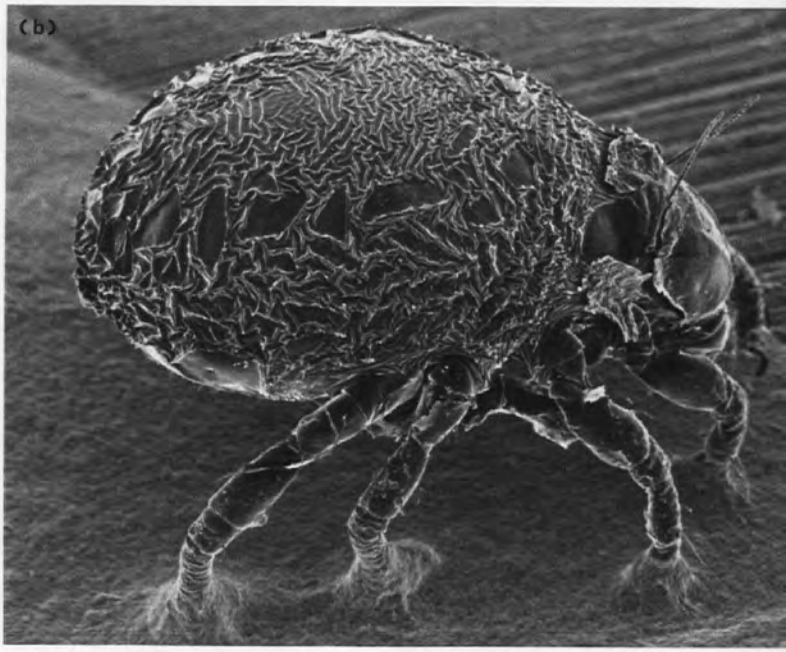
The ways in which terrestrial invertebrates survive the sub-ze peratures of polar regions is a primary facet of their ecology, biol physiology—indeed it underpins their existence in such areas. Col ness is defined as the ability of the organism to resist low temp which would normally be lethal. An invertebrate poikilotherm options in this respect: either to avoid freezing or to minimize da cells and tissues during the freezing process. The former species a

y termed "freezing-susceptible" and avoid freezing, which is always by supercooling, i.e. the maintenance of their body fluids in liquid elow the solution freezing point. Supercooling in such animals is ed by various solutes including polyhydric alcohols and sugars, and emperatures of *c.* −40°C may be reached before freezing occurs. The species are termed "freezing tolerant", and such animals survive ellular freezing in the supercooled condition. Freezing occurs at rela- igh sub-zero temperatures and ice nucleators may aid the process in ecies. Polyols such as glycerol may afford freezing tolerant species tion by reducing cell damage. Introductions to the background and re of insect cold-hardiness are available in Salt (1961) and Asahina whilst Meryman (1966) reviews biological freezing.

h of the early work was concentrated on arthropods, principally , and on northern species from the Arctic, sub-Arctic and Canada. ation is lacking on the levels of cold-hardiness of most non-arthro- vertebrate groups, which are key components of tundra soil nities in both the north and south. Early studies on Antarctic were concerned with lethal temperatures. Investigations of tic species to examine the mechanisms of survival have only recently and Block *et al.* (1978) and Sømme (1978a,b) working on micro- ods were the first to examine cold-hardiness in terms of super- potential and cryoprotectants. Supercooling ability is normally d by measurement of the individual's supercooling point (lowest emperature reached at which spontaneous freezing occurs) using rd cooling regimes (usually 1°C min^{-1}). Cryoprotectants are assayed ous chromatographic methods including ascending paper, thin layer and gas–liquid (GLC) techniques.

iminary observations showed that the cryptostigmatid mite *Maud- wilsoni* can survive experimental temperatures as low as −30°C, and us (1965) suggested that locomotion and possibly breeding could in sub-zero conditions. Pryor (1962) demonstrated that the lethal emperature for adults of the collembolan *Isotoma klovstadi* from Victoria Land was between −50 and −60°C. Apparently, another ail, *Gomphiocephalus hodgsoni* from the McMurdo area, is less cold t and dies between −20 and −28°C (Janetschek, 1963, 1967b). ons (1971b) found no evidence in his experiments with *G. hodgsoni* e prostigmatid mite *Stereotydeus mollis* that the presence of food in inhibits cold-hardiness, but rather that starved specimens succum- cold more quickly than well-fed animals. When supercooled to *G. hodgsoni* became frozen when touched with ice, while animals in e containers survived for longer at this temperature. Using adult *ydeus villosus* and cooling rates of *c.* −3°C h^{-1}, Graham (1974)


(a)


(b)

ied their survival after 12 h exposure to a range of sub-zero tem-
es. A marked increase in mortality occurred below −8°C and at
all the animals (86) were dead. It was thought that this level of
ardiness allowed the species to survive in the field at Palmer Station.
y of *Nanorchestes antarcticus* at low temperatures was examined by
evell (1977b). Detailed comparisons are, however, impossible due to
erent experimental procedures and in particular the varying rates of
utilized.

king with two species of Antarctic micro-arthropods (*Alaskozetes*
cus and *Cryptopygus antarcticus*), Block *et al.* (1978) showed that
ossessed the ability to supercool to −30°C, but the full realization of
tential was dependent on starvation. Additionally, the mite, *A.*
cus contained glycerol in a concentration of *c.* 1% fresh weight (*c.*
mg^{-1} fresh weight), when acclimated at 0°C for one week. No glycerol
tected in the collembolan. Field-fresh specimens of the mites
s tottanfjella and *Nanorchestes* spp. in the Vestfjella, Dronning
and had supercooling points between −20 and −30°C, and did not
freezing at these temperatures (Sømme, 1978a). In mid-summer,
nimals are subject to long periods of sub-zero temperatures in the
they face the problem of the necessity to feed as well as having a
percooling ability. Extending the work on *C. antarcticus*, Sømme
found that specimens from Bouvetøya supercooled to *c.* −25°C,
limation to −5, 0 and 12°C for various times had no affect on this
lycerol was not detected and all specimens examined were freezing
ible. The only freezing tolerant Antarctic species, the midge *Belgica*
ca has been studied at Palmer Station by Baust and Edwards (1979).
only are freezing tolerant to −15°C during the austral summer, and
several possible cryoprotectants including erythritol, glucose,
and trehalose. Adults are freezing susceptible and contain only
antities of the above substances. Larval feeding experiments using
l diets suggested that the cryoprotectant profiles were directly de-
t on food source and temperature. Adults and larvae had mean
oling points of −5.3 and −5.7°C respectively. Thus both freezing
ible and freezing tolerant strategies have been adopted by Antarctic
hropods.

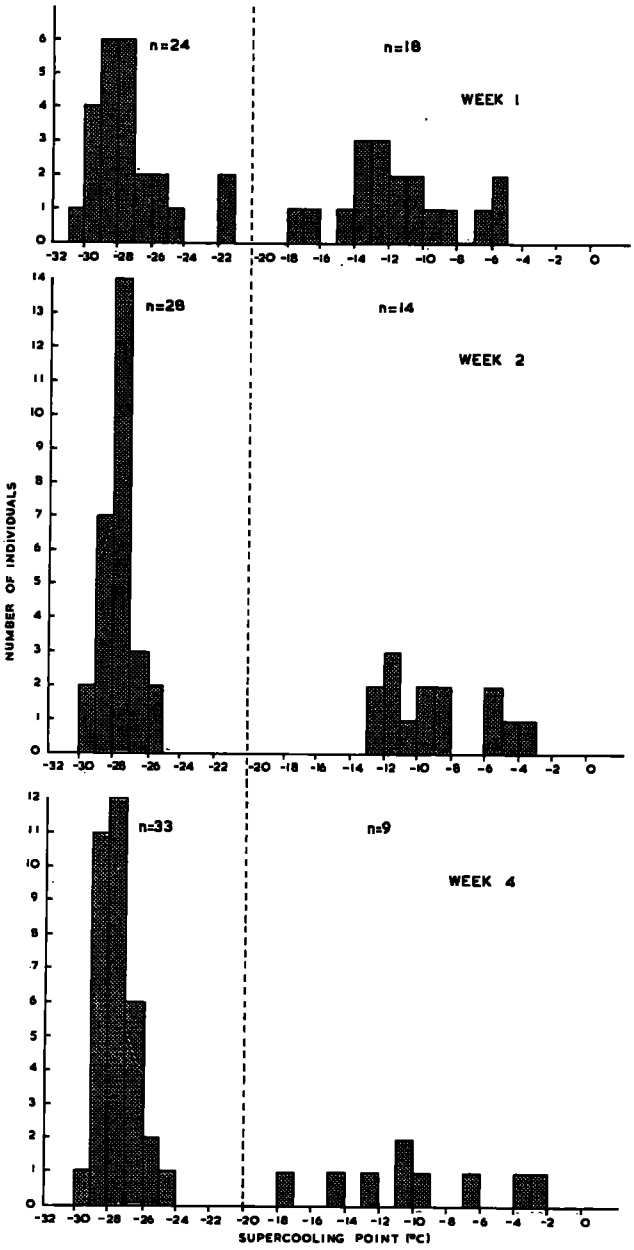
g the cultures of *Alaskozetes antarcticus* (Fig. 5a,b) from Signy
the mechanism of cold tolerance has been investigated (Young,

tereoscan electron micrographs of the oribatid mite *Alaskozetes antarcticus*.
specimen showing its robust exoskeleton and ceratotegument. The animal
m in length, 0.7 mm wide and has a live weight in the range 200–300 μg. (b)
ph (3rd nymphal instar), showing the pleated integument and sclerites on the dorsum,
.90 mm in length. (Photographs by kind permission of D. A. Wharton.)

1979c; Young and Block, 1980a), and freezing was found to be fat its life stages. Glycerol was identified as the major polyhydroxy co involved in its cold-hardiness, where it occurred in average concer of up to 50 μg mg^{-1} water (=0.55 g molecules kg^{-1} water). In supercooling points were as low as −31°C, but feeding detracted f ability by providing ice nucleators in the gut which initiated fre relatively high sub-zero temperatures (−2 to −24°C). Figure 6 sh increase in the number of individuals supercooling to >−20°C dur vation over four weeks. Although the mite can supercool to −26.5 out nucleators and without measurable glycerol in the boc temperature acclimation, this will only enable it to survive sumn peratures in the maritime Antarctic. This degree of cold-hardines be insufficient in winter and for a climatically severe austral autu process of supercooling is enhanced by glycerol, and an inverse relationship between its concentration and the supercooling pc demonstrated. In relating cold tolerance of the mites experimer environmental conditions in the field, it was clear that low tem acclimation increased glycerol concentrations and suppressed whilst desiccation also stimulated glycerol synthesis. This was report of an effect of low relative humidity on poikilotherm cold-ha Differences in photoperiod had no effect on cold tolerance, whic prising as this might be a reliable guide to seasonal changes in its ha

Experimental results suggest that much of the additional cold-h of *A. antarcticus* is built up during two phases in the autumn perio when mean daily ground surface temperatures are close to 0°C for ab month and oscillations are minimal (Walton, 1977, 1982), and se when mean daily temperatures occur between 0 and −10°C at the winter (although daily minima may be lower). During this period suppression is more important than supercooling point depression sub-zero conditions continue in early winter, glycerol production b critical for survival. Low relative atmospheric humidities are likely in the habitat of *A. antarcticus* before snow cover develops, and the accumulation that accompanies desiccation will play a crucial ro successful overwintering.

The nymphal stages of *A. antarcticus* (Fig. 5b) possess a greater d low temperature tolerance, as measured by supercooling points, t adults. Although glycerol was the main polyol found, ribitol, a xylitol, mannitol, inositol, rhamnitol and fucitol may also be These substances are likely to exert a similar influence to that of gly supercooling ability in these animals. Juvenile Collembola of Alpine species exhibit greater cold tolerance than the adults, an such as glucose may aid supercooling (Block and Zettel, 1980).



stograms showing the frequency distributions of individual supercooling points of *askozetes antarcticus*, during starvation over four weeks at 5°C. The increase in number p below −20°C can be seen clearly. (By permission of *Journal of Insect Physiology*.)

micro-arthropods have a cold-hardiness mechanism that allows a "safety margin" than in the adults, but why this should occu *antarcticus*, where all stages overwinter under similar temperatu tions, cannot be explained at present. Body size may be importa respect.

Glycerol and other solutes are thought to lower the homogene leating temperature of water, but in animals, nucleation is more fr heterogeneous, i.e. foreign particles act as centres for ice crystal f (Salt, 1961). This is apparent because freezing occurs above the h eous nucleating temperature of water. Comparison of the effect of on the heterogeneous nucleation temperature of individual *A. ar* and small droplets of distilled water (Block and Young, 1979), sugg a given quantity of glycerol depresses the supercooling point mor does the melting point. The effect is more marked in the mites, w supercooling point was depressed by more than twice the melti depression at any given glycerol concentration. It is of considerab tive significance in such cold tolerant micro-arthropods.

Supercooling in aqueous solutions in the absence of anti-free pounds is limited. Synthesis of such compounds may be meta costly, and at very low temperatures (−40 to −50°C), freezing t may be more difficult in terms of resource exploitation. If temp fluctuate around 0°C for long periods of time, it may be advanta avoid repeated freezing and thawing of the body, and supercoolin be the optimal strategy (e.g. *Alaskozetes antarcticus*). However exposure to positive temperatures, feeding will be necessary, and the gut will promote nucleation when the temperature declin balance resulting from the need, on the one hand, to avoid freezing the other, to ingest food to provide energy for growth, etc., is a deli in such poikilotherms.

The distribution of the two strategies of cold-hardiness in the A land fauna is interesting, in that the majority of the arthropods inv have adopted the freezing susceptible–supercooling approach in with many northern forms. It is significant that the only Antarcti found to be freezing tolerant is also the largest in size, and only i stages possess this ability. In the Arctic, adult insects may be tolerant, e.g. an Alaskan carabid beetle (Miller, 1969). Pre experiments with South Georgian enchytraeid worms suggest that tolerant mechanism may operate (Block, unpublished). Investiga other Antarctic soil invertebrates may yield other freezing toleran There is a need for a wider study of both the mechanisms themse their biochemical bases in the Antarctic terrestrial invertebrates. changes in cold-hardiness will need to be evaluated against the

conditions imposed on the organism in the field. Cold-hardiness is course, limited only to species inhabiting polar or indeed low tem- e environments (Block, 1979a; Sømme, 1979). Significant levels of istance have been found in desert centipedes and scorpions (Craw- d Riddle, 1974; Riddle and Pugach, 1976), in a temperate species of tigmatid mite (Young, 1980), and in tropical arthropods (Cloud- ompson, 1973, 1978). In several of the latter instances, however, the o supercool was thought to be a taxonomic rather than an adaptive

triguing feature of cold-hardiness in animals concerns the distribu- nong the various groups, of freezing susceptibility and freezing e. Freezing tolerant species have been found in some protozoans, des, rotifers (Koehler, 1967), molluscs, crustaceans, insects and les. Freezing susceptibility occurs in many insects, some intertidal s, spiders, mites and scorpions. Vertebrate poikilotherms cannot id whole body freezing and Antarctic fish may utilize glycoproteins reezes (DeVries *et al.*, 1970; Duman and DeVries, 1975). Both susceptible and tolerant forms occur in certain phyla (e.g. Mol- d Arthropoda), which raises some important questions. Is freezing e advantageous compared to freezing susceptibility, and if so, is phylogenetic component in the adoption of one strategy over the Study of the distribution of the two approaches in terrestrial herms will contribute to an understanding of their present-day dis- n in polar areas. Current evidence suggests that the colonization environments by such animals has not involved the evolution of physiological mechanisms, but development and/or extension of ting ones.

ystems

rable interest has been shown in recent years in the functional of total ecosystems, and the International Biological Programme examined productivity of a variety of ecosystems. The Antarctic al ecosystems were no exception to this interest (e.g. Holdgate, and in this region considerable progress has been made towards nding the structure and function of relatively simple (in terms of nt species) systems. During I.B.P., synthesis of information on arctic islands was undertaken: South Georgia (Smith and Walton, d Signy Island (Collins *et al.*, 1975). These were valuable assess- their terrestrial environments, primary and secondary production, sition processes and nutrient cycling.

The composition and structure of South Georgian terrestrial ecc
are determined by two principal factors, geographical isolation
northward extension of the Antarctic Convergence (Smith and
1975). This results in oceanic polar-alpine conditions, where the lc
and cold growing season permits high net annual production of
phanerogams and some bryophytes. Introduction of reindeer, rats a
has altered the plant communities in certain local areas of the isl
Signy Island further south (60°S 45°W), a severe summer climate
limited ice-free land area allows only two species of flowering p
survive, leaving bryophytes to dominate (Collins *et al.*, 1975). In
also, terrestrial invertebrate species diversity is greatly reduced ai
are no truly terrestrial mammals. An introduction to Signy Islanc
vided by Holdgate (1967a), whilst Jeffers and Holdgate (1976) have
terized the variability of environment and thus habitat on the
Considerable within-site diversity occurs, some of it on a very sma
but the island is representative of the maritime Antarctic zone
Antarctic Peninsula area (Holdgate, 1977). As conditions here are
larly favourable for terrestrial life, the terrestrial ecosystems c
Island are especially important for detailed study.

Net primary production, averaged over the total ice-free area
Island, amounts to *c.* 100 g dry weight m^{-2} y^{-1}, although up to 8(
weight m^{-2} y^{-1} is possible locally. Invertebrate herbivory, partici
bryophyte vegetation, is almost negligible, and most of the net
production passes to peat which may accumulate at rates up to 1 r
Decomposition is slow (Davis, 1980). In the peat-soil community,
brate predators are few (one species each of mite, nematode an
grade), but the saprovore-microbivore component is mucl
important. The ratio of total biomass to production, although
between sites on Signy Island, is comparable to those obtained f
tundra areas. Using the model of Heal and MacLean (1975), it h
suggested that maritime Antarctic habitats such as those at Signy
produce less invertebrate material than they should (Holdgate, 197
implies a basic functional difference compared to terrestrial ecosy
the Arctic and higher latitudes, but until information is availabl
vertebrate life cycles, growth and production, this cannot be substa

Two significant studies on terrestrial ecosystem processes ha
undertaken in the Antarctic: at Marion Island and Signy Island.

The studies at Marion Island were aimed at an understanding of t
cycles operating within the islands' general ecosystems. Vegetatio
ing crops, as in several other sub-Antarctic communities, were hig
cipally due to favourable environmental conditions during the
season and the virtual absence of herbivores (Smith, 1976). Only

tera and larval Lepidoptera feed directly on live plants (Smith, , and light aphid infestations occur on some grasses. Soil inverte- razing may be substantial, however. Introduced mice *Mus musculus* predominant above-ground herbivores, feeding on the seeds of at ur plant species. Predators include spiders and mites with the top res being the introduced cat *Felis cattus*, the brown skua *Catharacta nnbergi*, and two giant petrels *Macronectes giganteus* and *Macronec-*. Qualitative studies on terrestrial energy flow and nutrient cycling ion Island suggest that nutrient release is slow, leaching rates are d the main nutrient sources are via sea spray and vertebrate excre- vith some nitrogen-fixation by blue-green algae (Smith, 1977b; van en Bakker, 1978). Recycling of nutrients within the system is de- ased rather than grazer-based. Such features of the Marion Island may well be typical of many sub-Antarctic islands.

arch at Signy Island was concentrated on two bryophyte ecosystems stigate the details of their structure, both at the population and levels, and their function in terms of the major processes which nder maritime Antarctic conditions. The overall objective is a

TABLE III

annual respiration, net and gross primary production together with data for the nicroflora of a moss turf and a moss carpet at Signy Island, maritime Antarctic. y estimates are given in parenthesis (minimum–maximum). Efficiencies (%) of organic nsfer between trophic levels and selected parts of trophic levels are also given. From 81). *Ecological Monographs* 51(2) 125–143. With the permission of the Ecological f America.

	Moss turf	Moss carpet
g d.w. m^{-2})	546 (291–969)	180 (156–204)
n (g d.w. $m^{-2}y^{-1}$)	306 (277–418)	32 (26–38)
ary production (g d.w. $m^{-2}y^{-1}$)	409 (321–497)	392 (226–548)
mary production (g d.w. $m^{-2}y^{-1}$)	715 (597–857)	424 (258–580)
nicroflora		
g d.w. m^{-2})	56 (14–169)	5 (1–15)
n (g d.w. $m^{-2}y^{-1}$)	358 (182–486)[b]	229 (112–326)[a]
$\left(\text{ratio} \times \frac{100}{1}\right)$		
	7.0	9.1
	0.1	0.1
	49.4	75.6
	0.3	0.5
	0.01	0.04

respiration minus soil fauna respiration; [b], As [a] but also minus rhizoid respiration; P_0, Net primary ; P_1, Primary consumer production; P_2, Secondary consumer production; P_m, Moss net primary ; C_1, Consumption by primary consumers; C_2, Consumption by secondary consumers; C_m, on of moss by primary consumers; d.w., dry weight.

(a)

(b)

Fig. 7. Terrestrial ecosystem study sites at Signy Island, South Orkney Islands. (a) A
of *Polytrichum alpestre* and *Chorisodontium aciphyllum* showing a portion of the sample
A moss carpet of *Calliergon sarmentosum*, *Calliergidium austrostramineum* and *Drepa*
uncinatus, which contains extensive areas of the liverwort *Cephaloziella varians*.

tion model of each system, which will allow the testing of hypotheses ned with ecosystem dynamics as well as having a predictive capacity. ong-term programme commenced in 1970 and the communities d were a *Polytrichum–Chorisodontium* moss turf and a *Callier-alliergidium–Drepanocladus* moss carpet (Fig. 7a,b). The study sites rlier work on these and other Signy Island areas are described by ok (1973a). Initially, an analysis of the standing crops and transfers nic matter within communities was made, which involved a synthesis data for biomass, production and respiration of the plants (mosses, , liverworts and algae), the microflora (Table III) and the inverte-(Protozoa, Rotifera, Tardigrada, Nematoda, Acari and Collembola) IV) (Davis, 1981).

TABLE IV

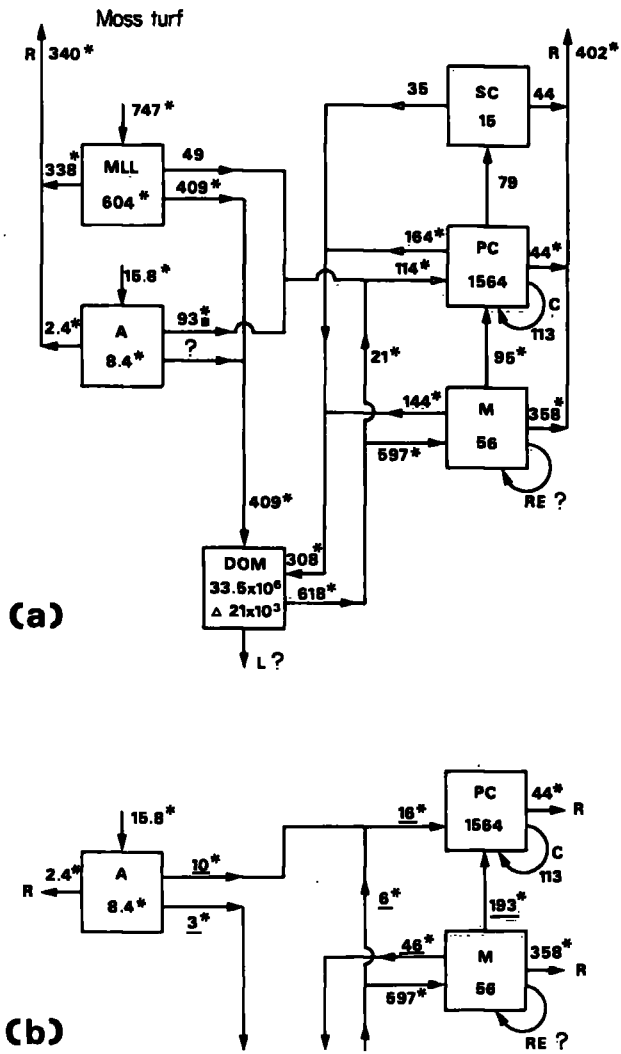
ght biomass and annual respiratory weight losses of the soil fauna of a moss turf and rpet at Signy Island. Variability estimates in parentheses (minimum–maximum). From 981). *Ecological Monographs* **51**(2), 125–143. With the permission of the Ecological of America.

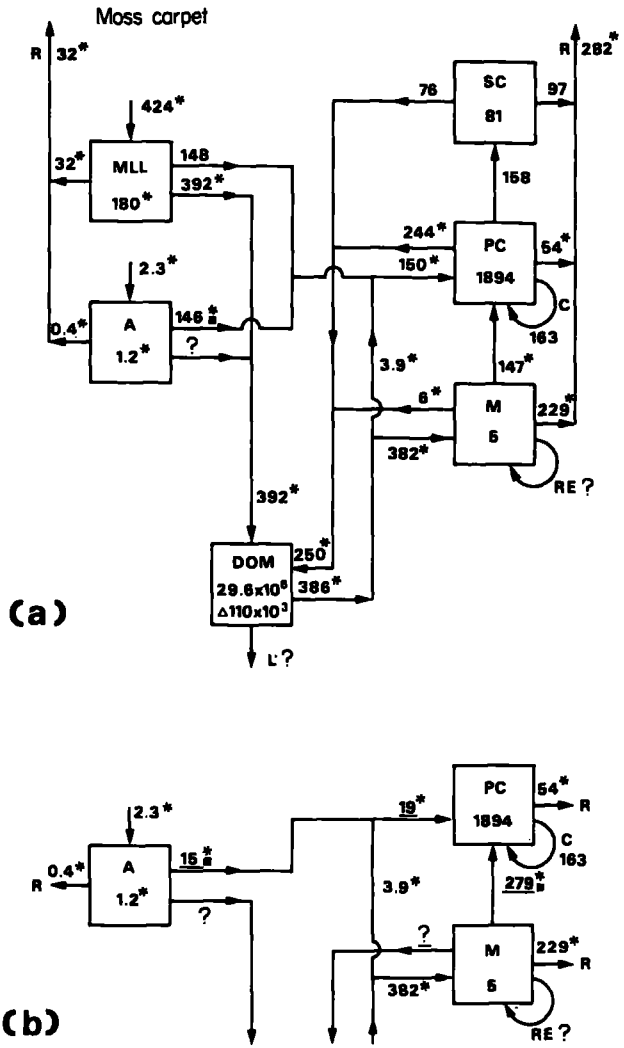
	Biomass (mg d.w. m^{-2})	Respiration (mg d.w. $m^{-2}y^{-1}$)
f		
	1240 (830–1700)	42400 (200–100600)
	25.3 (0.0–65.9)	169.0 (0.0–679.0)
da	47.0 (0.0–278.0)	236.9 (0.0–1557.7)
da	30.3 (6.7–33.9)	215.3 (83.6–347.0)
ola[a]	224.9 (96.7–353.1)	1192.0 (947.0–1442.0)
	12.1 (6.0–18.2)	115.9 (8.6–223.2)
pet		
	1660 (1169–2230)	52500 (500–122600)
	35.9 (0.0–117.2)	140.0 (0.0–560.0)
da	163.2 (0.2–652.1)	535.1 (0.0–2812.5)
la	60.6 (0.9–106.7)	297.3 (58.2–536.4)
ola[a]	55.5 (0.0–153.7)	186.0 (138.0–234.0)
	Absent	Absent

cies, *Cryptopygus antarcticus*.

ial rates of consumption, egestion, assimilation and production of ia and microflora were derived, together with efficiencies of organic transfer between trophic levels (Table III). The comparison re-n two flow diagrams representing the dynamics of organic matter (Fig. 8). Both communities have a simple trophic organization, grazers and with few micro-predators, which contrasts with those c and Alpine tundra (e.g. Wielgolaski, 1975a). Ecological efficien-the primary consumers (Table III) are within the normal range,

suggesting that their small size and the trophic structure do nc
energy flow at this level, although the pathways of material transfe
In both systems, <0.04% of moss net production is directly cor
and the invertebrate food base is largely algae, micro-organis
dead organic matter. An amount between 50 and 76% of anr
primary production is consumed, which differs from Arctic tundr





ganic matter standing crops (mg d.w. m^{-2}) and mean annual flow rates (mg d.w. m^{-2}
ntarctic moss turf and moss carpet communities at Signy Island, maritime Antarctic
vis (1981). *Ecological Monographs* **51**(2), 125–143. With the permission of the
l Society of America.)
osses, liverworts and lichens; A, micro-algae; DOM, dead organic matter; M, micro-
primary consumers; SC, secondary consumers; R, respiratory losses; L, leaching and
ion; C, carnivory; RE, recycling; *, value $\times 10^3$; ■, estimated rate of consumption of
nicroflora by primary consumers is greater than their net productivity, hence no
f their input to DOM has been made; ?, quantity unknown; Δ, estimated net annual
tion of DOM; (a) diet of Mastigophora is 100% DOM and of Sarcodina is 50% algae
microflora; (b) subsection redrawn with diet of Mastigophora being 95% microflora
OM, and of Sarcodina being 95% microflora and 5% algae.

exploitation efficiences are <1.5% (Whitfield, 1977). Conversely, c
production is only 0.3–0.5% of primary consumer production
Island, which is very low compared to the Arctic (15–33%).

Several similarities exist in the efficiencies and pathways of
matter transfer in the two maritime Antarctic moss communities,
differences in summer soil temperatures, nutrient levels, water regi
anaerobic conditions. The moss carpet had a much lower level of ar
activity (Acari and Collembola), a lower standing crop of mosses
faster turnover, and a higher decomposition rate reflected in the
accumulation of peat.

The accumulation of dead organic matter as peat on the Sign
moss turf and carpet sites has been modelled using data on peat res
and decomposition rates (Davis, 1980). Oxygen uptake by the p
converted to organic matter loss to derive the decomposition rate,
was evaluated using two mathematical models, which simula
accumulation of dead organic matter (29.6–33.5 kg dry weight m
from litter production (392–409 g d.w. m^{-2} y^{-1}) and mean decom
rate, i.e. fraction of standing crop lost y^{-1} (0.010–0.017 g d.w. g
From the models' predictions, the observed decay rate was too hig
moss turf and too low in the moss carpet, and greater precisio
measurement is clearly required. Nevertheless, it is certain that sir
modelling will enable a more precise definition of the processes
accumulation and organic matter decomposition in these
ecosystems.

From these two pioneer ecosystem studies, it is suggested that
sence of large, above-ground herbivores has a profound effect on
structure and function of the terrestrial system. Whether their ab
due to isolation and barriers to dispersal, or to the unpalatabilit
cryptogamic plants is not clear, but it shifts the emphasis of energy
nutrient circulation onto smaller organisms in the below-ground (s
system. This is essentially a decomposer community consisting o
bivores and saprovores with a few micro-predators. The functio
micro-organism component is thereby greatly enhanced in such
poor ecosystems, and clearly an understanding of the soil inver
microbial interactions is fundamental to any ecosystem analysis. Tl
face of these two components in moss dominated systems is likely t
phylloplane, where critical studies should now be concentrated.
these interactions, and the role of the soil invertebrate populatio
detritus-based trophic system of the coastal tundra at Point
Alaska, have been described by MacLean (1980). Such a synthesis
strates the importance of the soil community in tundra ecosyste
mics, and the difficulties of analysis in complexly structured sys

ions of the seasonal changes in microbial decomposer activity, using tic peat cores and Gilson respirometry techniques, Wynn-Williams has demonstrated the importance of the spring freeze–thaw cycles in ease of dissolved organic carbon from frost damaged moss cells. al biomass increased and diversified during summer as the carbon was depleted, and cellulose decomposition increased. Amending ucose was shown to restore partly the initial respiratory activity of ores. Oxygen uptake declined in summer, due not only to carbon on but also to microfaunal predation, and possibly desiccation. nental simulations of this sort have obvious advantages for the in- tion of processes at the microbial–microfaunal level, and for under- g the effects of perturbations upon such systems.

w ecosystem studies have been completed for Arctic and northern areas, e.g. Wielgolaski (1975b), Bliss (1977) and Brown *et al.* (1980), ave involved large numbers of personnel and research projects, due complexity of the systems. Very few satisfactory models either for lar ecosystems or for more general application across the tundra ave been developed. The terrestrial ecosystems of the maritime and ntal Antarctic offer the first possibility of constructing meaningful , which represent realistically the major processes inherent within n this context, such Antarctic systems may closely resemble those n certain species-poor hot deserts, and comparative studies may be ive.

clusions

ic terrestrial ecosystems and their living communities present the ntist with unparalleled opportunities to investigate a spectrum of al problems, the solution of which will contribute, not only to ic and polar biology, but also to general concepts in ecology and mental physiology. These encompass both autecological and ogical fields. At the microbial level, the relatively low levels of n in the Antarctic Region, compared to the northern hemisphere y, endows microbiological work there with a high degree of impor- or instance, the dominance of the yeast population in bryophyte during much of the growing season in the maritime Antarctic is not ed in northern tundra communities. Yeasts also appear to exhibit lerance to nutritional and environmental stresses and their epi- abit in moss, together with the micro-algae, may be a critical factor gy flow to the invertebrate components of the system. The

microbe–microbivore interaction is clearly of importance in these poor communities.

Invertebrate diversity, as measured by the number of resident s terrestrial communities, decreases markedly from the sub-Antarct South Pole. In the less harsh environments of the sub-Antarctic isl vertebrates are a key food source for certain overwintering birds. T large gaps in the knowledge of most of the non-arthropod grou Antarctic, in taxonomy, ecology and physiology. It is intrigu annelids such as the Enchytraeidae have been found in some of t sheltered areas of the maritime Antarctic, where they probably u the role of earthworms in other, warmer regions. The present pa faunal distribution, together with a knowledge of species ecology a ology, allow inferences to be made concerning the processes of past ation of the Antarctic land mass, and the position of the fauna d Pleistocene period. The sub-Antarctic provides a rich laborator testing of theories appertaining to island biogeography, and inve dispersal mechanisms. The numerical dominance in the invertebrat Acari and Collembola in the Antarctic is linked to their penetratio north and south in the world than many other phyla. These are clear which are highly successful in a wide range of environments, but especially adapted to low temperature conditions.

In the area of physiological adaptation to environment, the pro mites are of particular interest, as they exhibit a high degree of tol cold. In addition, their water relations would repay study in the lig possible effect of dehydration on cold tolerance and the use of anhyd as in representatives of hot desert faunas. The Antarctic can be consi subjecting poikilotherms to the most stressful environmental m earth, and it is eminently suitable for the testing of ideas on the t biological cold tolerance and on the survival mechanisms of in species. The interplay of the species' physiology with environmen ables to produce a successful life cycle highlights the overall ada strategy which has been adopted over a long time period.

Finally, terrestrial ecosystems in the Antarctic, being devoid above-ground herbivores and containing mainly decomposer-or communities, provide ideal test-beds for examining perturbation e so doing, their ecological fragility and the dynamics of the natural p of repair and rehabilitation will be understood.

7. References

Aoki, K. and Konno, M. (1961). Frost-resistance of the rotifer in Antarcti *Bulletin of the Marine Biology Station of Asamushi* **10,** 247–250.

, P., Arnaud, F. and Hureau, J.-C. (1967). General bibliography of ctic and sub-Antarctic Biology. *Comité National Français des Recherches ctiques* **18,** 1–180.
, E. (1969). Frost resistance in insects. *Advances in Insect Physiology* **6,**

, W. R. and Davis, B. L. (1979). Chromosomal variability in the Antarctic *Belgica antarctica*. *Annals of the Entomological Society of America* **72,** 52.
:. M., di Menna, M. E. and Cameron, R. E. (1978). Ecological investiga- of yeasts in Antarctic soils. *Antarctic Research Series* **30,** 27–34.
W. T. and Peterson, P. C. (1967). Astigmata (Sarcoptiformes): Procto- didae, Avenzoariidae (feather mites). *Antarctic Research Series* **10,** 3.
W. T. and Peterson, P. C. (1970). Acarina: Astigmata: Analgoidea: feather of South Georgia and Heard Islands. *Pacific Insects Monograph* **23,** 51.
A. D. and Wynn-Williams, D. D. (1982). Soil microbiological studies at Island, South Orkney Islands. *British Antarctic Survey Bulletin* No. 51, 91.
. H. (1970a). Yeasts, moulds and bacteria from an acid peat on Signy Island. ntarctic Ecology" (M. W. Holdgate, ed.), pp. 717–722. Academic Press, ork and London.
. H. (1970b). Quantitative study of yeasts and bacteria in a Signy Island *British Antarctic Survey Bulletin* No. 23, 51–55.
. H. (1974). Use of a temperature gradient incubator to investigate the rature characteristics of some bacteria from Antarctic peat. *British tic Survey Bulletin* No. 39, 49–59.
. H. and Smith, D. G. (1972). The bacteria in an Antarctic peat. *Journal of d Bacteriology* **35,** 589–596.
. E., Holdgate, M. W., Longton, R. E., Tilbrook, P. J., Tamblin, J. F., an, R. W. and Wynne-Edwards, W. C. (1964). A survey of the South ich Islands. *Nature* (Lond.) **203,** 691–693.
Browne, J. and Tilbrook, P. J. (1966). Coleoptera collected in the South y and South Shetland Islands. *British Antarctic Survey Bulletin* No. 9,

rn, E. S. and Nichols, R. L. (1961). Sulfate-reducing bacteria and pyritic nts in Antarctica. *Science* (New York) **134,** 190.
. G. and Edwards, J. (1979). Mechanisms of freezing tolerance in an tic insect (*Belgica antarctica*). *Physiological Entomology* **4,** 1–5.
, W. B. (1922). Oligochaeta of Macquarie Island. *Australasian Antarctic ition*, 1911–1914. *Scientific Report* **6,** 1–38.
C. (ed.) (1977). "Truelove Lowland, Devon Island, Canada: a High Arctic stem". University of Alberta Press, Edmonton.
V. (1976). Oxygen uptake by *Nanorchestes antarcticus* (Acari). *Oikos* **27,** 3.
W. (1977). Oxygen consumption of the terrestrial mite *Alaskozetes icus* (Acari: Cryptostigmata). *Journal of Experimental Biology* **68,** 69–87.
W. (1979a). Cold tolerance of micro-arthropods from Alaskan taiga. ical Entomology **4,** 103–110.
V. (1979b). Oxygen consumption of the Antarctic springtail *Parisotoma*

octooculata (Willem) (Isotomidae). *Revue d'Écologie et de Biologie d* 227–233.
Block, W. (1979c). Terrestrial invertebrates. *In* "Elephant Island: an Expedition" (C. Furse, ed.), pp. 226–229. Anthony Nelson, Shrewsbury
Block, W. (1979d). *Nanorchestes antarcticus* Strandtmann (Prostigma Antarctic ice. *Acarologia* **11,** 173–176.
Block, W. (1980a). Aspects of the ecology of Antarctic soil fauna. *In* "Soil E Related to Land Use Practices" (D. L. Dindal, ed.), pp. 741–758. [*Soi Colloquium* **VII,** Syracuse, New York, 29 July–3 August 1979.] Envir Protection Agency, Washington D.C.
Block, W. (1980b). Survival strategies in polar terrestrial arthropods. *Journal of the Linnean Society* **14,** 29–38.
Block, W. (1982a). The Signy Island terrestrial reference sites: XIV. P studies on the Collembola. *British Antarctic Survey Bulletin* No. 55, 33–
Block, W. (1982b). Respiration studies on some South Georgian Coleopter *National Français des Recherches Antarctiques* **51,** 183–192.
Block, W. and Tilbrook, P. J. (1975). Respiration studies on the Antarcti bolan *Cryptopygus antarcticus*. *Oikos* **26,** 15–25.
Block, W. and Tilbrook, P. J. (1977). Effects of long term storage on th uptake of *Cryptopygus antarcticus* (Collembola). *Oikos* **29,** 284–289.
Block, W. and Tilbrook, P. J. (1978). Oxygen uptake by *Cryptopygus a* (Collembola) at South Georgia. *Oikos* **30,** 61–67.
Block, W. and Young, S. R. (1978). Metabolic adaptations of Antarctic micro-arthropods. *Comparative Biochemistry and Physiology* **61A,** 363–
Block, W. and Young, S. R. (1979). Measurement of supercooling in sma pods and water droplets. *Cryo-Letters* **1,** 85–91.
Block, W. and Zettel, J. (1980). Cold hardiness of some Alpine Co *Ecological Entomology* **5,** 1–9.
Block, W., Young, S. R., Conradi-Larsen, E.-M. and Sømme, L. (19 tolerance of two Antarctic terrestrial arthropods. *Experientia* **34,** 1166–1
Bowra, G. T., Holdgate, M. W. and Tilbrook, P. J. (1966). Biological inve in Tottanfjella and Central Heimefrontfjella. *British Antarctic Survey* No. 9, 63–70.
Boyd, W. L. (1967). Ecology and physiology of soil micro-organisms in pola *Japanese Antarctic Research Expedition, Scientific Reports, Special Iss* 265–275.
Boyd, W. L. and Boyd, J. W. (1962). Presence of *Azotobacter* species regions. *Journal of Bacteriology* **83,** 429–430.
Boyd, W. L. and Boyd, J. W. (1963). Soil organisms of the McMurdo So Antarctica. *Applied Microbiology* **11,** 116–121.
Boyd, W. L. and Rothenberg, I. (1968). Ecology of soil micro-organis vicinity of Almirante Brown Base. *Antarctic Journal of the United States*
Boyd, W. L., Staley, J. T. and Boyd, J. W. (1966). Ecology of soil micro-org Antarctica. *Antarctic Research Series* **8,** 125–159.
Boyd, W. L., Rothenberg, I. and Boyd, J. W. (1970). Soil micro-org Paradise Harbour, Antarctica. *Ecology* **51,** 1040–1045.
Brinck, P. (1945). Coleoptera. *Scientific results of the Norwegian Antarcti tion, 1927–1928* (Oslo) **24,** 1–23.
Broady, P. A. (1975). "Studies on the terrestrial algae of Signy Island, Sout Islands." Ph.D. thesis, University of Bristol.
Broady, P. A. (1976). Six new species of terrestrial algae from Signy Isla

y Islands, Antarctica. *British Phycological Journal* **11**, 387–405.
P. A. (1977a). A new genus and two new species of terrestrial chloro-an algae from Signy Island, South Orkney Islands, Antarctica. *British logical Journal* **12**, 7–15.
P. A. (1977b). The Signy Island terrestrial reference sites: VII. The ec-of the algae of site 1, a moss turf. *British Antarctic Survey Bulletin* No. 45,

P. A. (1979a). The Signy Island terrestrial reference sites: IX. The ec-of the algae of site 2, a moss carpet. *British Antarctic Survey Bulletin* No. -29.
P. A. (1979b). Quantitative studies on the terrestrial algae of Signy , South Orkney Islands. *British Antarctic Survey Bulletin* No. 47, 31–41.
P. A. (1979c). Feeding studies on the collembolan *Cryptopygus ticus* Willem at Signy Island, South Orkney Islands. *British Antarctic Bulletin* No. 48, 37–46.
P. A. (1979d). A preliminary survey of the terrestrial algae of the tic Peninsula and South Georgia. *British Antarctic Survey Bulletin* No. -70.
P. A. (1979e). Wind dispersal of terrestrial algae at Signy Island, South y Islands. *British Antarctic Survey Bulletin* No. 48, 99–102.
P. A. (1979f). The terrestrial algae of Signy Island, South Orkney s. *British Antarctic Survey Scientific Reports* No. 98, 1–117.
., Bunnell, F. L., MacLean, S. F., Miller, P. L. and Tiezen, L. C. (eds) . "An Arctic Ecosystem: the Coastal Tundra at Barrow, Alaska". *B.P. Synthesis Series* **12**, 1–571. Dowden, Hutchinson and Ross, elphia.
L. (1970). Antarctic land faunas and their history. *In* "Antarctic Ec-' (M. W. Holdgate, ed.) Vol. 1, pp. 41–53. Academic Press, New York ndon.
S. (1954a). The soil inhabiting nematodes of Macquarie Island. *Aus-Journal of Zoology* **2**, 264–274.
S. (1954b). A comparative account of the terrestrial diatoms of Mac-Island. *Proceedings of the Linnean Society of New South Wales* **79**,

S. (1954c). Notes on the bacteria belonging to the *Rhodobacteriineae* , Murray & Hitchens, and the *Chlamydobacteriales* Buchanan occurring at arie Island. *Proceedings of the Linnean Society of New South Wales* **79**,

S. (1955). A note on the faecal flora of some Antarctic birds and mammals quarie Island. *Proceedings of the Linnean Society of New South Wales* **80**,

S. (1965). Observations on the fungi of Macquarie Island. *Australian al Antarctic Research Expedition* Ser. B, **2**, No. 78, 1–22.
S. and Rovira, A. D. (1955a). Microbiological studies of some sub-tic soils. *Journal of Soil Science* **6**, 119–128.
S. and Rovira, A. D. (1955b). The effect of temperature and heat treat-n soil metabolism. *Journal of Soil Science* **6**, 129–136.
A. E. (1978). Terrestrial invertebrates: a food resource for birds at 1 Island. *South African Journal of Antarctic Research* **8**, 87–99.
A. E. (1979). Sampling of terrestrial invertebrates using sticky-traps at 1 Island. *Polar Record* **19**, 618–620.

Burn, A. J. (1981). Feeding and growth in the Antarctic collembolan *Cry antarcticus* (Willem). *Oikos* **36,** 59–64.
Caldwell, J. R. (1981). The Signy Island terrestrial reference sites: XIII tion dynamics of the nematode fauna. *British Antarctic Survey Bulleti* 33–46.
Cameron, R. E. (1971). Antarctic soil microbiology and ecological inves *In* "Research in the Antarctic" (L. O. Quam and H. D. Porter, 137–189. American Association for the Advancement of Science, W D.C.
Cameron, R. E. (1972a). Microbial and ecologic investigations in Victori Southern Victoria Land, Antarctica. *Antarctic Research Series* **20,** 195–2
Cameron, R. E. (1972b). Farthest south algae and associated bacteria. *P* **11,** 133–139.
Cameron, R. E. (1972c). Pollution and conservation of the Antarctic t ecosystem. *In* "Colloquium on Conservation Problems in Antarctica Parker, ed.), pp. 267–308. Allen Press, Lawrence, Kansas.
Cameron, R. E. and Benoit, R. E. (1970). Microbial and ecological inve of recent cinder cones, Deception Island, Antarctica—a preliminar *Ecology* **51,** 802–809.
Cameron, R. E. and Conrow, H. P. (1969). Soil moisture, relative humi microbial abundance in dry valleys of southern Victoria Land. *Antarcti of the United States* **4,** 23–28.
Cameron, R. E. and Ford, A. B. (1974). Baseline analysis of soils Pensacola Mountains. *Antarctic Journal of the United States* **9,** 116–119.
Cameron, R. E. and Morelli, F. A. (1974). Viable micro-organisms fro Ross Island and Taylor Valley drill cores. *Antarctic Journal of the Uni* **9,** 113–116.
Cameron, R. E., King, J. and David, C. N. (1970). Microbiology, eco microclimatology of soil sites in dry valleys of southern Victoria "Antarctic Ecology" (M. W. Holdgate, ed.), pp. 702–716. Academic Pr York and London.
Cameron, R. E., Lacy, G. H., Morelli, F. A. and Marsh, J. R. (1971). south soil microbial and ecological investigations. *Antarctic Journ United States* **6,** 105–106.
Cameron, R. E., Morelli, F. A. and Johnson, R. M. (1972). Bacterial s soil and air of the Antarctic Continent. *Antarctic Journal of the United* 187–189.
Cameron, R. E., Honour, R. C. and Morelli, F. A. (1977). Environment studies of Antarctic sites. *In* "Adaptations within Antarctic Ecosystems Llano, ed.), pp. 1157–1176. Gulf Publishing Co., Houston, Texas.
Caretta, G. and Piontelli, E. (1977). *Microsporum magellanicum* a *ninghamella antarctica*, new species isolated from Australic and Anta of Chile. *Sabouraudia* **15,** 1–10.
Carmichael, J. W. (1962). *Chrysosporium* and some other aleurospori mycetes. *Canadian Journal of Botany* **40,** 1137–1173.
Carpenter, G. H. (1902). Insecta. Aptera. Collembola. *In* "Report Collections of Natural History made in the Antarctic Regions du Voyage of the 'Southern Cross'", pp. 1–344. British Museum (Natural London.
Castrelos, O. D., Ikonicoff, S. I., Del Prete, L., Milano, O. C. and Marg

). Microbiologia de la Antártica. *Contribución del Instituto Antártico ıtino* No. 209, 1–25.
H. B. (1966). Trapping of air-borne insects in the Atlantic–Antarctic *Pacific Insects* **8,** 455–466.
'. (1967). Mallophaga (biting lice) and Anoplura (sucking lice). Part I: *ogoniodes* (Mallophaga) parasitic on penguins (Sphenisciformes). *ctic Research Series* **10,** 149–155.
. and Moreby, C. (1967). Mallophaga (biting lice) and Anoplura (sucking Part II: Keys and locality lists of Mallophaga and Anoplura. *Antarctic rch Series* **10,** 157–196.
'. and Moreby, C. (1970). Mallophaga and Anoplura of subantarctic s. *Pacific Insects Monograph* **23,** 216–220.
ɜy-Thompson, J. L. (1973). Factors influencing supercooling of tropical ɔpods, especially locusts. *Journal of Natural History* **7,** 471–480.
ɜy-Thompson, J. L. (1978). Diurnal rhythms of supercooling in locusts. *ational Journal of Biometeorology* **22,** 112–115.
N. J., Baker, J. H. and Tilbrook, P. J. (1975). Signy Island, maritime ctic. *In* "Structure and Function of Tundra Ecosystems" (T. Rosswall ɔ. W. Heal, eds), pp. 345–374. Swedish Natural Science Research ɔil, Stockholm. (*Ecological Bulletins* (Stockholm) **20.**)
n, I. F. B. (1962). Insects of Macquarie Island. Lepidoptera: Pyralidae: riinae. *Pacific Insects* **4,** 975–978.
n, I. F. B. (1970). Lepidoptera: Yponomeutidae of Heard Island. *Pacific s Monograph* **23,** 229–233.
G. R. (1963). The occurrence of the beetle *Hydromedion sparsutum*) in a peat profile from Jason Island, South Georgia. *British Antarctic y Bulletin* No. 1, 25–26.
A. and Daglio, C. A. N. (1963). Micromicetes aislados en el Antártico. *ibución del Instituto Antártico Argentino* No. 74, 1–27.
A. and Daglio, C. A. N. (1964). A mycological study of Antarctic air. *In* ɔgie Antarctique" (R. Carrick, M. W. Holdgate and J. Prévost, eds), pp. 20. Hermann, Paris.
bias, R. (1966). Observaciónes cuantitatives sobre los invertebrados tres Antárticos y pueantárticos. *Instituto Antártico Chileno* **9,** 1–62.
bias, R. (1968). Some observations on Antarctic Oribatei (Acarina) *Lio- ius australis* sp. n, and two *Oppia* spp. n. *Acarologia* **10,** 313–356.
d, C. S. and Riddle, W. A. (1974). Cold hardiness in centipedes and ons in New Mexico. *Oikos* **25,** 86–92.
, A. R. (1977). First record of *Ereynetes macquariensis* (Acarina: Erey- e) from Anvers Island, Antarctic Peninsula. *Pacific Insects* **17,** 489.
E. A. (1970). Prostigmata: Tarsonemoidea: Pyemotidae of South Geo- *Pacific Insects Monograph* **23,** 115–120.
s, P. (1965). The Acarology of the Antarctic regions. *Monographiae ɣicae* **15,** 414–430.
s, P. and Wilson, O. (1958). On the soil fauna of the Antarctic and of ıb-Antarctic Islands. The Oribatidae (Acari). *Arkiv för Zoologi* **2,** 25.
C. A. and Siple, P. A. (1941). Bacteria of Antarctica. *Journal of iology* **42,** 83–98.
L. (1973). Observations on the distribution of surface-living land arthro-

pods on the Subantarctic Île de la Possession, Îles Crozet. *Journal of History* **7**, 241–253.
Davis, R. C. (1980). Peat respiration and decomposition in Antarctic te moss communities. *Biological Journal of the Linnean Society* **14**, 39–49.
Davis, R. C. (1981). Structure and function of two Antarctic terrestri communities. *Ecological Monographs* **51**, 125–143.
Delettre, Y. R. (1978). Biologie et écologie de *Limnophyes pusillus* Eat (Diptera, Chironomidae) aux Îles Kerguelen. I.—Présentation générale des populations larvaires. *Revue d'écologie et de Biologie du Sol* **15**, 475–
Delettre, Y. R. and Cancela da Fonseca, J. P. (1978). II.—Étude des pop imaginates et discussion. *Revue d'Écologie et de Biologie du Sol* **16**, 355–
Dell, R. K. (1964). Land snails from sub-Antarctic islands. *Transactio Royal Society of New Zealand (Zoology)* **4**, 167–173.
De Man, J. G. (1904). Nématodes libres. *In* "Resultats du voyage du S. Y. ' en 1897–1898 sous le commandement de A. de Gerlache de Gomer *Zoologie* 55 pp. Anvers.
DeVries, A. L., Komatsu, S. K. and Feeney, R. E. (1970). Chemical and properties of freezing point depressing glycoproteins from Antarctic fish *nal of Biological Chemistry* **245**, 2901–2908.
di Menna, M. E. (1960). Yeasts from Antarctica. *Journal of General Micr* **23**, 295–300.
di Menna, M. E. (1966a). Three new yeasts from Antarctic soils: *Candida Candida gelida* and *Candida frigida*. *Antonie van Leeuwenhoek* **32**, 25–28
di Menna, M. E. (1966b). Yeasts in Antarctic soils. *Antonie van Leeuwen* 29–38.
Dougherty, E. C. (1964). Cultivation and nutrition of Micrometazoa. Antarctic strain of the tardigrade *Hypsibius arcticus* (Murray 1907) Marc *Transactions of the American Microscopical Society* **83**, 1–6.
Doutt, R. L. and Yoshimoto, C. M. (1970). Hymenoptera: Chalcidoidea: idae of South Georgia. *Pacific Insects Monograph* **23**, 293–294.
Dreux, P. (1965). Faune entomologique de l'Île de la Possession (Archipel *Terres australes et antarctiques françaises* No. 30, 58–73.
Dreux, P. (1966). La faune entomologique de l'Archipel Crozet et son end *Comité National Français des Recherches Antarctiques* **15**, 35–55.
Dreux, P. (1970). Contribution à l'étude des Arthropodes terrestres et d'ea des terres australe françaises. *Terres australes et antarctiques françai* 50–51, 41–44.
Dreux, P. (1971a). Premières données sur la faune entomologique de l'Île (Archipel Crozet). *Terres australes et antarctiques françaises* No. 55–56, 4
Dreux, P. (1971b). Insecta. La faune entomologique des Îles Marion et d Edward. *In* "Marion and Prince Edward Islands". Report on the South Biological and Geological Expedition, 1965–66 (E. M. van Zinderen J. M. Winterbottom, R. A. Dyer, eds), pp. 336–343. Balkema, Cape To
Duddington, C. L., Wyborn, C. H. E. and Smith, R. I. L. (1973). Predacio from the Antarctic. *British Antarctic Survey Bulletin* No. 35, 87–90.
Duman, J. G. and DeVries, A. L. (1975). The role of macromolecular antifr cold water fishes. *Comparative Biochemistry and Physiology* **52A**, 193–19
Dunkle, R. and Strong, F. (1972). A digital electrolytic micro-respirometer. *of the Entomological Society of America* **65**, 705–710.
Dunnet, G. M. (1961). Fleas from Macquarie Island, with a description o

es of *Parapsyllus* Enderlein. *Proceedings of the Royal Entomological Society* ndon Ser. B, **30**, 43–49.
:, G. M. (1962). Insects of Macquarie Island; Siphonoptera. *Pacific Insects* **4**,
:, G. M. (1964). Distribution and host relationship of fleas in the Antarctic and ntarctic. *In* "Biologie Antarctique" (R. Carrick, M. W. Holdgate and J. Pré- eds), pp. 223–239. Hermann, Paris.
, V. F. (1962). Insects of Macquarie Island. Hemiptera: Homoptera: didae. *Pacific Insects* **4**, 937–938.
, V. F. (1970). Hemiptera: Homoptera: Aphididae of South Georgia. *Pacific ts Monograph* **23**, 227.
E. (1908a). Bakteriologische Studien während der Schwedischen Südpolar- dition 1901–1903. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar- dition 1901–1903* **4**, 1–120.
E. (1908b). Studien über den Bakteriengehalt der Luft und des Erdbodens ntarktischen Gegenden, ausgeführt während der Schwedischen Südpolar dition 1901–1903. *Zeitschrift für Hygiene und Infektion* (Leipzig) **56**, 370.
ein, G. (1905). *Pringleophaga*, eine neue Schmetterlingsgattung aus dem ktischen Gebiet. *Zoologischer Anzeiger* **29**, 119–125.
ıray, J., Sáiz, F. and Hajek, E. R. (1977). Análisis de las relaciones entre fauna antártica y algunos factores climáticos. *Instituto Antártico Chileno* No. -44.
ons, J. M. (1971a). On the food habits of certain Antarctic arthropods from al Victoria Land and adjacent islands. *Pacific Insects Monograph* **25**, 121–125.
ons, J. M. (1971b). Temperature and three species of Antarctic arthropods. ic *Insects Monograph* **25**, 127–135.
ın, P. W. and Veum, A. K. (1974). Relationships between respiration, weight temperature and moisture in organic residues in tundra. *In* "Soil Organisms Decomposition in Tundra" (A. J. Holding, O. W. Heal, S. F. MacLean and P. lanagan, eds), pp. 249–277. Tundra Biome Steering Committee, Stockholm.
:. A. and Stout, J. D. (1960). Microbiology of some soils from Antarctica *re* (Lond.) **188**, 767–768.
i. E. (1967). Observations on the snow algae of the South Orkney Islands. *In* iscussion on the terrestrial Antarctic ecosystem" (J. E. Smith, organizer). *sophical Transactions of the Royal Society* **B 252**, 279–287.
J. E. and Stewart, W. D. P. (1968). *In situ* determinations of biological gen fixation in Antarctica. *British Antarctic Survey Bulletin* No. 15, 39–46.
, R. R. (1962). Insects of Macquarie Island. Araneida (spiders). *Pacific Insects* 1–919.
, R. R. (1970). Araneae: spiders of South Georgia. *Pacific Insects Monograph* 1–42.
, R. R. (1971). Notes on an airborne spider found in Antarctica. *Pacific Insects* ograph **25**, 119–120.
ann, E. I. (1977). Microorganisms in Antarctic desert rocks from dry valleys Dufek Massif. *Antarctic Journal of the United States* **12**, 26–29.
H. (1912). Untersuchungen über Meeresbakterien und ihren Einfluss auf den vecksel im Meere. *Deutsche Südpolar-expedition 1901–1903, Berlin*, **7**, 96.
ham, C. H. and Smith, R. I. L. (1970). Bryophyte and lichen communities in

the maritime Antarctic. *In* "Antarctic Ecology" (M. W. Holdgate, ed.), pp. 752–785. Academic Press, New York and London.
Gless, E. E. (1967). Notes on the biology of *Coccorhagidia gressitti* Wo and Strandtmann. *Antarctic Research Series* **10,** 321–324.
Gless, E. E. (1972). Life cycle studies of some Antarctic mites and descript new species, *Protereunetes paulinae* (Acari: Eupodidae). *Antarctic I Series* **20,** 289–306.
Goddard, D. G. (1977a). The Signy Island terrestrial reference sites: VI. uptake of *Gamasellus racovitzai* (Trouessart) (Acari: Mesostigmata). *Antarctic Survey Bulletin* No. 45, 1–11.
Goddard, D. G. (1977b). The Signy Island terrestrial reference sites Oxygen uptake of some Antarctic prostigmatid mites (Acari: Prosti *British Antarctic Survey Bulletin* No. 45, 101–115.
Goddard, D. G. (1977c). "Ecological studies on the terrestrial Acari c Island, South Orkney Islands, in the maritime Antarctic". Ph.D. University of Leicester.
Goddard, D. G. (1979a). The Signy Island terrestrial reference sit Population studies on the Acari. *British Antarctic Survey Bulletin* 71–92.
Goddard, D. G. (1979b). Biological observations on the free-living mites Island in the maritime Antarctic. *British Antarctic Survey Bulletin* 181–205.
Goddard, D. G. (1982). Feeding biology of free-living Acari at Signy South Orkney Islands. *British Antarctic Survey Bulletin* No. 51, 290–293.
Goto, S., Sugiyama, J. and Iizuka, H. (1969). Taxonomic study of A yeasts. *Mycologia* **61,** 748–774.
Graham, W. L. (1974). Arthropods near Palmer Station, Anvers Island. *A Journal of the United States* **9,** 306–307.
Graham, W. L. (1975). "Morphology and biology of *Stereotydeus* (Trouessart) (Acarina: Penthalodidae) from Antarctica". M.Sc. thesis Technical University, Lubbock, Texas.
Greene, S. W., Gressitt, J. L., Koob, D., Llano, G. A., Rudolf, E. D., Sin Steere, W. C. and Ugolini, F. C. (1967). Terrestrial life of Antarctica. *A Map Folio Series* **5,** 1–24. American Geographical Society, New York.
Gressitt, J. L. (1961). Problems in the zoogeography of Pacific and A insects. *Pacific Insects Monograph* **2,** 1–94.
Gressitt, J. L. (1962). Insects of Macquarie Island. Introduction. *Pacific In* 905–915.
Gressitt, J. L. (1964). Ecology and biogeography of land arthropods in Ant *In* "Biologie Antarctique" (R. Carrick, M. W. Holdgate and J. Prévos pp. 211–222. Hermann, Paris.
Gressitt, J. L. (1965a). Terrestrial animals. *In* "Antarctica" (T. Hatherto pp. 351–371. Methuen, London.
Gressitt, J. L. (1965b). Biogeography and ecology of land arthrop Antarctica. *Monographiae Biologicae* **XV,** 431–490.
Gressitt, J. L. (ed.) (1967a). Entomology of Antarctica. *Antarctic Researc* **10,** 1–395.
Gressitt, J. L. (1967b). Introduction. *In* "Entomology of Antarctica" Gressitt, ed.). *Antarctic Research Series* **10,** 1–33.
Gressitt, J. L. (1967c). Notes on arthropod populations in the Antarct

a–South Shetland Islands–South Orkney Islands Area. *Antarctic Research s* **10,** 373–392.
t, J. L. (ed.) (1970a). Subantarctic entomology, particularly of South gia and Heard Island. *Pacific Insects Monograph* **23,** 1–374.
t, J. L. (1970b). Subantarctic entomology and biogeography. *Pacific Insects ograph* **23,** 295–374.
t, J. L. (1971). Antarctic entomology with emphasis on biogeographical cts. *Pacific Insects Monograph* **25,** 167–178.
t, J. L. and Leech, R. E. (1961). Insect habitats in Antarctica. *Polar Record* 01–504.
t, J. L. and Pryor, M. E. (1961). Supplement to "Bibliographic introduction ntarctic–Subantarctic entomology". *Pacific Insects* **3,** 563–567.
t, J. L. and Shoup, J. (1967). Ecological notes on free-living mites in North ria Land. *In* "Entomology of Antarctica" (J. L. Gressitt, ed.). *Antarctic rch Series* **10,** 307–320.
t, J. L. and Weber, N. A. (1959). Bibliographic introduction to Antarctic-antarctic entomology. *Pacific Insects* **1,** 441–480.
t, J. L., Leech, R. E., Leech, T. S., Sedlacek, J. and Wise, K. A. J. (1961). ping of air-borne insects in the Antarctic area. (Part 2). *Pacific Insects* **3,** 562.
t, J. L., Leech, R. E. and Wise, K. A. J. (1963). Entomological investiga- in Antarctica. *Pacific Insects* **5,** 287–304.
t, J. L., Fearon, C. E. and Rennell, K. (1964). Antarctic mite populations negative arthropod surveys. *Pacific Insects* **6,** 531–540.
s, D. A. (1977). A new family of astigmatid mites from the Îles Crozet, Antarctica: introducing a new concept relating to ontogenetic development osomal setae. *Journal of Zoology* (Lond.) **182,** 291–308.
er, M. and Wallwork, J. A. (1979). A review of the world distribution of tid mites (Acari: Cryptostigmata) in relation to continental drift. *Kongelige ke Videnskabernes Selskabs, Biologiske Skrifter* **22,** 1–31.
, W. H. and Hooker, J. D. (1844). Algae. *In* "The Botany of the Antarctic ge of H. M. 'Erebus' and 'Terror' in the Years 1839–1843. Flora Antarctica" . Hooker, ed.), Vol. 1, pp. 175–193 and Vol. 2, pp. 254–519. Reeve Brothers, on.
worth, D. L. (1973). *Thyronectria antarctica* (Speg.) Seeler var. *hyper- ctica* D. Hawksw. var. nov. *British Antarctic Survey Bulletin* No. 32, 51–54.
). W. (1965). Observations on testate amoebae (Protozoa: Rhizopoda) from Island, South Orkney Islands. *British Antarctic Survey Bulletin* No. 6, .
). W. and MacLean, S. F. (1975). Comparative productivity in ecosystems— dary productivity. *In* "Unifying Concepts in Ecology" (W. H. van Dobben R. H. Lowe-McConnell, eds), pp. 89–108. Junk, The Hague; Pudoc, ningen.
). W., Bailey, A. D. and Latter, P. M. (1967). Bacteria, fungi and protozoa my Island soils compared with those from a temperate moorland. *Philo- cal Transactions of the Royal Society* **B252,** 191–197.
, M. (1965). Freshwater algae in the Antarctic regions. *In* "Biogeography cology in Antarctica" (J. van Mieghem and P. van Oye, eds), pp. 127–193. The Hague. [*Monographiae Biologicae* **15.**]
te, M. W. (1964). Terrestrial ecology in the maritime Antarctic. *In*

"Biologie Antarctique" (R. Carrick, M. W. Holdgate and J. Prévost, e
181–194. Hermann, Paris.
Holdgate, M. W. (1967a). Signy Island. *Philosophical Transactions of th
Society* **B252,** 173–177.
Holdgate, M. W. (1967b). The Antarctic ecosystem. *Philosophical Transac
the Royal Society* **B252,** 363–383.
Holdgate, M. W. (ed.) (1970). "Antarctic Ecology", Vols 1 and 2. Academi
New York and London.
Holdgate, M. W. (1977). Terrestrial ecosystems in the Antarctic. *In* "S
Research in the Antarctic" (V. E. Fuchs and R. M. Laws, eds). *Philos
Transactions of the Royal Society of London* **B279,** 5–25.
Holdgate, M. W. and Baker, P. E. (1979). The South Sandwich Islands: I. (
description. *British Antarctic Survey Scientific Reports* No. 91, 1–76.
Holdgate, M. W., Tilbrook, P. J. and Vaughan, R. W. (1968). The bio
Bouvetøya. *British Antarctic Survey Bulletin* No. 15, 1–7.
Holm-Hansen, O. (1963). Algae: Nitrogen fixation by Antarctic species.
(New York) **139,** 1059–1060.
Hughes, A. M. (1970). Acarina: Astigmata: Saproglyphidae of South G
Pacific Insects Monograph **23,** 153–160.
Hughes, A. M. and Tilbrook, P. J. (1966). A new species of *Calvolia* (Ac
Acarina) from the South Sandwich Islands. *British Antarctic Survey Bulle
10, 45–53.
Hunter, P. E. (1964). Laelaptid mites from Auckland and Macquarie Islan
arina: Laelaptidae). *Pacific Insects Monograph* **7,** 630–641.
Hunter, P. E. (1967a). Mesostigmata: Rhodacaridae, Laelapidae (Mesost
mites). *Antarctic Research Series* **10,** 35–39.
Hunter, P. E. (1967b). Rhodacaridae and Parasitidae mites (Acarina: M
mata) collected by the British Antarctic Survey 1961–64. *British Antarctic
Bulletin* No. 13, 31–39.
Hunter, P. E. (1970). Acarina: Mesostigmata: Free-living mites of South (
and Heard Island. *Pacific Insects Monograph* **23,** 43–70.
Inoue, K. and Komagata, K. (1976). Taxonomic study on obligately psych
bacteria isolated from Antarctica. *Journal of Applied Microbiology* **22,** 16
Janetschek, H. (1963). On the terrestrial fauna of the Ross-Sea area, Ant
(preliminary report). *Pacific Insects* **5,** 305–311.
Janetschek, H. (1967a). Arthropod ecology of South Victoria Land. *A
Research Series* **10,** 205–293.
Janetschek, H. (1967b). Growth and maturity of the springtail *Gomphioc
hodgsoni* Carpenter, from South Victoria Land and Ross Island. *A
Research Series* **10,** 295–305.
Janetschek, H. (1970). Environments and ecology of terrestrial arthropod
high Antarctic. *In* "Antarctic Ecology" (M. W. Holdgate, ed.), Vol.
871–885. Academic Press, New York and London.
Jeffers, J. N. R. and Holdgate, M. W. (1976). Signy Island: a case study of ec
characterisation. *Merlewood Research and Development Paper* **66,** 1–29.
Jenkin, J. F. (1975). Macquarie Island, Subantarctic. *In* "Structure and Fun
Tundra Ecosystems" (T. Rosswall and O. W. Heal, eds), pp. 375–398. S
Natural Science Research Council, Stockholm. [*Ecological B
(Stockholm),* **20.**]
Jennings, P. G. (1975). The Signy Island terrestrial reference sites: V. (

: of *Macrobiotus furciger* J. Murray (Tardigrada). *British Antarctic Survey etin* No. 41/42, 161–168.
gs, P. G. (1976a). The Tardigrada of Signy Island, South Orkney ıds, with a note on the Rotifera. *British Antarctic Survey Bulletin* No. 44, ;.
gs, P. G. (1976b). Tardigrada from the Antarctic Peninsula and Scotia Ridge ɔn. *British Antarctic Survey Bulletin* No. 44, 77–95.
gs, P. G. (1976c). "Ecological studies on Antarctic tardigrades and rotifers".). thesis, University of Leicester.
gs, P. G. (1979). The Signy Island terrestrial reference sites: X. Population ımics of Tardigrada and Rotifera. *British Antarctic Survey Bulletin* No. 47, 06.
ın, R. M., Madden, J. M. and Swafford, J. R. (1978). Taxonomy of Antarctic ɛria from soils and air primarily of the McMurdo Station and Victoria Land Valleys region. *Antarctic Research Series* **30,** 35–64.
t, J. J. (1971). Preliminary microbiological studies. *In* "Marion and Prince ard Islands. Report of the South African Biological and Geological Expedi- 1965–1966" (E. M. van Zinderen Bakker, J. M. Winterbottom and R. A. r, eds), pp. 237–240. Balkema, Capetown.
ır, J. K. (1967). Studies on the survival of the rotifer *Philodina* after freezing :hawing. *Cryobiology* **5,** 392–399.
ır, J. K. and Johnson, L. K. (1969). Food supply as a factor in the survival of ın and thawed rotifers. *Cryobiology* **5,** 375–378.
. (1968). Algae from the Antarctica. *Annales Historico-Naturales Musei ɔnalis Hungarici, Pars botanica* **60,** 71–77.
P. M. and Heal, O. W. (1971). A preliminary study of the growth of fungi ɔacteria from temperate and Antarctic soils in relation to temperature. *Soil ɔgy and Biochemistry* **3,** 365–379.
. C. and Hunter, P. E. (1974). Arthropoda of the subantarctic islands of New and 6. Rhodacaridae (Acari: Mesostigmata). *New Zealand Journal of ogy* **1,** 295–328.
y, K. L. (1972). *Nanorchestes antarcticus* Strandtmann; a taxonomic descrip- of the instars. *Acarologia* **8,** 593–606.
, G. (1971). Occurrence of arthropods in mosses at Anvers Island, Antarctic ısula. *Pacific Insects Monograph* **25,** 137–144.
J. H. (1978). Man's impact along the Antarctic Peninsula. *In* "Environ- al Impact in Antarctica" (B. C. Parker, ed.), pp. 333–371. Virginia Poly- ıic Institute and State University, Blacksburg, Virginia.
G. (1965). The flora of Antarctica. *In* "Antarctica" (T. Hatherton, ed.), pp. 350. Methuen, London.
n, R. E. (1973). The occurrence of radial infection patterns in colonies of bryophytes. *British Antarctic Survey Bulletin* No. 32, 41–49.
. A. (1975). Dorylaimoidea from some Sub-Antarctic islands. *Nematologica* 19–255.
an, S. F. (1980). The detritus-based trophic system. *In* "An Arctic Ec- em: the Coastal Tundra at Barrow, Alaska" (J. Brown, F. L. Bunnel, S. F. ean, P. Miller and L. L. Tiezen, eds), pp. 411–457. Dowden, Hutchinson oss, Philadelphia.
ı, A. L. (1918). Bacteria of ice and snow in Antarctica. *Nature* (Lond.) **102,**).

McLean, A. L. (1919). Bacteriological and other researches. *Australasian A Expedition 1911–1914. Scientific Report* **7**, 1–128.

Madden, J. M., Siegel, S. K. and Johnson, R. M. (1979). Taxonomy Antarctic *Bacillus* and *Corynebacterium* species. *Antarctic Research Se* 77–103.

Margni, R. A. and Castrelos, O. D. (1963). Examenes bacteriologicos de air y suelo de Cabo Primavera y Estacion Ellsworth. *Instituto Antártico A* No. 76, 1–15.

Margni, R. A. and Castrelos, O. D. (1964). Quelques aspects de la bacté antarctique. *In* "Biologie Antarctique" (R. Carrick, M. W. Holdgate and vost, eds), pp. 121–139. Hermann, Paris.

Margni, R. A. and Castrelos, O. D. (1971). Las bacterias del Antartico y su con la epoca del ano. *Instituto Antártico Argentina* No. 141, 1–19.

Margni, R. and Corte, A. (1962). Bacteriological analysis of some contam with exposure in South American Antarctic sector air. *Polar Record* **11**, 3

Marsh, J. B. (1973). "Radioisotopic determination of the ingestion rates species of Antarctic arthropods: *Cryptopygus antarcticus* Willem (Coll Isotomidae). *Belgica antarctica* Jacobs (Diptera: Chironomidae) and *Ala antarcticus* (Michael) (Cryptostigmata: Podacaridae)". M.Sc. thesis, Un of California, Davis.

Marshall, B. J. and Ohye, D. F. (1966). *Bacillus macquariensis* (a new sp psychrotrophic bacterium from a sub-Antarctic soil. *Journal of Genera biology* **44**, 41–46.

Martin, J. (1962). Inversion polymorphism in an Antarctic species living in environment (*Belgica antarctica* Jacobs). *American Naturalist* **96**, 317–318

Maslen, N. R. (1979a). Six new nematode species from the maritime An *Nematologica* **25**, 288–308.

Maslen, N. R. (1979b). "Terrestrial nematodes of the Antarctic region: tax biogeography and an ecological study". Ph.D. thesis, University of Readi

Maslen, N. R. (1980). Additions to the nematode fauna of the Antarctic reg keys to taxa. *British Antarctic Survey Bulletin* No. 49, 207–229.

Maslen, N. R. (1981). The Signy Island terrestrial reference sites: XII. Po ecology of nematodes with additions to the fauna. *British Antarctic Bulletin* No. 53, 57–75.

Maslen, N. R. (1982). An unidentified nematode-trapping fungus from a Alexander Island. *British Antarctic Survey Bulletin* No. 51, 285–287.

Matsuda, T. (1968). Ecological study of the moss community and micro-or in the vicinity of Syowa Station, Antarctica. *Biological Results of the J Antarctic Research Expedition, Series E* No. 29, 1–45.

Matsuda, T. (1977). Ecological investigations on free-living mites near Station, Antarctica. *In* "Adaptations within Antarctic Ecosystems" Llano, ed.), pp. 1015–1021. Gulf Publishing Co., Houston, Texas.

Meryman, H. T. (1966). Review of biological freezing. *In* "Cryobiology" Meryman, ed.), pp. 1–106. Academic Press, New York and London.

Meyer, G. H., Morrow, M. B. and Wyss, O. (1962). Viable microorganisms year old yeast preparation in Antarctica. *Nature* (Lond.) **196**, 598–599.

Meyer, G. H., Morrow, M. B. and Wyss, O. (1963). Viable microorganis faeces and foodstuffs from early Antarctic expeditions. *Canadian Jo Microbiology* **9**, 163–167.

Meyer, G. H., Morrow, M. B. and Wyss, O. (1967). Bacteria, fungi and oth

e vicinity of Mirny Observatory. *Antarctic Journal of the United States* **2,** 251.
l, A. D. (1895). Über die auf Süd-Georgien von der deutschen Station -1883 gesammelten Oribatiden. *Jahrbuch der Hamburgischen enschaftlichen Anstalten* 1894, XII, 69–72.
L. K. (1969). Freezing tolerance in an adult insect. *Science* (New York) **166,** 106.
T. (1975a). Clostridia isolated from the soil in the east coast of Lutzow-Holm East Antarctica. *Antarctic Record* **53,** 89–99.
T. (1975b). Clostridia in the soil of the Antarctic. *Japanese Journal of cal Science and Biology* **28,** 201–213.
T. (1976). Anaerobic bacteria of Antarctica—Isolation of Clostridia from oil around Syowa Station. *National Institute for Polar Research Memoirs* E, **32,** 56–63.
wa, K. (1962). Notes on some Tardigrada from the Antarctic Region. *Bio- al Results of the Japanese Antarctic Research Expedition Series E* No. 17, 1–6.
, J. (1906). Scottish National Antarctic Expedition: Tardigrada of the South eys. *Transactions of the Royal Society of Edinburgh* **45,** 323–334.
, J. (ed.) (1910a). Antarctic Rotifera. *In* "British Antarctic Expedition, -1909. Reports on the Scientific Investigations. Biology", pp. 41–65. emann, London.
, J. (ed.) (1910b). Tardigrada. *In* "British Antarctic Expedition, 1907–1909. rts on the Scientific Investigations. Biology", pp. 83–185. Heinemann, on.
, M. D. (1958). Ecology of the louse *Lepidopthirus macrorhini* Enderlein on the elephant seal *Mirounga leonina* (L.). *Nature* (Lond.) **182,** 404–405.
, M. D., Orton, M. N. and Cameron, A. S. (1967). The Antarctic flea *opsyllus antarcticus* Smit and Dunnet. *Antarctic Research Series* **10,** 95.
a, Y. (1977). Population density of free-living mites in ice-free areas around a Station, east Antarctica. *Antarctic Record* **60,** 47–56.
a, Y. (1979). Notes on the free-living mites in the ice-free areas around a Station. *Memoirs of National Institute of Polar Research, Special Issue* **11,** 29.
a, Y. and Matsuda, T. (1977). Free-living prostigmatic mites found around a Station, east Antarctica. *Antarctic Record* **59,** 172–176.
B. C., Howard, R. V. and Allnutt, F. C. T. (1978). Summary of environ- al monitoring and impact assessment of the DVDP. *In* "Environmental ct in Antarctica" (B. C. Parker, ed.), pp. 211–251. Virginia Polytechnic ute and State University, Blacksburg, Virginia.
n, R. A. and Knox, J. S. (1972). Occurrence of aquatic fungi in Victoria and Ross Island. *In* "Colloquium on Conservation Problems in Antarctica" . Parker, ed.), pp. 185–192. Allen Press, Lawrence, Kansas.
n, V. (1971). Notes on the Chironomid midge *Belgica antarctica* Jacobs at rs Island in the maritime Antarctic. *Pacific Insects Monograph* **25,** 145–166.
D. N., Spooner, B. M. and Smith, R. I. L. (1980). Higher fungi of ctica, the subantarctic zone and Falkland Islands. *Kew Bulletin* **35,** 62.
n, A. J. (1971). Population studies on the Antarctic collembolan *Gom- ephalus hodgsoni* Carpenter. *Pacific Insects Monograph* **25,** 75–98.

Pickford, G. E. (1932). Oligochaeta 2. Earthworms. *Discovery Reports* (
265–290.
Pirie, J. H. H. (1904). First Antarctic voyage of the 'Scotia'. 6. Bacteriology
Geographical Magazine (Edinburgh) **20,** 129–132.
Pirie, J. H. H. (1912). Notes on Antarctic Bacteriology. *Report of Scientific I
the S. Y. Scotia* **3,** 137–148.
Pittard, D. A. (1971). A comparative study of the life stages of the mite *Ster
mollis* W. & S. (Acarina). *Pacific Insects Monograph* **25,** 1–14.
Pittard, D. A., Roberts, L. A. and Strandtmann, R. W. (1971). Morpl
variations in three populations of the Antarctic mite *Stereotydeus mollis*
ley and Strandtmann. *Acarologia* **13,** 88–97.
Pryor, M. E. (1962). Some environmental features of Hallett Station, Ar
with special reference to soil arthropods. *Pacific Insects* **4,** 681–728.
Quinlan, J. (1964). A new species of *Aphiloptera* Forster (Hyme
Cynipoidea) from the Crozet Islands. *Entomologist* **97,** 232.
Ramazzotti, G. (1972). Tardigrada della Isole Kerguelen e discrizione del
specie *Hypsibius* (I) *renaudi. Memorie dell'Istituto Italiano di Idrobiolo*
(Marco di Marchi, Milano) **29,** 141–144.
Rapoport, E. H. (1971). The geographical distribution of Neotropical and
Collembola. *Pacific Insects Monograph* **25,** 99–118.
Richters, F. (1907). Die Fauna der Moosrasen der Gausskengs und einiger S
Inseln. *Deutsches Südpolar-Expedition* **9,** 259–302.
Riddle, W. A. and Pugach, S. (1976). Cold hardiness in the scorpion *Paru
aquilonalis. Cryobiology* **12,** 248–253.
Rounsevell, D. E. (1977a). Geographic variation in the size of an Antar
Tydeus erebus Strandtmann (Acarina: Prostigmata). *Acarologia* **9,** 209–2
Rounsevell, D. E. (1977b). The ecology of the pan-Antarctic mite *Nan
antarcticus. In.* "Adaptation within Antarctic Ecosystems" (G. A. Llano,
1023–1033. Gulf Publishing Co., Houston, Texas.
Rounsevell, D. E. (1977c). "A population of *Nanorchestes antarcticus* (Acar
gmata) at the Vestfold Hills, Antarctica". M.Sc. thesis, University of Me
Rounsevell, D. E. (1978). Populations of introduced arthropods at A
Antarctic Stations. *Pacific Insects* **18,** 199–202.
Rounsevell, D. E. (1979). Arthropods in a botanical collection from th
Charles Mountains, Antarctica. *Pacific Insects* **20,** 83–85.
Rountree, P. M. (1938). Soils from the subantarctic Islands. Sect
Bacteriological examination of soils from Macquarie Island. *British
Zealand Antarctic Research Expedition (1929–1931) Reports* Ser. A, **2,** 1
Rudolph, E. D. (1970). Local dissemination of plant propagules in Antar
"Antarctic Ecology" (M. W. Holdgate, ed.), Vol. 2, pp. 812–817. Acaden
New York and London.
Saiz, F., Hajek, E. T. and Hermosilla, W. (1970). The colonization of in
litter by subantarctic soil and moss arthropods. *In* "Antarctic Ecology"
Holdgate, ed.), Vol. 2, pp. 897–907. Academic Press, New York and Lo
Salt, R. W. (1961). Principles of insect cold-hardiness. *Annual Review
mology* **6,** 55–74.
Schaefer, P. W. and Strandtmann, R. W. (1971). Notes on the incidence a
preference of Mallophaga and Analgoidea ectoparasitic on south po
(*Catharacta skua maccormicki*) on Ross Island, Antarctica. *Pacific Insec
graph* **25,** 15–16.

r, U. (1974a). Two Pauropodidae species (Myriapoda, Pauropoda) from the ntarctic Crozet Islands. *Entomologica Scandinavica* **5**, 59–65.
r, U. (1974b). Symphyla (Myriapoda) from the Subantarctic Crozet Islands. *mologica Scandinavica* **5**, 240–246.
h, J. M. (1965). Microbiology of Antarctica. *In* "Biogeography and Ecology ıtarctica" (J. van Mieghem and P. van Oye, eds), pp. 267–295. Junk, The ıe. [*Monographiae Biologicae* **15**.]
, N. A. and Stokes, J. L. (1965). Obligately psychrophilic yeasts from the regions. *Canadian Journal of Microbiology* **11**, 259–269.
R. (1967). Fungi distribution. *In* "Terrestrial Life of Antarctica" (S. W. ne, J. L. Gressitt, D. Koob, G. A. Llano, E. D. Rudolf, R. Singer, W. C. e and F. C. Ugolini, eds), pp. 16–17. American Geographical Society, New . [*Antarctic Map Folio Series* **5**.]
R. (1972). New Basidiomycete from the Antarctic. *Antarctic Research* **20**, 179–180.
R. and Corte, A. (1962). Estudio sobre los basidiomicetes antarticos. *Instiıntártico Argentino* No. 71, 1–45.
R. and Corte, A. (1964). A study of Antarctic Basidiomycetes. *In* "Biologie rctique" (R. Carrick, M. W. Holdgate and J. Prévost, eds), pp. 161–163. ıann, Paris.
G. A. M. (1970). Siphonaptera of South Georgia and Heard Island. *Pacific s Monograph* **23**, 291–292.
G. A. M. and Dunnet, G. M. (1962). A new genus and species of flea from rctica (Siphonaptera: Ceratophyllidae). *Pacific Insects* **4**, 895–903.
H. G. (1972). The terrestrial Protozoa of Elephant Island, South Shetland ls. *British Antarctic Survey Bulletin* No. 31, 55–62.
H. G. (1973a). The Signy Island terrestrial reference sites: II. The Protozoa. *h Antarctic Survey Bulletin* Nos 33 and 34, 83–87.
H. G. (1973b). The Signy Island terrestrial reference sites: III. Population gy of *Corythion dubium* (Rhizopoda: Testacida) in site 1. *British Antarctic y Bulletin* Nos 33 and 34, 123–135.
H. G. (1973c). The ecology of Protozoa in chinstrap penguin guano. *British ctic Survey Bulletin* No. 35, 33–50.
H. G. (1973d). The temperature relations and bi-polar biogeography of the genus *Colpoda*. *British Antarctic Survey Bulletin* No. 37, 7–13.
H. G. (1973e). "Studies on the terrestrial Protozoa of the maritime ctic". Ph.D. thesis, University of Edinburgh.
H. G. (1974a). A comparative study of Protozoa inhabiting *Drepanocladus* carpet in the South Orkney Islands. *British Antarctic Survey Bulletin* No. 16.
H. G. (1974b). The colonization of volcanic tephra on Deception Island by zoa. *British Antarctic Survey Bulletin* No. 38, 49–58.
H. G. (1975). Protozaires terricoles de l'Île de la Possession. *Revue logie et de Biologie du Sol* **12**, 523–530.
H. G. (1978). The distribution and ecology of terrestrial Protozoa of subctic and maritime Antarctic islands. *British Antarctic Survey Scientific ts* No. 95, 1–104.
R. I. L. and Stephenson, C. (1975). Preliminary growth studies on *Festuca ıcta* Kirk and *Deschampsia antarctica* Desv. on South Georgia. *British ctic Survey Bulletin* Nos. 41 and 42, 59–75.

Smith, R. I. L. and Walton, D. W. H. (1975). South Georgia, Subanta
"Structure and Function of Tundra Ecosystems" (T. Rosswall and O. V
eds), pp. 399–423. Swedish Natural Science Research Council, Sto
[*Ecological Bulletins* (Stockholm) **20**.]
Smith, V. R. (1976). Standing crop and nutrient status of Marion Isla
Antarctic) vegetation. *Journal of South African Botany* **42**, 231–236.
Smith, V. R. (1977a). Notes on the feeding of *Ectemnorrhinus similis*
ouse (Curculionidae) adults on Marion Island. *Oecologia* (Berlin) **29**, 269
Smith, V. R. (1977b). A qualitative description of energy flow and
cycling on Marion Island. *Polar Record* **18**, 361–370.
Solem, A. (1968). The subantarctic land snail *Notodiscus hookeri* (Reev
(Pulmonata, Endodontidae). *Proceedings of the Malacological So
London* **38**, 251–266.
Sømme, L. (1978a). Notes on the cold hardiness of prostigmate mit
Vestfjella, Dronning Maud Land. *Norwegian Journal of Entomol*
51–55.
Sømme, L. (1978b). Cold hardiness of *Cryptopygus antarcticus* (Coll
from Bouvetøya. *Oikos* **31**, 94–97.
Sømme, L. (1979). Overwintering ecology of alpine Collembola and
mites from the Austrian Alps. *Ecological Entomology* **4**, 175–180.
Sømme, L. (1980). Terrestrial arthropods from Vestfjella, Dronning Ma
(Acari, Collembola), with notes on their taxonomy. *Entor
Scandinavica* **11**, 61–64.
Spain, A. V. (1971). Some aspects of soil conditions and arthropod dis
in Antarctica. *Pacific Insects Monograph* **25**, 21–26.
Spaull, V. W. (1972). *Antarctenchus hooperi* n.g., n. sp. (Nematod
chodoridae) from Signy Island, South Orkney Islands, with the erect
new subfamily. *Nematologica* **18**, 353–359.
Spaull, V. W. (1973a). Seasonal variation in numbers of soil nematodes
Island, South Orkney Islands. *British Antarctic Survey Bulletin* Nos 33
47–56.
Spaull, V. W. (1973b). Qualitative and quantitative distribution of soil
des of Signy Island, South Orkney Islands. *British Antarctic Survey*
Nos 33 and 34, 177–184.
Spaull, V. W. (1973c). Distribution of soil nematodes in the maritime A
British Antarctic Survey Bulletin No. 37, 1–6.
Spaull, V. W. (1973d). Distribution of nematode feeding groups at Signy
South Orkney Islands, with an estimate of their biomass and oxygen c
tion. *British Antarctic Survey Bulletin* No. 37, 21–32.
Spaull, V. W. (1973e). The Signy Island terrestrial reference sites:
nematode fauna. *British Antarctic Survey Bulletin* No. 37, 94–96.
Spaull, V. W. (1973f). "Some aspects of the ecology of soil nematode
maritime Antarctic". Ph.D. thesis, University of Reading.
Spellerberg, I. F. (1971). Mallophaga on the south polar skua (*Cathara
maccormicki*). *Pacific Insects Monograph* **25**, 19–20.
Staley, J. T. and Boyd, W. L. (1967). L-Serine dehydratase (deaminase
chrophiles and mesophiles from polar and temperate habitats. *Canadi
nal of Microbiology* **13**, 1333–1342.
Stannard, L. J. (1962). Insects of Macquarie Island. Thysanoptera: Th
Pacific Insects **4**, 933–936.

R. P. and Stokes, J. L. (1960). Psychrophilic bacteria from Antarctica. *al of Bacteriology* **80,** 622–625.
nann, R. W. (1967). Terrestrial Prostigmata (Trombidiform mites). *ctic Research Series* **10,** 51–80.
nann, R. W. (1970). Acarina; eupodiform Prostigmata of South Georgia. *Insects Monograph* **23,** 89–106.
nann, R. W. (1978a). Redescription of *Nanorchestes bifurcatus* (Acarina: gmata: Nanorchestidae). *Pacific Insects* **19,** 101–104.
nann, R. W. (1978b). Terrestrial arthropods, Marie Byrd Land, Antarctica. *ctic Journal* **13,** 166–168.
nann, R. W. and Davies, L. (1972). Eupodiform mites from Possession , Crozet Islands, with a key to the species of *Eupodes* (Acarina: Pro- ita). *Pacific Insects* **14,** 39–56.
nann, R. W. and George, J. E. (1973). Distribution of the Antarctic mite *tydeus mollis* Womersley and Strandtmann in southern Victoria Land. *ctic Journal* **8,** 209–211.
nann, R. W. and Sømme, L. (1977). Prostigmate mites (Acari: Pro- ta) from Sverdrupfjella, Dronning Maud Land, with description of four ecies. *Norwegian Journal of Entomology* **24,** 137–146.
nann, R. W. and Tilbrook, P. J. (1968). Some Prostigmata (Acari) from Island, South Orkney Islands, and Deception Island, South Shetland s. *British Antarctic Survey Bulletin* No. 17, 51–57.
. E., Dunkle, R. L. and Dunn, R. L. (1970). Low temperature physiology arctic arthropods. *Antarctic Journal* **5,** 123.
. (1967). Ecology of terrestrial arthropods at Palmer Station, Antarctic ula. *Antarctic Research Series* **10,** 357–371.
M. (1964). On the microfauna of the Antarctic region. I. Moss-water unity at Langhovde. *Biological results of the Japanese Antarctic Research ition, Series E* No. 19, 1–41.
M. (1979). On the microfauna of the Antarctic region. III. Micro-biota of restrial interstices. *Memoirs of the National Institute of Polar Research, , Special Issue* **11,** 104–126. [Proceedings of the Symposium on Terrestrial stems.]
I., Huppert, M. and Cameron, R. E. (1978). Identification of some fungi oil and air of Antarctica. *Antarctic Research Series* **30,** 1–26.
yche, H. (1954). Arachnoidea from South Georgia and the Crozet Islands emarks on the subfamily Masoninae. *Scientific Results of the Norwegian tic Expeditions 1927–1928* (Oslo) **35,** 1–19.
n, J. C. (1972). Ciliated Protozoa of the Antarctic Peninsula. *Antarctic ch Series* **20,** 261–288.
, P. J. (1967a). Arthropod ecology in the maritime Antarctic. *Antarctic ch Series* **10,** 331–356.
, P. J. (1967b). The terrestrial invertebrate fauna of the mari- Antarctic. *In* "A Discussion of the Terrestrial Antarctic" (J. E. organizer). *Philosophical Transactions of the Royal Society* **B252,** 8.
, P. J. (1970a). The terrestrial environment and invertebrate fauna of the ne Antarctic. *In* "Antarctic Ecology" (M. W. Holdgate, ed.), Vol. 2, pp. 6, Academic Press, New York and London.
, P. J. (1970b). The biology of *Cryptopygus antarcticus*. *In* "Antarctic

Ecology" (M. W. Holdgate, ed.), Vol. 2, pp. 908–918. Academic Pı York and London.
Tilbrook, P. J. (1973a). The Signy Island terrestrial reference sites: I. An tion. *British Antarctic Survey Bulletin* Nos 33 and 34, 65–76.
Tilbrook, P. J. (1973b). "Terrestrial arthropod ecology at Signy Islar Orkney Islands". Ph.D. thesis, University of London.
Tilbrook, P. J. (1977). Energy flow through a population of the collembola *pygus antarcticus*. *In* "Adaptations within Antarctic Ecosystems' (G. ed.), pp. 935–946. Gulf Publishing Co., Houston, Texas.
Tilbrook, P. J. and Block, W. (1972). Oxygen uptake in an Antarctic c *Cryptopygus antarcticus*. *Oikos* **23**, 313–317.
Travé, J. (1976a). Les Oribates (Acariens) des Archipels de Kerguelen essai biogeographique. *Comité National Français des Recherches An* **41**, 61–72.
Travé, J. (1976b). Recherches sur les Microarthropodes terrestres de l'ar Kerguelen. Données quantitatives—Analyse de deux groupes d Oribatida et Acaridida. *Revue d'Écologie et de Biologie du Sol* **13**, 55–6
Travé, J. (1977). Investigations on the land micro-arthropods of the K Archipelago—quantitative data. *In* "Adaptations within Antarctic Ecc (G. A. Llano, ed.), pp. 1035–1053. Gulf Publishing Co., Houston, Texa
Trehen, P. and Delettre, Y. (1976). Aspects originaux de la biologie et l'é *Limnophyes pusillus* Eaton à Kerguelen. *Comité National Français de ches Antarctiques* **41**, 73–84.
Tsiklinsky, Mlle. (1908). La flore microbienne dans les régions du Pôl "Expedition Antarctique Française 1903–1905", No. 3, 1–33. Masso Paris.
Tubaki, K. and Asano, I. (1965). Additional species of fungi isolated Antarctic materials. *Japanese Antarctic Research Expedition, Series I* 1–12.
Tyndale-Biscoe, H. C. (1960). On the occurrence of life near the B Glacier, Antarctica. *Pacific Insects* **2**, 251–253.
van Zinderen Bakker, E. M. (1978). Geoecology of Marion and Prince Islands (subantarctic). *In* "Geoecological Relations between the Temperate Zone and the Tropical Mountains" (C. Troll and W. Lauer, 495–515. Franz Steiner Verlag, Wiesbaden.
Viette, P. E. L. (1952). Lepidoptera. *Scientific Results of the Norwegian Expedition* 1927–1928 (Oslo) **33**, 1–4.
von Grospietsch, T. (1971). Beitrag zur Ökologie der testaceen Rhizop Marion Island. *In* "Marion and Prince Edward Islands" (E. M. van Bakker, J. M. Winterbottom and R. A. Dyer, eds), pp. 411–423. A. A. Cape Town. [Report on the South African Biological and Geological Ex 1965–1966.]
Wallace, M. M. H. (1970). Acarina: Prostigmata: Bdellidae Georgia. *Pacific Insects Monograph* **23**, 107–113.
Wallwork, J. A. (1962a). *Maudhemia petronia* n. sp. (Acari: Orib oribatid mite from Antarctica. *Pacific Insects* **4**, 865–868.
Wallwork, J. A. (1962b). A redescription of *Notaspis antarctica* Mich (Acari: Oribatei). *Pacific Insects* **4**, 869–880.
Wallwork, J. A. (1962c). Notes on the genus *Pertorgunia* Dalenius 1 Antarctica and Macquarie (Acari: Oribatei). *Pacific Insects* **4**, 881–885.

:, J. A. (1963). The Oribatei (Acari) of Macquarie Island. *Pacific Insects* **5,** 9.
:, J. A. (1965). The Cryptostigmata (Acari) of Antarctica with special ce to the Antarctic Peninsula and South Shetland Islands. *Pacific Insects* **7,** 8.
:, J. A. (1966). Some Cryptostigmata (Acari) from South Georgia. *British tic Survey Bulletin* No. 9, 1–20.
:, J. A. (1967). Cryptostigmata (oribatid mites). *Antarctic Research Series* –122.
:, J. A. (1969). The zoogeography of Antarctic Cryptostigmata. *In* "Pro- s of 2nd International Congress of Acarology" (G. O. Evans, ed.), pp. Hungarian Academy of Sciences, Budapest.
:, J. A. (1970a). Acarina: Cryptostigmata of South Georgia. *Pacific Insects raph* **23,** 161–178.
:, J. A. (1970b). Acarina: Cryptostigmata of Heard and Kerguelen. *Pacific Monograph* **23,** 179–182.
:, J. A. (1972a). Some cryptostigmatid mites (Acari: Cryptostigmata) from Islands. *Pacific Insects* **14,** 27–37.
:, J. A. (1972b). Distribution patterns of cryptostigmatid mites (Arachnida: in South Georgia. *Pacific Insects* **14,** 615–625.
:, J. A. (1973). Zoogeography of some terrestrial micro-Arthropoda in tica. *Biological Reviews* **48,** 233–259.
). W. H. (1977). Radiation and soil temperatures 1972–74: Signy Island ial reference sites. *British Antarctic Survey Data* **1.**
). W. H. (1982). The Signy Island terrestrial reference sites: XV. Micro- monitoring, 1972–74. *British Antarctic Survey Bulletin* No. 55, 111–126.
K. (1967). The terrestrial Arthropoda of Macquarie Island. *Australian il Antarctic Research Expedition Reports, Series B, Zoology* **99,** 1–90.
, D. W. A. (1977). Energy budgets and ecological efficiencies of Truelove l. *In* "Truelove Lowland, Devon Island, Canada; a High Arctic Ecosystem" 3liss, ed.), pp. 607–620. University of Alberta Press, Edmonton, Alberta.
ki, F. E. (ed.) (1975a). Functioning of Fennoscandian tundra ecosystems. inoscandian Tundra Ecosystems", Vol. 17 pp. 300–326. Springer-Verlag,

ki, F. E. (ed.) (1975b). Ecological studies. Analysis and synthesis. *In* scandian Tundra Ecosystems", Vol. 17, pp. 1–337. Springer-Verlag,

'. (1901). Les Collemboles recueillis par l'Expedition Antarctique Belge. *of the Society for Entomology of Belgium* **45,** 260–262.
V. (1902). Collemboles. Résultats du Voyage du S. Y. Belgica en 398–1899. "Rapports Scientifiques de la Commission de la Belgica" 11, pp. E. Buschmann, Anvers.
J. (1967). Mesostigmata: Rhinonyssidae: Halarachnidae (nasal mites); gmata: Ixodidae (Ticks). *Antarctic Research Series* **10,** 41–49.
'. (1970a). Acarina: Mesostigmata: Halarchnidae, Rhyninyssidae of South a, Heard and Kerguelen. *Pacific Insects Monograph* **23,** 71–77.
J. (1970b). Metastigmata: Ixodidae of South Georgia, Heard and Ker- *Pacific Insects Monograph* **23,** 78–88.
. H. and Standard, L. J. (1970). Thysanoptera of South Georgia. *Pacific Monograph* **23,** 221–226.

Wirth, W. W. and Gressitt, J. L. (1967). Diptera: Chironomidae (midges). *Research Series* **10,** 197–203.
Wise, K. A. J. (1967). Collembola (springtails). *Antarctic Research* 123–148.
Wise, K. A. J. (1970a). Collembola of South Georgia. *Pacific Insects M* **23,** 183–208.
Wise, K. A. J. (1970b). Collembola of Heard Island. *Pacific Insects Mono* 209–215.
Wise, K. A. J. (1971). The Collembola of Antarctica. *Pacific Insects Mono* 57–74.
Wise, K. A. J. and Gressitt, J. L. (1965). Far southern animals and plant (Lond.) **207,** 101–102.
Wise, K. A. J. and Shoup, J. (1967). Distribution of Collembola at Cap *Antarctic Research Series* **10,** 325–330.
Wise, K. A. J. and Shoup, J. (1971). Entomological investigations in A *Pacific Insects Monograph* **25,** 27–56.
Wise, K. A. J. and Spain, A. V. (1967). Entomological investigations in A 1963–64 season. *Pacific Insects* **9,** 271–293.
Wise, K. A. J., Fearon, C. E. and Wilkes, O. R. (1964). Entomological tions in Antarctica, 1962–63 season. *Pacific Insects* **6,** 541–576.
Womersley, H. and Strandtmann, R. W. (1963). On some free living pro mites of Antarctica. *Pacific Insects* **5,** 451–472.
Wynn-Williams, D. D. (1979). Techniques used for studying microbial e the maritime Antarctic. *Society for Applied Bacteriology, Technical S* 13, 67–81.
Wynn-Williams, D. D. (1980). Seasonal fluctuations in microbial a Antarctic moss peat. *Biological Journal of the Linnean Society* **14,** 11–28
Wynn-Williams, D. D. (1982). Simulation of seasonal changes in microbi of maritime Antarctic peat. *Soil Biology and Biochemistry* **14,** 1–12.
Yoshimoto, C. M. (1962). Insects of Macquarie Island. Hymenoptera: D *Pacific Insects* **4,** 973–974.
Young, S. R. (1979a). Respiratory metabolism of *Alaskozetes antarcticus of Insect Physiology* **25,** 361–369.
Young, S. R. (1979b). Effect of temperature change on the metabolic r Antarctic mite. *Journal of Comparative Physiology* **131,** 341–346.
Young, S. R. (1979c). "Aspects of the environmental physiology of an terrestrial mite". Ph.D. thesis, University of Leicester.
Young, S. R. (1980). Cold hardiness in a temperate cryptostigmatid mite. 350–352.
Young, S. R. and Block, W. (1980a). Experimental studies on the cold tol *Alaskozetes antarcticus. Journal of Insect Physiology* **26,** 189–200.
Young, S. R. and Block, W. (1980b). Some factors affecting metabolic r Antarctic mite. *Oikos* **34,** 178–185.

INVERTEBRATES AND FREEZING

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ABSTRACT

Invertebrate poikilotherms have adopted are of two possible strategies to overcome the problems of freezing temperatures. Avoidance of lethal ice formation in the body by supercooling is a common strategy, whilst tolerance of extra-cellular ice is rare. The former are termed freeze sensitive, whilst the latter freeze tolerant species are restricted to marine molluscs, some freshwater benthic invertebrates and insects (mainly Coleoptera, Diptera and Hymenoptera). The physiological and biochemical mechanisms behind these strategies are reviewed in the light of possible environmental triggers, the activity of potential nucleators and the role of body water. Finally, the evolution of such strategies, which together form a suite of adaptations to low temperature and freezing conditions, is discussed.

SOME ARCTIC ORIBATEI

BY

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This paper gives a list of oribatid mites (Acarina : Cryptostigmata) collected from three near arctic sites in Iceland, Spitzbergen and Alaska. Adult specimens were found except where otherwise stated, and the list follows the order of TURK (1953). Notes on the collection and extraction of the samples are also given.

ICELAND.

This material was collected in August, 1959 from five sites along the margin of the Lang Jökull ice cap in Iceland at a height of 5,000 ft (:1,525 m) by Dr. J. B. WHITTAKER of the Department of Zoology, University of Durham. The mites were extracted from moss, litter and soil in a Tullgren funnel apparatus in camp near the collecting sites.

1. *Trimalaconothrus* Berlese 1916.
2. *Nothrus pratensis* Sellnick 1929, nymphae.
3. *N. borussicus* Sellnick 1928, nymphae.
4. *Nothrus* Koch 1935, nymphae.
5. *Camisia horrida* (Hermann 1804), nymphae.
6. *Heminothrus thori* (Berlese 1904), nymphae.
7. *Platynothrus punctatus* (L. Koch 1879).
8. *Tectocepheus velatus* (Michael 1880).
9. *Liebstadia similis* (Michael 1888).
10. *Edwardzetes edwardsii* (Nicolet 1855).

SPITZBERGEN.

The mite specimens were extracted by a Tullgren funnel apparatus at Durham University from *Dryas* plant material and litter. The material was collected in King's Bay, Spitzbergen by Mr. P. J. TILLBROOK of the Durham University Spitzbergen Expedition in 1960.

11. *Camisia horrida* (Hermann 1804).
12. *Ameronothrus lineatus* (Thorell 1871).
13. *Hermannia reticulata* (Thorell 1888).
14. *Diapterobates notatus* (Thorell 1871).

ALASKA.

This material was collected in *Sphagnum* moss from the Samovar Hills, Gulf of Alaska (ref. 60° 17′ N, 140° 37′ W) at a height of 1,200 ft (:366 m) in September, 1961 by Dr. W. S. WATT. The specimens were extracted by means of a Tullgren funnel apparatus at Durham University.

15. *Trimalaconothrus foveolatus* Willmann 1931.
16. *T. novus* (Sellnick 1921).
17. *Nothrus pratensis* Sellnick 1929.
18. *Chamobates pusillus* (Berlese 1914).
19. *Pelops* C. L. Koch 1836.

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REFERENCE

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17: 1–9. Copenhagen 1966

Some characteristics of the Macfadyen high gradient extractor for soil micro-arthropods

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Abstract

ls are given of the temperatures and ature gradients developed in peat and l soil samples in a model of the Mac- high gradient extractor for soil micro- ods. Temperature gradients were steeper samples than in samples of mineral soil hout the entire extraction process. Changes idity in mineral soil samples, and emer- of the fauna during extraction are shown. nt emergence patterns are shown for a and Collembola, and for groups and of mites. An efficiency of 76% is esti- for the recovery of Acarina from mineral mples by this extractor.

Резюме

Некоторые показатели градиентного зктрактора Макфедьена для почвообитающих мелких членистоногих.

Приводятся данные о температуре и температурном градиенте почвенных образцов из торфяных и минеральных почв, взятых с помощью градиентного экстрактора Макфедьена для почвообитающих мелких членистоногих. Температурные колебания в торфе более резкие, чем в минеральных почвах в течение всего процесса зкстракции. Установлены колебания влажности в образцах минеральных почв, и получены данные об зффективности зкстракции отдельых групп беспозвоночных. Показано, что полнота зкстракции *Acarina* и *Collembola* различна, отмечены колебания зффективности зкстракции представителей разных видов и групп клещей. Полнота выхода *Acarina* из минеральных почв с помощью зкстрактора Макфедьена достигает 76%.

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1. Introduction

The extraction of micro-arthropods from soil presents great problems. Methods of extraction have been reviewed in Balogh (1958), Kevan (1962), Kuhnelt (1955, 1961), Macfadyen (1955, 1962), and Murphy (1962). They can be grouped into two main types. Firstly, those which operate by the movement of the animals out of the soil sample in response to attractant or repellent stimuli or a combination of both sets of stimuli (e.g. light, heat, desiccation and humidity). Secondly, physical methods involving sieving, flotation or sedimentation in which arthropods are removed from the soil sample independent of their activity. The former methods are referred to as behaviour methods, and the latter as mechanical methods in this paper.

Macfadyen (1953, 1955, 1961, 1962) has described and compared behaviour methods for the extraction of soil micro-arthropods. Nef (1962) has discussed the roles of desiccation and temperature in the Tullgren-funnel behaviour type extractor, whilst Satchell and Nelson (1962) have compared the Tullgren-funnel and flotation methods for extracting Acarina from woodland soils. Recently, Hale (1964) has compared a new flotation process for the extraction of Collembola from peat soil with a model of the Macfadyen high gradient extractor. Few accurate measurements of the percentage recovery (extraction efficiency) or of the factors affecting the recovery of micro-arthropods in any method have been made. Data are given in this paper of the temperature and humidity gradients established in soil samples in the Macfadyen high gradient extractor, of the emergence of the fauna during the extraction process, and of the percentage recovery.

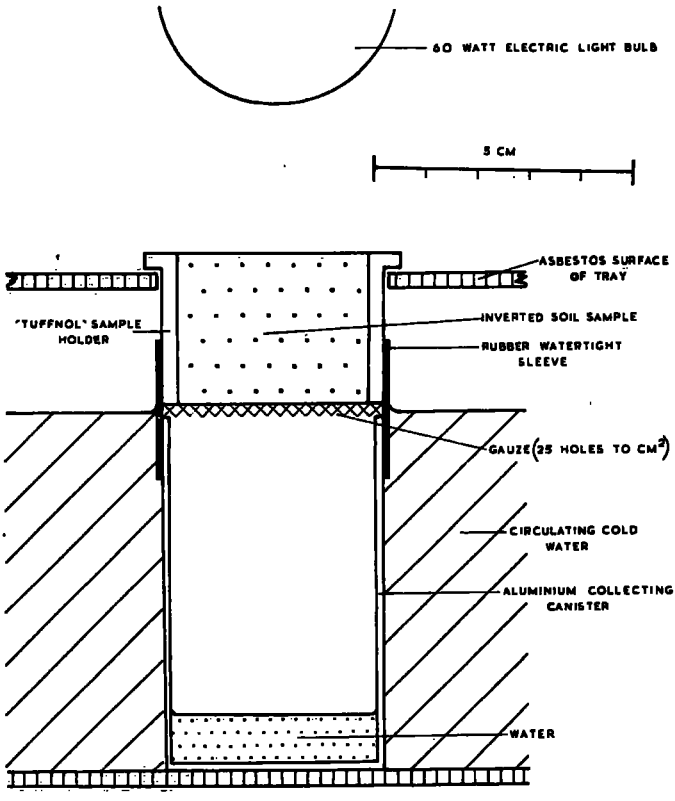
2. The extractor

In studies on the ecology and biology of soil mites of Pennine moorland (Block 1965 a, b, c, 1966) a model of the Macfadyen high gradient apparatus was used to Acarina from a variety of soils. Fl techniques and other mechanical n were considered unsuitable due to th amounts of organic matter in the s The high gradient extractor designed b fadyen (1961) was considered to be th efficient and most suitable for thes and a model was used which had bee and used for ecological studies on Coll of the same area by Hale (1963, 1964 extractor was up to ten times as effi the Tullgren-funnel under the conditio soils used by Macfadyen (1961).

The extractor used in these expe takes 32 extractor units, each hol circular soil core of 11.35 cm^2 in surfa (1/881 m^2) and of 3 cm depth. Fig. 1 s single extractor unit with the soil c verted (vegetation downwards) over a gauze (25 meshes per cm^2) fitted to the an aluminium canister, which contain to a depth of 1 cm. The sample ho made of heat resistant laminated p plastic and is held in place on top canister by a watertight rubber sleeve. temperature gradient is established an tained throughout the soil sample by from above by a 60 watt pearl electri and cooling the canister from below culating cold-water in a bath.

The apparatus consists of two tra holding 16 extractor units. The trays f water baths for cooling the collecti isters, and a Zenith variac transforme 100 M) controls the voltage passing t the electric light bulb above each unit, this way controls the temperature g within each soil sample. Pilot warnin on the control panel of the extractor i when a bulb has ceased to function. T no controlled draught system in thi ratus.

It was found by experiment that a th extraction régime was the most suita soil mites and the soils in the study, v



. A single unit of the high gradient extractor showing the orientation of the soil sample. Size sample unit is 11.35 cm² in surface area and 3 cm deep. Scale approximately natural size.

g controlled at the following voltages: hours at 60 volts, 24–48 hours at 100 and 48–72 hours at 140 volts. The mples were completely dry by 72 hours. o the relatively short extraction régime not found necessary to use fixatives or ides in the collecting canisters. The ted fauna was killed at the end of the tion by washing down the walls of the ting canisters and by spraying with lcohol.

mperature

been claimed by Macfadyen (1961) that mperature gradient in the soil sample in igh gradient extractor is steep, being ly dependent upon the temperature of the cold water bath and the heating bulb. Using the same extractor as used in the present experiments, and the same extraction régime, Hale (1962) recorded temperatures with mercury thermometers at the top and bottom of a soil sample after 60 hours extraction. A temperature gradient of 60°C was measured in this way. In the present study the temperatures were recorded at three points in a soil sample throughout a normal three day extraction régime in order to show the establishment and maintenance of a gradient, and to attempt to correlate this with humidity and the emergence of the fauna.

Temperature recordings were made at three points in the soil sample as follows: (1) at the surface and in the centre of the soil sample nearest the heating bulb; (2) at a depth of 1.5

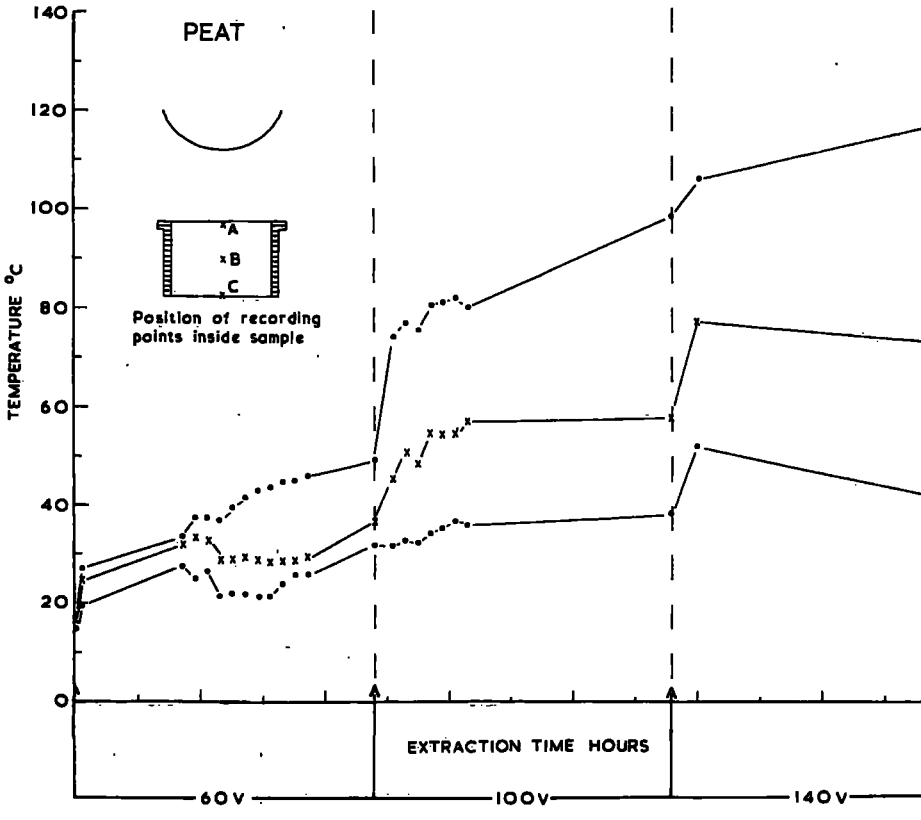


Fig. 2. Graph of the temperatures recorded in a peat soil sample during extraction in the high g extractor. The position of the three thermistor recording points (A, B and C) within the sam shown in the inset. Temperatures recorded with mercury thermometers in the water bath and in the extraction room were the same as those shown in Fig. 3. The time scale is the sam Fig. 3. The voltages to the heating bulbs are also indicated

cm from the surface and in the centre of the soil sample; (3) at the bottom and in the centre of the soil sample, i.e. in the vegetation layer and furthest away from the heating bulb (see Fig. 2). The temperatures were measured by Stantel 'Type F' thermistors using a Wheatstone bridge circuit. The thermistor probes were sited in the soil sample by insertion from the side in previously drilled holes in the plastic sample holder, and were sealed in position with a sealing agent. The temperatures at these points in samples of both peat and mineral soils were recorded at intervals throughout a normal extraction. The experiment was replicated four times for each soil type.

Thus a picture of the temperature g throughout the extraction was obtaine temperature gradient is the differe temperature measured between the t bottom of the soil sample at any on A temperature curve typical of those re in samples of peat soil is shown in and that typical of mineral is shown in The development of the temperature g with extraction time in a sample of m soil is shown in Fig. 4. It shows that t an immediate establishment of a grad about 8°C throughout the sample, whic after 22 hours to 12°C. At 24 hours t face temperature of mineral soil sam this experiment is 32°C, which is that

ed by Macfadyen (1962). For peat es, a higher surface temperature of 45°C orded. The increase of voltage by the after 24 hours extraction causes a steady se in the temperature gradient to 38°C hours, which is maintained until the ge is increased again at 48 hours. This ces an immediate increase in the tem- ire gradient to 59°C, and thereafter is a general increase in the gradient to 70°C at the end of the extraction (72). The unexpected drop in the tempera- gradient to 44°C at 53 hours may be ned by condensation on a thermistor. nperature gradients at three stages in ctraction in peat and mineral soils are ared in Tab. 1. It is clear that the nt in peat soil is steeper than in the al soil at the three recorded times.

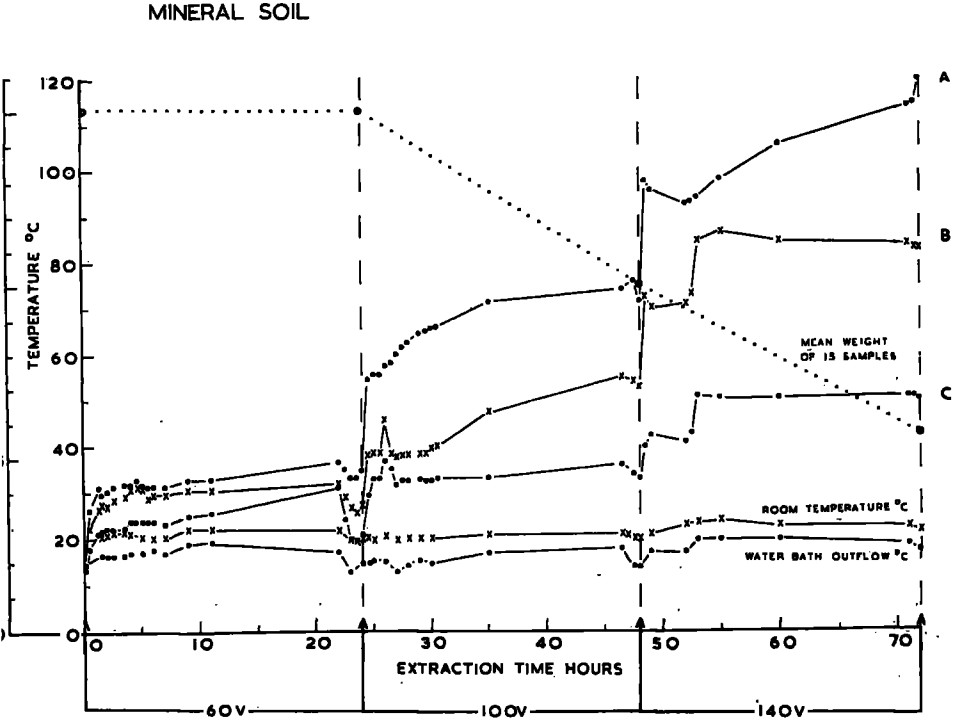
Table 1. Temperature gradients recorded in soil samples in the high gradient extractor. Each figure is the mean of four readings.

Extraction stage	Temperature gradient (°C) in 3 cm in mineral soil	Temperature gradient (°C) in 3 cm in peat soil
At 24 hours....	13.2	19.0
At 48 hours....	43.9	53.0
At 72 hours....	67.4	77.7

Reference to Figs. 2 and 3 shows that this is the case throughout the whole extraction period. This is caused by the difference in physical properties of the two soils studied.

4. Humidity

Macfadyen (1962) has suggested that there is a steep humidity gradient in the soil samples throughout the extraction in the high gradient



. Graph of the temperatures recorded in a mineral soil sample during extraction in the high nt extractor. The positions of the three thermistor recording points (A, B and C) are as shown . 2. The weight of 15 samples of mineral soil are shown throughout the extraction, indicating e rate of water loss from the samples. The voltages to the heating bulbs are also indicated.

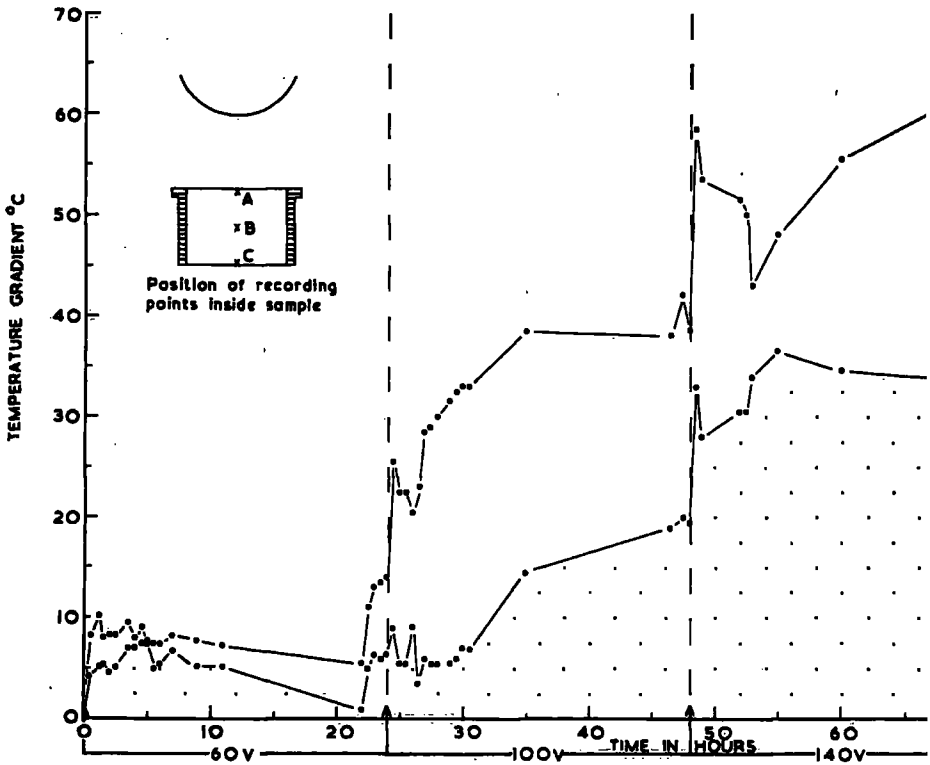
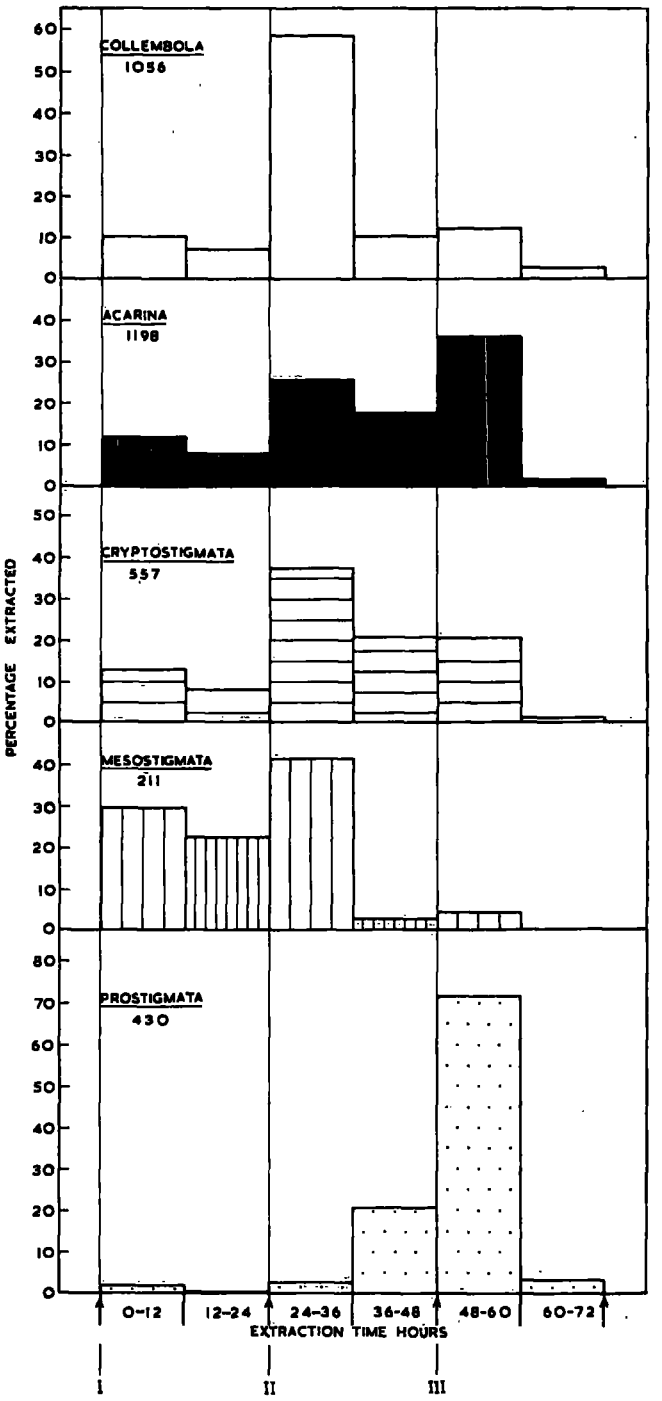


Fig. 4. The temperature gradient (in °C) in a sample of mineral soil throughout extraction high gradient apparatus. The positions of the three thermistor recording points (A, B and C) soil sample are shown in the inset. The voltages to the heating bulbs are also indicated.

apparatus, which results in condensation normally occurring below the level of the sample in the collecting canister. It has been suggested above that condensation may occur within the soil sample with a consequent lowering of the temperature gradient. The humidity was not measured in samples extracted by the Durham model of the high gradient extractor, but notes were made on the condition of 15 soil samples at intervals throughout a normal extraction, and these are summarised below:

1. After 24 hours extraction, the soil samples were beginning to dry at the upper surface, but the lower vegetation surfaces were extremely moist. Heavy condensation had appeared on the walls of the collecting canisters, below the level of the sample.
2. After 48 hours extraction, the soil sa had thoroughly dried out on the surfaces, the lower vegetation surface drier than at 24 hours, but still ren damp. Condensation was again pres the walls of the collecting canisters.
3. After 72 hours extraction, the soil sa were completely dry throughout thei thickness. A small amount of conden remained on the walls of the coll canisters at the end of the extraction.

The mean rate of water loss from 15 s units of mineral soil during a three d traction is shown in Fig. 3. Little water during the first 24 hours of extractio thereafter there is a steady loss of wat corded by loss in weight of the sample) the end of the extraction.



. The emergence of the fauna from a mineral soil sample during the extraction process in the gradient extractor. The total number of each animal group extracted from 15 sample units 11.35 cm^2 in surface area and 3 cm deep) is shown below the group name. The histograms e percentages of the total of each animal group extracted per 12 hour period. The voltage to the heating bulbs was increased every 24 hours as in a normal extraction.

5. Emergence of fauna

The emergence of the fauna from soil samples in the high gradient extraction is shown in Fig. 5. The three day extraction was divided into six periods each of 12 hours duration, when the collecting canisters were changed. The percentages of the total number of animals extracted from 15 sample units were calculated and are plotted in each period in Fig. 5. The sample was of mineral soil. The extraction patterns for total mites and Collembola and for three groups of Acarina, are shown in Fig. 5.

The extraction pattern of mites differs from that of Collembola. For both mites and Collembola about 10% of the total numbers are extracted in the first 24 hours. There is a main peak of emergence of Collembola (58% of the total) from the sample during the 24–36 hours period, whereas only 25% of the total mites emerge over the same period. The majority (about 75%) of the mites are extracted over a much longer time (between 24 and 60 hours) in the extraction. The greatest proportion of the Cryptostigmata emerge during the 24–60 hours of extraction, but egress of the Mesostigmata is confined to the early stages (0–36 hours) of the process. Over 70% of the total prostigmatid mites emerge late in the extraction during the 48–60 hour period. Thus there are different emergence patterns for the constituent groups of Acarina, and for Collembola, depending on the reactions of the different species to the temperature gradient and humidity in the soil samples in the extractor.

The majority of the total juvenile oribatids emerge from the samples during the 24–36 hour period of the extraction along with the following species: *Achipteria coleoptrata* (Linnaeus 1758), *Pelops plicatus* (C. L. Koch 1836) and species of *Oppia* and *Suctobelba*. *Platynothrus peltifer* (C. L. Koch 1839), a moisture loving species, emerges even earlier (39% of the total number are collected in the first 12 hours). *Nanhermannia nana* Willmann 1931 emerges in the greatest numbers in the first 12 hours of the extraction and has a peak also in the period 24–60 hours. Similarly, *Tectocepheus velatus* (Michael 1880) has two of egress: 24–36 hours and 48–60 hour greatest numbers of *Trachytes pyr* (Kramer 1876), *Olodiscus minima* (K 1882), and specimens of parasitids ar conids leave the samples during the hour extraction period.

It is not possible to separate the eff heat and desiccation in the extraction p It has been suggested by Nef (1962) th most species of mites the peak of mo out of litter in the Tullgren-funnel is rel the degree of desiccation. Species of *Op Tectocepheus velatus* were definitely infl by temperature in his experiments. present study, the bulk of the Acarina soil samples in two main groups, in the hour and the 48–60 hour extraction p when the rate of water loss from the s was increasing rapidly (Fig. 3) result lowering of relative humidity within t samples, and when there was a sharp ir in the temperature gradient in the s (se Fig. 4).

6. Percentage recovery

The efficiency of the extractor used ir experiments for Acarina was estimat placing live mites into sterile soil sa extracting over a normal three day r and calculating the percentage recover teen sample units of mineral soil were sterilised in an air oven for three day temperature of 105°C to kill the faun then allowed to recover by soaking water for three days. The water content sterile samples was made as near as p to that in the field. Into the vegetatio

Table 2. Recovery of Acarina inserte sterile soil samples by the high gradie tractor. The figures are the total num specimens for 15 sample units of miner

Group	No. introduced	No. recovered	Pe r
Cryptostigmata.....	90	69	
Mesostigmata.....	40	34	
Prostigmata.....	20	11	
Total Acarina.....	150	114	

ch sterile sample were placed 10 live mites, recently extracted in a Tullgren- l from mineral soil and collected alive ater. After one hour, the sample units placed in the extractor and the extraction ı. The number and percentage recovery ; introduced fauna are shown in Tab. 2.)verall percentage recovery for mites in ctractor tested was 76%. The high per- ge recovery of the Mesostigmata may e to their greater mobility. It should be ed that these figures are estimates of the ncy of the extractor used, and should not be regarded as actual efficiencies for the groups investigated. As Murphy (1962) has shown, using the split-funnel extractor, extraction efficiency can be influenced by many different factors.

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It is a pleasure for the writer to thank Professor J. B. Cragg and Dr. J. C. Coulson for direction and encouragement in these studies, and Drs. W. G. Hale and J. B. Whittaker for advice on the extractor and thermistors respectively. Thanks also due to the East Suffolk County Education Committee for a postgraduate grant.

References

ɜH, J. 1958. Lebensgemeinschaften der Landtiere. Ihre Erforschung unter besonderer Berücksichtigung der zoozönologischen Arbeitsmethoden. – Budapest: Verlag der Ungarischen Akademie der Wissenschaften.

:, W. 1965a. The life histories of *Platynothrus peltifer* (Koch 1839) and *Damaeus clavipes* Hermann 1804) (Acarina: Cryptostigmata) in soils of Pennine moorland. – Acarologia 7: 35–743.

965b. Distribution of soil mites (Acarina) on the Moor House National Nature Reserve, Westmorland, with notes on their numerical abundance. – Pedobiologia 5: 244–251.

965c. The distribution of soil Acarina on eroding blanket bog. – Pedobiologia 5: in press.

966. Seasonal fluctuations and distribution of mite populations in moorland soils, with a note n biomass. – In press.

W. G. 1962. Studies on the biology of moorland Collembola. – Ph. D. thesis, University of)urham, England.

963. The Collembola of eroding blanket bog. – In: Soil Organisms (ed. by J. Doeksen and VAN DER DRIFT), pp. 406–413. North-Holland, Amsterdam.

964. A flotation method for extracting Collembola from organic soils. – J. Anim. Ecol. 33: 53–369.

ɨ, D. K. Mc. 1962. Soil Animals. – Witherby, London.

ELT, W. 1955. A preliminary note on sampling for soil animals. – In: Soil Zoology (ed. by). K. Mc. Kevan), pp. 313–314. Butterworths, London.

961. Soil Biology: with special reference to the animal kingdom. – Faber & Faber, London.

ADYEN, A. 1953. Notes on methods for the extraction of small soil arthropods. – J. Anim. col. 22: 65–77.

955. A comparison of methods for extracting soil arthropods. – In: Soil Zoology (ed. by . K. Mc. Kevan), pp. 315–332. Butterworths, London.

961. Improved funnel-type extractor for soil arthropods. – J. Anim. Ecol. 30: 171–184.

962. Control of humidity in three funnel-type extractors for soil arthropods. – In: Progress in oil Zoology (ed. by P. W. Murphy), pp. 158–168. Butterworths, London.

HY, P. W. 1962. Effect of sample treatment on extraction efficiency with the split-funnel ;tractor. – In: Progress in Soil Zoology (ed. by P. W. Murphy), pp. 182–188. Butterworths, ondon.

.. 1962. The roles of desiccation and temperature in the Tullgren-funnel method of extraction. In: Progress in Soil Zoology (ed. by P. W. Murphy), pp. 169–173. Butterworths, London.

ELL, J. E., and Nelson, J. M. 1962. A comparison of the Tullgren-funnel and flotation methods r extracting Acarina from woodland soil. – In: Progress in Soil Zoology (ed. by P. W. Murphy), ɔ. 212–216. Butterworths, London.

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SOME LAMELLICORN BEETLES (COL., SCARABAEOIDEA) FROM EAST AFRICA

By William Block

The following is a list of lamellicorn beetles collected from five sites East Africa. At three sites the beetles were collected by light traps, ilst the material from Murchison Falls National Park in Uganda and Kilimanjaro in Tanzania was obtained from animal dung.

1. Nightly collections were made by mercury-vapour light trap iated close to the laboratory of the Nuffield Unit of Tropical Animal)logy at Mweya (0° 12′ S., 29° 53′ E.) in the Queen Elizabeth National 'k, Uganda. They were made over a period of nine months (October 4 to July 1965) which covered two rainy seasons. Fifteen species of rabaeidae have been identified:

)oprinae.—*Catharsius opacus* Waterhouse, 9.i.65; *C. pandion* Harold, 11.xii.64; *is fallaciosus* Gillet, 12.ii.65; *C. muticus* Boheman, 11.xi.64; *Onitis robustus* eman, 8.xi.64; *O. viridulus* Lansberge, 12.xi.64; *Onthophagus gazella* Fabricius, .65.

)ynastinae.—*Augosoma centaurus* (Fabricius), 18.xi.64; *Cyphonistes vallatus* deman), 10.i.65; *Heteronychus gerstaeckeri* Kolbe, 12.i.65; *H. licas* (Klug), 64; *Hetroligus gazanus* Arrow, 8.i.65; *Pycnoschema diversum* ssp. *diversum* ıguey, 7.i.65; *Rhizoplatys auriculatus* Burmeister, 10.i.65; *Temnorrhynchus atus* Klug, 10.i.65.

2. At Serere Experiment Station (1° 31′ N., 33° 27′ E.) of the artment of Agriculture, near Soroti, Teso, Uganda the collection mercury-vapour light trap was over a week (3–9 June, 1964) in dry season. Three species are recorded:

)prinae.—*Catharsius polynices* Kolbe, 3.vi.64; *Copris evanidus* Klug, 4.vi.63; *s sphinx* Fabricius, 5.vi.64.

3. In Murchison Falls National Park (Paraa airfield grid ref.; 9′ N., 31° 29′ E.) collections were made from elephant and buffalo ; at the end of the main rains in May, 1964, and at the end of the season in February, 1965. Ten species were found:

)prinae.—*Allogymnopleurus alluaudi* (Garreta) ex elephant dung, Buliga circuit 4; ex buffalo dung, Paraa airfield, 20.ii.65; *Aptychonitis anomalis* Gestro (?), ephant droppings, 16.v.64; *Catharsius polynices* Kolbe, ex elephant dung, circuit, 21.ii.65; *Copris ovanidus* Klug, ex elephant dung, Buliga circuit, 5; *Heteronychus atratus* Klug, ex elephant dung, Paraa airfield, 20.ii.65; *mgus militaris* Castelnau, ex elephant dung, Paraa airfield, 20.ii.65; *Onitis tus* Klug, ex elephant droppings, 16.v.64; *O. viridulus* Boheman, ex elephant Paraa airfield, 20.ii.65; *Onthophagus gazella* Fabricius, ex elephant and buffalo Paraa airfield, 20.ii.65; *O. brucei* Reiche, ex elephant and buffalo dung, Paraa d, 20.ii.65.

4. At Mlingano Sisal Estate near Morogoro (6° 49′ S., 37° 38′ E.). ania mercury-vapour light trap collections were made over three hs (January to March, 1965), and thus covered the end of the dry n and the beginning of the rains. Ten species have been identified:

)rinae.—*Anachalcos convexus* Boheman, 11.ii.65; *Catharsius opacus* Waterhouse; *Copris integer* Reiche, 3.i.65; *Garreta nitens* (Olivier) var. *lacvis* Arrow, 20.iii.65,

Onitis inversidens Lansberge, 10.i.65; *Onthophagus gazella* Fabricius, 21.ii.6
Pycnoschema subulatum Quedenfeldt, 11.i.65.

Dynastinae.—*Hetroligus gazanus* Arrow, 4.i.65; *Oryctes boas* (Fabricius), 24.iii.6
O. monoceros (Olivier), 6.ii.65.

5. Mt. Kilimanjaro (3° 05′ S., 37° 22′ E.), Tanzania, at abo
11,500 ft., on open moorland:

Trogidae.—*Trox* sp., ex leopard dung, 7.i.65.

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References

BOWLER, G. E. (1948). Sarcosporidiosis in a Cow. *J. Am. vet. med. Ass.*, **113**: 266.

MADDY, K. T. (1955). Sarcosporidiosis. *N. Am. Vet.* **36**:455-457.

MILLER, A. R. (1952). Meat Hygiene. 2nd Ed. *Lea and Febiger, Philadelphia.* pp. 98.

RICHARDSON, U. F. and KENDALL, S. B. (1963). Veterinary Protozoology. 3rd Ed. Revised. *Oliver & Boyd, Edinburgh and London.* pp. 200.

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Ticks from waterbuck and warthog in the Queen Elizabeth National Park, Uganda

The ticks listed below were collected on 14th May, 1964 from animals shot in the Kamulikwezi area of the Queen Elizabeth National Park, to the north of Lake George (0°08′ N., 30° 07′ E.). The habitat is mixed savanna grassland at an altitude of about 914 m (c. 3,000 ft.) The ticks were obtained by one collector from animals which had been shot a few minutes previously. Each collection took about 30 min and special attention was paid to ears, eyes, nostrils, mouth, axils of legs, flanks and anus of the host animals. All stages of ticks were collected and placed in 75 per cent. alcohol to kill and preserve them. The specimens were identified using Hoogstraal (1956). Two species were obtained from waterbuck and six from warthog.

Defassa waterbuck (*Kobus defassa* Rüppell):

Six waterbuck (1 ♂, 5 ♀♀) were examined from which 184 ticks were collected. The number of ticks ranged from 27 to 38 per animal and two species were found.

The commonest species was *Amblyomma cohaerens* Dönitz (the East African buffalo tick) with a total of 175 nymphae. Individual hosts yielded from 27 to 35 ticks. No adults of this species were found on waterbuck. Eight larvae of an *Amblyomma* sp. were also collected from three waterbuck. A single nymph of *Rhipicephalus appendiculatus* Ne umann (the brown ear tick) was found on th only ♂ waterbuck examined.

Warthog (*Phacochoerus aethiopicus* Pallas):

Seven warthogs (2 ♂♂, 5 ♀♀) were examine and yielded 124 ticks. The number of tick per animal ranged from 1 to 36 and si species were found.

The commonest species was again *A cohaerens*, with a total of 135 specimens i infestations ranging from 1 to 35 per anima This total included 11 adults from thre hosts (ratio of ♂♂ : ♀♀ was 1 : 1, 2 : 1 an 4 : 2). Nine adults of *Rhipicephalus simu* Koch (the glossy tick) were collected fro three warthogs (ratio of ♂♂ : ♀♀ was 1 : 0 5 : 1 and 1 : 1). Three ♂♂ of *Rhipicephalu longus* Neumann (the scimitar-shield Cap brown tick) as defined by Clifford an Anastos (1962), were collected from one warthog and, from two other animals, a of *Amblyomma variegatum* Fabricius (th tropical bont tick) and two nymphae o *R. appendiculatus* were obtained. A singl nymph of *Ornithodoros moubata* Murra (the eyeless tampan) was recorded fro another ♀ warthog. Dinnik *et al.* (196 also collected both *A. cohaerens* and *R simus* from warthogs in western Uganda

A. cohaerens has been found mostly o African buffalo (*Syncerus caffer* Sparrma but it has been recorded also from warthog. I is a common tick on old buffalo grazin grounds in Uganda. *R. simus* has a predile tion for pigs and carnivores, with antelope as second choice hosts. The specimens c this species reported here are very lightl punctate. *O. moubata* is widely distribute locally throughout East Africa and th warthog is a common host.

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References

CLIFFORD, C. M. and ANASTOS, G. (1962). Ticks. *Explor. Parc natn. Upemba Miss. G. F. de Witte*, **66**, 45 pp., 23 pls.

DINNIK, J. A., WALKER, JANE B., BARNETT, S. F. and BROCKLESBY, D. W. (1963). Some parasites obtained from game animals in Western Uganda. *Bull. epizoot. Dis. Afr.*, **11**: 37-44.

HOOGSTRAAL, H. (1956). African Ixodoidea. Vol. 1. Ticks of the Sudan. *Dep. Navy, Washington*, 1101 pp., 103 pls.

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The nestling plumage of four East African coursers

Of the five coursers occurring in East Africa only the cream-coloured courser (*Cursorius cursor* (Latham)) has its nestling plumage described in Mackworth-Praed and Grant (1957). I have seen downy young of the other four species in the following localities in Tanzania:—Temminck's courser (*C. temminckii* Swainson) on the flood plains of the Wembere and Ugalla rivers, two-banded courser (*Hemerodromus africanus* (Temminck)) on the Wembere flood plains, Heuglin's courser (*H. cinctus* Heuglin) around Tabora, and violet-tipped courser (*Rhinoptilus chalcopterus* (Temminck)) in the Ugalla River Game Reserve. One fairly striking difference between the chicks of coursers and plovers is that the down of the former is rather longer and coarser, especially on the posterior parts of the body. This characteristic is particularly evident in *H. cinctus*.

Temminck's courser:—All upperparts mottled buffish-chestnut, black and off-white with a distinct off-white collar. Apart from a buff chest band underparts all white. Legs and bill grey. Steyn (1965) describes the upperparts as "mottled black, buff and red-brown" and the chest band as "dull reddish-brown".

Two-banded courser:—The general appearance is very similar to that of Temminck's courser. Unfortunately I did not note down an exact description when I found a young chick as I did not realise at the time that the nestling plumage was undescribed.

Heuglin's courser:— Upperparts buffish-grey with black blotches and no white collar. Underparts white except for a very faint pale buff chest band. Legs pale "dirty" yellow, bill horn.

Violet-tipped courser:—Upperparts black with some buffish-chestnut patches and a broad white collar. Underparts white. Legs dark grey, bill black.

References

MACKWORTH-PRAED, C. W. and GRANT, C. H. B. (1957). Birds of Eastern and North Eastern Africa, 2nd Edition. *Longmans, Green & Co., London.*

STEYN, P. (1965). Temminck's courser. *Afr. wild Life*, **19** (1):29-32.

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Protective threat display of young nightjar

On 20th November, 1966 I was driving through rather open *miombo* woodland near Tabora, Tanzania when a nightjar (*Caprimulgus* sp.) flushed from near the front wheels of my Landrover. The bird went through a typical "broken wing display", but flew away when I alighted from the cab.

Looking over the ground from which the bird had flushed I found two well-feathered young nightjars which remained motionless while I photographed them. When I touched the larger of the two young birds its behaviour changed completely; it spread its wings, widely opened its gape and repeatedly hurled itself at my finger. This behaviour had the same startling effect as the sudden wing-opening display of stick insects and might well have deterred a small predator. After photographing the threat display I searched carefully for the parent but was unable to find her/him again.

As the adult bird was not collected it is not possible to state for certain the species concerned in this observation. The only species known to occur regularly around

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Oxygen uptake by Nanorchestes antarcticus (Acari)

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Block, W. 1976. Oxygen uptake by *Nanorchestes antarcticus* (Acari). – O
27: 320–323.

Oxygen consumption rates of the minute terrestrial mite, *Nanorchestes arcticus* Strandtmann were measured at +5°C with a Cartesian Diver mi respirometer. Individual respiration rates were in the range 0.156 (deutonym to 1.135 (tritonymph) × 10^{-3} µl O_2 $ind^{-1}h^{-1}$. Mean estimated live weights v 1.59 to 3.57 µg, and metabolic rate was highest in the adult female (367.73 O_2 $g^{-1}h^{-1}$) and lowest in the deutonymph (161.045 µl O_2 $g^{-1}h^{-1}$). These res are discussed with reference to other terrestrial mites and cold adaptation.

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Скорость потребления кислорода у мелких почвенных клещей *Nanorche antarcticus* измеряли при 5°C с помощью поплавкового микрореспироме Индивидуальные колебания активности дыхания составляли от 0,156 /л тонимфа/ до 1,135 /тритонимфа/ × 10^{-3} µл O_2/экз$^{-1}$/час/$^{-1}$. Средний вес основе измерений составлял 1,59–3,57 мг, метаболическая активность б наибольшей у зрелых самок /367,734 µл O_2/г$^{-1}$ /час$^{-1}$/. Обсуждаются полу ные результаты в сравнении с другими почвенными клещами и адаптаци холоду.

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oduction

orchestes antarcticus Strandtmann is one of the llest terrestrial mites (average length 240 µm), and the southernmost arthropod collected at 85° 32'S se and Gressitt 1965). It is widely distributed in the ·itime Antarctic zone (Tilbrook 1967). On continental arctica, *N. antarcticus* is often the most abundant ropod (Janetschek 1967). Rounsevell (1975) recorded high population densities near Davis Station (68°): 12700 ind m^{-2} in August (winter) and 158600 ind in January (summer), where it was the only arpod present. This species is active down to 0°C, and ɔwer lethal temperature is in the region of −23° to °C (Fitzsimons 1971).

. *antarcticus* was first described by Womersley and ndtmann (1963), and Lindsay (1972) separated its nstars, which include a prelarval stage passed in the ıle.

uring a visit to Signy Island (60° 43'S, 45° 38' W) ıe South Orkney Islands from November to March 1/72), some measurements of the rate of oxygen conption of individual *N. antarcticus* were made. Con·ing the ecological importance and the intrinsic iological interest in this species, the results are re·ed here.

ıods

imens of *N. antarcticus* were extracted from samples :hen encrusted *Polytrichum – Chorisodontium* moss collected near Factory Cove Bluffs on Signy Island. l temperatures were +1.5° to +7.5°C. Extraction ıe mites was by Tullgren funnels using very gentle , the animals being collected on moist filter paper, h was changed every 3 h, and removed to a stock ıre containing food material and maintained at C. Animals for respirometry were removed from the culture after 24 h with a fine brush.

ɛygen uptake was measured with a Cartesian Diver ɔ-respirometer (Zeuthen 1964) using stoppered div- f gas volumes in the range 1.20 to 9.41 µl. The diver ıique used was as described in Block and Tilbrook 5). Respiration rates of resting individuals were ıured at +5°C over 6–8 h periods. In some cases, than one animal of similar size was used per diver, mean individual respiration rates have been calcu- for these results.

ter measurement, each animal was preserved in 75% ıol, mounted in Hoyer's medium on a slide, and ified to life stage using phase contrast microscopy axonomic descriptions given in Lindsay (1972). The eter of the idiosoma was measured in each case ; an eyepiece graticule and, on the assumption that ıody of *N. antarcticus* approximated to a sphere, measurement was converted to live weight by the wing linear regression equation (Goddard 1976): $y = 146.27 + 13.81\ x$, where y : diameter of idiosoma (µm) and x : live weight (µg).

Results

The individual live weights for proto-, deuto-, and tritonymphs together with adult females are given in Tab. 1, and the mean weight for each life stage. Adult males were not found. The weights of individual tritonymphs are very variable. The mean tritonymph and adult female weights are similar, and there is a x2 weight increment between deuto- and tritonymphs. These findings are of a similar order to those reported by Block (1976) for the Antarctic cryptostigmatid mite, *Alaskozetes antarcticus* (Michael). Compared to Goddard (1976) the live weights derived for *N. antarcticus* are slightly lower for deuto-, tritonymph and adult.

The mean rates of oxygen uptake per individual and g (Tab. 2) show that on an individual basis, at +5°C, there was a similarity in respiration of the adult and tritonymph, with deutonymphal respiration being much lower. Metabolic rate of the adult female (mean: 367.73 µl O_2 g^{-1} h^{-1}) exceeded both the trito- and deutonymphal stages. These results are broadly similar to Goddard (1976).

The individual respiration rates for *N. antarcticus* are considerably lower than those reported for *A. antarcticus* at the same temperature; these fell within the range 2.138 to 23.765 × 10^{-3} µl O_2 ind $^{-1}$ h^{-1} (Block 1976). However, on a weight basis the metabolism of *N. antarcticus* is comparable to *A. antarcticus* at +5°C. Under Signy Island conditions, *N. antarcticus* is metabolically

Tab. 1. Live weights of individual *Nanorchestes antarcticus* derived from measurements of idiosomal diameter (see text for details).

Life stage	Animal number	Live weight (µg)
Protonymph	1	0.035
Deutonymph	2	0.162
–	3	2.627
–	4	1.055
–	5	2.515
Mean deutonymph		1.590
Tritonymph	6	8.748
–	7	0.927
–	8	6.070
–	9	0.247
–	10	1.310
–	11	4.115
Mean tritonymph		3.570
Adult female (+ egg)	12	4.158
–	13	2.585
Mean adult female		3.371

Tab. 2. Respiration rates of *Nanorchestes antarcticus* at +5°C on an individual and a weight basis. Mean individual ± SE are given for each life stage.

Life stage	Number of animals per diver measurement	Respiration rate $\times 10^{-3}$ µl O_2 ind^{-1} h^{-1}	µl O_2 g^{-1} h
Protonymph	3	0.1749	–
Deutonymph	1	0.0693	–
–	2	0.2965	161.045
–	2	0.1549	–
–	2	0.0875	–
–	3	0.1748	–
Mean deutonymph		0.1565 ± 0.040	
Tritonymph	1	2.5903	296.091
–	3	0.2062	58.932
–	3	0.6099	224.847
Mean tritonymph		1.1354 ± 0.737	193.290
Adult female (+ egg)	1	0.5515	132.645
–	1	1.5583	602.823
Mean adult female		1.0549 ± 0.503	367.734

as active as the larger oribatid mite at summer temperatures, disregarding the difference in size and weight. This may have important implications for terrestrial poikilotherms living in cold environments, in that whatever its size or weight the animal must be able to support a relatively high metabolic rate (Block 1976).

In general, the metabolic rates of *N. antarcticus* are much higher than those calculated from the data given by Berthet (1964) for temperate cryptostigmatid mites. The metabolism of 16 species ranged from 26.80 to 126.64 µl 0_2 g^{-1} h^{-1} at +5°C. The only information on respiratory rates of prostigmatid mites has been provided by Wood and Lawton (1973) for adults of five species at +10°C. Using a Q_{10} of 2.0 these rates were reduced to provide a range of 369.61 (*Lorryia* sp.) to 758.92 (*Bdella* sp.) µl 0_2 g^{-1} h^{-1} at +5°C. The metabolic rate of adult female *N. antarcticus* compares closely with the lower end of this range for temperate species.

The extremely small size of *N. antarcticus*, together with its obvious success in colonizing extreme habitats, reflects its ecological importance in a variety of Antarctic terrestrial ecosystems. Concomitant with this are the large variations in population density recorded for this species, and its activity at low temperatures. In cold adapted species it is probable that more of the assimilated energy is utilised for maintenance and less for growth and reproduction than in temperate species. The high metabolic cost of cold adaptation will result in slow growth rates and protracted life cycles. However, a higher level of metabolism during short periods when environmental temperatures are suitable for activity, growth and reproduction is a necessary requisite for these species.

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References

Berthet, P. 1964. L'activité des Oribatides (Acari: batei) d'une Chênaie. – Mém. Inst. r. Sci. nat. Belg. 1–152.

Block, W. 1976. Oxygen consumption of the terres mite *Alaskozetes antarcticus* (Acari: Cryptostigmat J. exp. Biol. (in press).

– and Tilbrook, P. J. 1975. Respiration studies on Antarctic collembolan *Cryptopygus antarcticus*. – O 26: 15–25.

Fitzsimons, J. M. 1971. Temperature and three specie Antarctic arthropods. – Pacif. Ins. Monogr. 25: 127–

Goddard, D. G. 1976. The Signy Island Terrestrial R ence Sites: VIII. Oxygen uptake of some prostigm mites (Acari: Prostigmata). – Bull. Br. Antarct. S (in press).

Janetschek, H. 1967. Arthropod ecology of South toria Land. – Antarct. Res. Ser. 10: 205–293.

Lindsay, K. L. 1972. *Nanorchestes antarcticus* Strandtm a taxonomic description of the instars. – Acarologi 593–606.

Rounsevell, D. E. 1976. Ecological adaptation in the Antarctic mite *Nanorchestes antarcticus* (Strandtma – In: Llano, C. A. (ed.). Adaptations within Anta ecosystems. 3rd Symp. Antarctic Biol., SCAR, W ington, USA (in press).

Tilbrook, P. J. 1967. The terrestrial invertebrate faun the Maritime Antarctic. – Phil. Trans. R. Soc. Se 252: 261–278.

Wise, K. A. J. and Gressitt, J. L. 1965. Far southern mals and plants. – Nature, Lond. 207: 101–102.

MERSLEY, H. and STRANDTMANN, R. W. 1963. On some free living prostigmatid mites of Antarctica. – Pacif. Ins. 5: 451–472.
OD, T. G. and LAWTON, J. H. 1973. Experimental studies on the respiratory rates of mites (Acari) from beech-woodland leaf litter. – Oecologia (Berl.) 12: 169–191.
ZEUTHEN, E. 1964. Microgasometric methods: Cartesian Divers. – In: Schiebler, T. H., Pearse, A. G. E., and Wolff, H. H. (ed.). 2nd Int. Congr. of Histo-and Cytochemistry. Wiley, New York.

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Cold tolerance of two Antarctic terrestrial arthropods

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Summary. Two Antarctic arthropods, *Alaskozetes antarcticus* (Acari) and *Cryptopygus antarcticus* (Collembola) possess the ability to supercool to −30 °C, but the realisation of this potential is dependent on starvation. The mite contains glycerol in a concentration of about 1% fresh weight.

Much effort has been devoted to elucidating the mechanisms involved in the survival of subzero temperatures by Arctic[2-5] and other terrestrial invertebrates[6], but surprisingly little attention has been directed towards Antarctic animals of this kind. Apart from results of temperature preferance and tolerance experiments[7-10], there has been no reported instance of the occurrence of supercooling or the presence of cryoprotectants such as glycerol or other polyhydric alcohols in the Antarctic terrestrial invertebrate fauna. Recent work has demonstrated the ability of 2 microarthropod species (a mite and a springtail) to supercool and the presence, in the mite, of glycerol, a compound often associated with the capacity to survive exposure to low subzero temperatures[4,5].

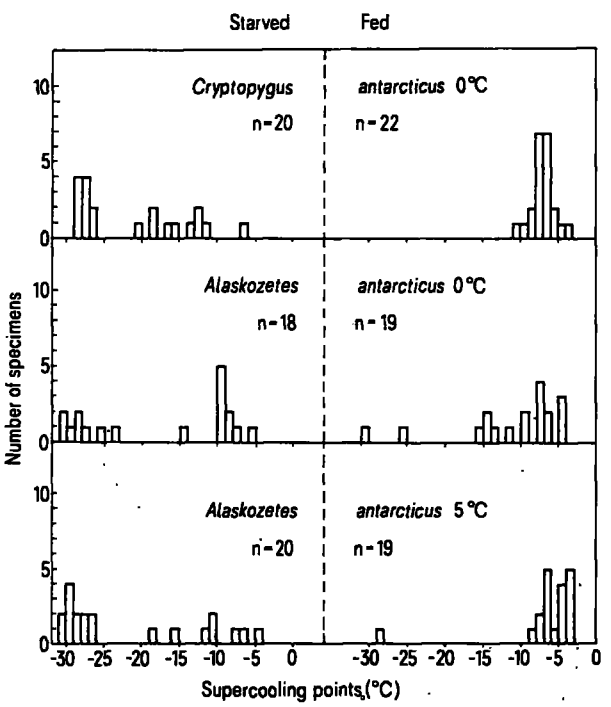
The 2 species involved in the present work are the mite *Alaskozetes antarcticus* (Michael), (Acari: Cryptostigmata) and the springtail *Cryptopygus antarcticus* Willem, (Insecta: Collembola). Both species are widespread in the maritime Antarctic and sub-Antarctic zones[11,12]. The individuals used in the experiments were collected during the austral summer of 1976–1977 near the British Antarctic Survey research station at Signy Island (60°43'S, 45°36'W), South Orkney Islands, a typical maritime Antarctic locality[13]. Here winter air temperatures may reach −25 to −39 °C and minimum temperatures within the animals' habitat are in the region of −20 to −25 °C[14]. Animals were maintained in culture at 5±2 °C from the time of their collection until they were used in the experiments (about 6 months).

Before measurements of supercooling points (lowest temperature reached before spontaneous freezing) and glycerol contents were made, *C. antarcticus* was acclimated at 0 °C, and *A. antarcticus* at 0 and 5 °C for 1 week. At each temperature 1 group of animals was fed and 1 group starved. Supercooling points were determined by the method of Salt[15], using fine copper-constantan thermocouples, for both starved and fed individuals of both species, while a paper chromatographic method[5,16] was used to test for the presence of polyhydric alchols in extracts of the animals concerned. 3 samples of each species were prepared for each acclimation temperature, using 12 individuals of *A. antarcticus* and 25 of *C. antarcticus* per sample. Use of glycerol standards on each chromatogram allowed an estimate of the concentration of unknowns to be made, since spot area is related to concentration of solution.

Results of supercooling experiments (figure) show that both species have supercooling points in the range −25 to −30 °C, which would enable them to survive winter temperatures in their habitats at Signy Island. It is also clear from the figure that the ability to supercool is strongly influenced by feeding or starvation of the animals concerned, although this is not so evident in 0 °C acclimated *A. antarcticus*. In general the results support those of Salt[15] and Sømme and Conradi-Larsen[17], who suggest that the presence of food material in the gut increases the probability of freezing occurring in a supercooled animal because such material contains efficient nucleating agents. If *A. antarcticus* had been starved for more than 1 week, a shift of more specimens to lower supercooling points would have been expected. Further experiments to this effect are being undertaken. None of the individuals used in the experiments survived the freezing process, indicating strongly that both species are freezing-susceptible and therefore depend on supercooling for survival.

The results of tests for the presence of polyhydric alcohols show that *C. antarcticus* contained no glycerol when acclimated at 0 °C, but did show the presence of another, as yet unidentified, compound on the chromatograms. *A. antarcticus*, on the other hand, contained glycerol when acclimated at 0 °C, but the substance was absent in animals maintained at 5 °C. The mean concentration (±SD) of glycerol found in the 3 samples from 0 °C was 10.1±0.35 µg mg^{-1} fresh weight (about 1%), which is a relatively low value compared to those found by Sømme and Conradi-Larsen[17] in Norwegian oribatid mites. It apparently does not affect supercooling points in this concentration, since 0 °C acclimated animals did not show lower supercooling points than those kept at 5 °C, but larger amounts may be accumulated during more prolonged storage at 0 °C or lower temperatures.

Previous work on arthropods inhabiting cold environments has suggested that there are 2 alternative ways in which such animals can survive temperatures far below the freezing point of water. 1 alternative is to avoid freezing altogether by supercooling which, apart from its ready occurrence in the absence of nucleating agents, seems to be



Supercooling point distribution histograms of *Alaskozetes antarcticus* acclimated to 0 and 5 °C, and *Cryptopygus antarcticus* acclimated to 0 °C. Number of determination is also given (n).

enhanced by the presence of glycerol[18] and other compounds[19]. The other alternative is to tolerate the extracellular freezing of the body[20], in which case the animal may produce its own nucleating agents which ensure that freezing occurs at relatively high subzero temperatures[21]. It is evident from the present data that 2 prominent and widespread members of the Antarctic terrestrial fauna have adopted the first solution, in common with mites and some insects from northern tundra environments. It is also apparent that *Nanorchestes antarcticus* Strandtmann (Acari: Prostigmata), another widely distributed Antarctic mite has solved the problem in a similar way, since it is reported to be active at $-23\,^{\circ}C$[7].

The discovery of glycerol in extracts of *A. antarcticus* indicates another striking similarity between the strategies of north and south polar cold tolerant organisms. Research is being undertaken to clarify the role of this compound with those of starvation and acclimation to low temperatures in the development of supercooling ability.

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2 A.W. MacPhee, Can. Ent. *96*, 617 (1964).
3 L.K. Miller, Science *66*, 105 (1969).
4 R.W. Salt, A. Rev. Ent. *6*, 55 (1961).
5 L. Sømme, Can. J. Zool. *42*, 87 (1964).
6 C.S. Crawford and W.A. Riddle, Oikos *25*, 86 (1974).
7 J.M. Fitzsimons, Pac. Insects Monogr. *25*, 127 (1971).
8 H. Janetschek, Pacif. Insects *5*, 305 (1963).
9 M.E. Pryor, Pacif. Insects *4*, 681 (1962).
10 P. Dalenius and O. Wilson, Ark. Zool. *11*, 393 (1958).
11 P.J. Tilbrook Phil. Trans. R. Soc. *252 B*, 261 (1967).
12 J.A. Wallwork, Biol. Rev. *48*, 233 (1973).
13 M.W. Holdgate, in: Biologie Antarctique, p. 181. Hermann Paris 1964. M.W. Holdgate, Phil. Trans. R. Soc. *252 B*, 17 (1967).
14 D.W.H. Walton, Br. Antarct. Surv. data, No. 1 (1977).
15 R.W. Salt, Can. J. Zool. *44*, 117 (1966).
16 R.L. Metzenburg and H.K. Mitchell, J. Am. chem. Soc. *76* 4187 (1954).
17 L. Sømme and E.M. Conradi-Larsen, Oikos *29*, 118 (1977).
18 R.W. Salt, Can. J. Zool. *37*, 59 (1959).
19 L. Sømme, Can. J. Zool. *43*, 881 (1965).
20 E. Asahina, Adv. Insect Physiol. *6*, 1 (1969).
21 K.E. Zachariassen and H.T. Hammel, Nature, Lond. *262*, 28 (1976).

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old tolerance of micro-arthropods from Alaskan taiga

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ABSTRACT. Mean supercooling points for a variety of soil and litter arthropods including mites, springtails, a heteropteran and immature spiders from a central Alaskan taiga site ranged from −6.3 to −28.5°C during autumn. Variation in supercooling ability of five species of cryptostigmatid mites occurred throughout the year with increased cold tolerance in autumn and early winter concomitant with the temperature pattern of the habitat. No correlation between the level of supercooling and water content of the mites was evident. Changes in the frequency distribution of individual supercooling points occurred in autumn, winter, spring and summer samples which were species specific. All arthropods tested were susceptible to freezing, and the mites utilize supercooling to avoid freezing.

oduction

y terrestrial arthropods in cold environ-
its overcome low habitat temperatures by
rcooling (e.g. Salt, 1958, 1961; Miller,
9; Crawford & Riddle. 1974), but there
few data (Macphee, 1964; Sømme &
radi-Larsen, 1977) for the mites (Acari),
e of the most abundant members of the
fauna throughout both temperate and
r regions. The objectives of the present
y were to determine the degree of cold
ance as exemplified by individual super-
ing points, of prominent species of soil
litter dwelling micro-arthropods in a
it habitat in central Alaska; and to examine
effects of body water content, season and
e environmental temperature, on their
ty to supercool. Information would also
ie from such experiments as to their
anism of cold hardiness and whether or
such taxa are tolerant of, or susceptible to, freezing. For these studies the supercooling point is defined as the lowest temperature reached before the body fluids freeze spontaneously.

Early research on cold hardiness of Acari was concentrated on phytophagous pest species and associated predators (Macphee, 1961, 1963, 1964; Sømme, 1965), whilst later Sømme & Conradi-Larsen (1977) and Block *et al.* (1978) investigated soil forms. Glycerol has been found in Norwegian and Antarctic soil mites by the latter workers. It remains to be seen if similar physiological mechanisms exist in mites as have been found in northern cold hardy insects (e.g. Baust & Miller, 1970; Sømme, 1974). A preliminary study of collembolan cold tolerance was made at Point Barrow, Alaska, by Tanno (1975).

Methods

The arthropods for study were collected in samples of leaf litter and soil taken from two sites close together in the Biological Reserve on the campus of the University of Alaska at Fairbanks. The area is typical of the taiga of

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central Alaska. The first site was a birch–aspen–alder community (*Betula papyrifera* Marsh, *Populus tremuloides* Michx., *Alnus incana* (L.) Moench.) with well-developed litter and humus layers, and the second site was a black spruce community (*Picea mariana* (Mill.) B.S.P.) with a moss field layer (mostly *Polytrichum* and *Sphagnum* spp.).

Sampling was extensive during autumn (October to early December) in 1974, and further collections were made in winter (January), spring (March–April) and summer (July) in 1975. Ten samples each of *c.* 10 cm^3 of leaf material, humus and soil from the deciduous site and of moss and peat from the evergreen site were collected on each occasion either by means of a knife or, when the substrate was frozen, they were chopped out using an axe. All samples were stored in a refrigerator at 0 to +3°C for 24 h or until they had thawed, which was never more than 36 h. Field temperatures in the humus layer on each site were measured at sampling and, in addition, maximum and minimum temperatures were recorded in the litter layer at each site between sampling occasions.

The thawed samples were placed in Tullgren funnels for extraction of the arthropods. Gentle heating was provided by 25 W electric bulbs, and the fauna was extracted into cooled containers lined with moist filter paper. The live animals were removed and stored at 0°C within 1 h of extraction. The time between field collection and the determination of supercooling points was kept as short as possible; it was often as little as 2 h, and never more than 36 h.

Supercooling points were measured in the four main seasons of 1974–75. Measurements were made in the autumn period of a variety of micro-arthropods including several species of mites, Collembola, pentatomids and spiders (a total of nineteen taxa). During succeeding seasons the study was concentrated on five common cryptostigmatid mites: *Eremaeus foveolatus* Hammer, *Cepheus corae* Jacot, *Epidamaeus gibbofemorata* Hammer, *Ceratoppia sphaerica* (L. Koch) and *Ceratoppia bipilis* (Hermann). These were extracted in sufficient numbers for experimental work during the difficult winter conditions. The Cryptostigmata were determined using Hammer (1952, 1955).

The live mites were sorted in an ice-co dish under low power and manipulated wi fine, moist paintbrush. Individual animals supercooling were weighed quickly usin Cahn gram microbalance and stored in n bered tubes at 0°C for a short time u required. Each specimen was attached to tip of a fine (40 swg) copper–constar thermocouple by means of a small spot vaseline on the dorsum. A good contact ensured between specimen and thermocou and each was positioned in a small air-fi glass tube and suspended from an expan polystyrene float in a methanol bath c cryostat (Ultra Kryostat UK 30L) at (Five specimens were monitored at one t with the thermocouples connected to a m point potentiometric dotting recorder (F elect) to record their body temperatures. experiments started at 0°C and a cooling of *c.* 1°C min^{-1} was used throughout. A supercooling, freezing was indicated b sharp rise in body temperature, which recorded. After the experiment, the ani was carefully removed from the thermocou placed in a clean tube, its condition n then and after 24 h of storage at 0°C. specimens were degreased by washing bri in acetone followed by distillled water, d in a vacuum oven at 60°C for 48 h, reweighed. The animals were preserved s rately in 70% ethyl alcohol for later spe confirmation.

Supercooling points were read dire from the chart record and tabulated. In dual live and dry weights were used to calcu body water contents, and mean values v derived for each taxon in each seasonal gro

Results

Preliminary faunal extractions, freezing d minations and preliminary data anal showed that there were no differences betv the two sites, so the data have been tre together.

Autumn supercooling points

The data for the taxa examined only in autumn are given in Table 1, where su cooling points and water contents of

E 1. Mean (±SE) supercooling points and body water contents of micro-arthropods from two Alaskan ites during October–November 1974. The number of determinations is given in parentheses.

		Supercooling point (°C)		Body water content (%)
ostigmata				
pelops septentrionalis (Trägårdh)	Adult	−28.5	(1)	56.1
emaeus foveolatus Hammer	Nymph	−7.7±1.4	(5)	62.2
cobates consimilis Hammer	Adult	−23.4±3.2	(8)	66.9
thrus pratensis Sellnick	Adult	−10.2	(1)	71.4
misia spinifer (C. L. Koch)	Adult	−7.9	(1)	34.7
pterobates variabilis Hammer	Adult	−7.3	(1)	75.5
tigmata				
ctoseius ornatus Evans	Adult	−7.8±1.2	(9)	35.9
gmata				
ellid sp.	Adult	−6.3±0.6	(3)	52.2
ombidiid sp.	Adult	−15.7±0.8	(6)	70.5
identified sp.	Adult	−7.0	(1)	54.0
nbola				
tomid sp.	Adult	−17.3±2.4	(2)	77.5
duridae	Adult	−22.7±1.1	(2)	78.4
ptera				
ntatomid sp.	Nymph	−7.2±0.9	(10)	64.5
ida	Juvenile	−8.4±0.3	(9)	76.2

es of cryptostigmatid, one mesostigmatid three prostigmatid mites are given her with those for Collembola, a penta- l and some araneids. The spiders tested all juveniles belonging to the families diidae, Thomisidae (*Xysticus* sp.), Lyco- (*Lycosa* sp.) and Linyphyiidae. Addi- data collected in the autumn for adults e species of cryptostigmatid mites are in parts of Tables 2 and 3.

nsiderable variation in supercooling s was recorded in the autumn period mean values of −6.3 to −28.5°C. In the , the only nymphs (*Eremaeus foveolatus*) ined were as cold tolerant as their adult and comparable to adults of other s. No clear correlation of supercooling with body water content was apparent. With five exceptions (out of nineteen), individual water contents were >60% of fresh weight with a range of supercooling points from −7.2°C (pentatomid species) to −23.5°C (*Epidamaeus gibbofemorata*). Of the five exceptions with body water content <60%, four had supercooling points *c.* −7°C and the fifth was the mite *Eupelops septentrionalis* (Tragårdh) at −28.5°C. Of the adult mites whose sex could be determined, no significant differences in supercooling points occurred between males and females.

Seasonal variation in mean supercooling points

Changes in mean supercooling levels of adults of five species of cryptostigmatid mites

E 2. Seasonal variation in supercooling points of adult cryptostigmatid mites from two Alaskan taiga n 1974–75. Mean values (±SE) are given with the number of determinations in parentheses. NM: not ed.

	Autumn	Winter	Spring	Summer
eus foveolatus Hammer	−10.7±1.0 (10)	−13.2±1.6 (27)	−7.0±0.3 (25)	−10.1±0.7 (24)
s corae Jacot	−22.0±1.2 (11)	−7.3±2.0 (3)	−7.0±1.0 (2)	−10.3±0.6 (21)
naeus gibbofemorata Hammer	−23.5±1.9 (21)	−8.2±1.5 (18)	−6.1±0.3 (24)	−7.4±0.2 (25)
ppia sphaerica (L. Koch)	−11.9±1.2 (29)	NM	NM	−11.1±1.1 (14)
ppia bipilis (Hermann)	−8.3±1.5 (9)	NM	NM	−9.0±0.0 (2)

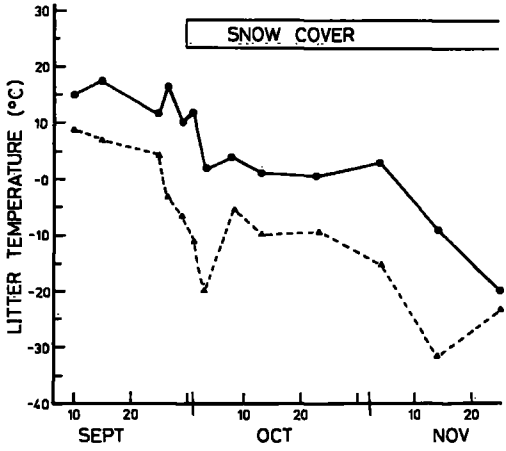


FIG. 1. Maximum (●) and minimum (▲) temperatures in the litter layer of the birch–aspen–alder site at Fairbanks during autumn 1974.

throughout the year are given in Table 2. Both *Ceratoppia sphaerica* and *Ceratoppia bipilis* were unobtainable in winter and spring samples together with low numbers of *Cepheus corae* in the same seasons. Both *E.gibbofemorata* and *C.corae* exhibited a significant depression of mean supercooling point from autumn to winter ($P < 0.001$). A similar significant downward shift in supercooling capability occurred in *E.foveolatus* between winter and spring. Between spring and summer three species increased their supercooling ability, of which two were significant at $P < 0.001$. In general, the lowest supercooling points occurred in autumn and winter, indicating that these mites were most cold tolerant at that time. The spring was a period of poor supercooling ability (mean of $-6.7°C$ for three species), and there was a general build up in cold tolerance preceding winter.

Reference to the temperature of the litter layer in the taiga habitat for the autumn period (Fig. 1) and for the other seasons vides support for these observed sea changes in mean supercooling points. O snow cover was formed in early Oc 1974, temperatures in the forest floor ranged from 0 to 4°C (maximum) and -5 to $-31°C$ (minimum) for approxim 6 weeks thereafter. There were conside fluctuations in temperature during this In January 1975 subnivean spot temper readings of between -11 and $-18°C$ recorded at sampling, and in May temperatures were 0–14°C. During late the leaf litter was at *c.* 14°C at the tir sampling. Subnivean temperatures in w (January) were greatly ameliorated by layer insulation as indicated by an air tem ture at 1 m height of $-47°C$. It seems the critical period for survival in such ar pods is autumn and early winter, when ambient temperatures may occur bef sufficient snow layer has formed to pr the subnivean habitat. The cold toleran the mites investigated generally followe seasonal temperature pattern in their hab

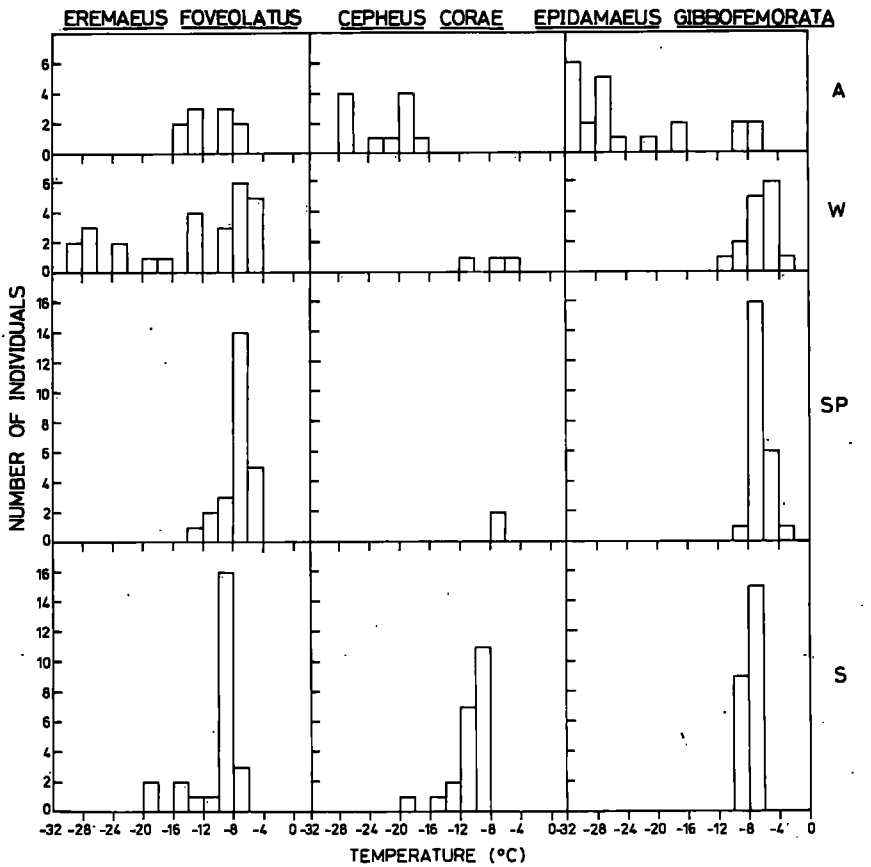
In terms of mean water content the species altered markedly during the (Table 3). The trend was for high body contents (63–72%) in autumn with decr levels in winter, spring and summer. pattern during autumn and winter ma correlated with the withdrawal of free water in connection with the synthes cryoprotective substances such as gly and other polyhydric alcohols. However, was no clear correlation of mean supercc point and water content of the mites.

Individual supercooling points

Analyses of the individual data of s cooling points reveal several inter

TABLE 3. Seasonal variation in mean (%) body water contents of adult cryptostigmatid mites fron Alaskan taiga sites in 1974–75. The number of determinations is given in parentheses. NM: not mea

Taxon	Autumn	Winter	Spring	Sum
Eremaeus foveolatus Hammer	67.1 (12)	60.5 (42)	58.6 (33)	53.7
Cepheus corae Jacot	64.1 (12)	45.8 (3)	54.9 (3)	52.9
Epidamaeus gibbofemorata Hammer	71.7 (26)	58.6 (22)	59.8 (29)	59.8
Ceratoppia sphaerica (L. Koch)	62.7 (23)	NM	NM	63.1
Ceratoppia bipilis (Hermann)	69.7 (10)	NM	NM	52.5



IG. 2. Frequency distributions of supercooling points of three species of cryptostigmatid mites in utumn (A) 1974, winter (W), spring (SP) and summer (S) 1975 from Alaskan taiga.

ures. The frequency distribution of the ples throughout the year for individuals of *veolatus*, *C.corae* and *E.gibbofemorata* are vn in Fig. 2, with corresponding data for *haerica* and *C.bipilis* in autumn and mer in Fig. 3. The autumn data highlight iderable differences between the five ies. *E.foveolatus* and the two *Ceratoppia* have the majority of their supercooling ts between 0 and -16°C, whereas *C.corae* *E.gibbofemorata* have supercooling points veen -16 and -32°C for this period. It is y therefore that some of these forms with supercooling potential suffer heavy tality at this season if environmental peratures fall below *c.* -16°C, as all ies investigated were susceptible to freez- The winter experiment showed further rences in that two-thirds of *E.foveolatus* and all the individuals of *E.gibbofemorata* tested had supercooling points above -16°C. In the spring samples there were clear frequency distributions of both these latter species in the upper temperature zone (i.e. 0 to -16°C). The summer distributions of supercooling points were essentially similar to those of spring.

Within species the seasonal frequency distributions of supercooling points were different. *E.foveolatus* had a similar distribution pattern in autumn, spring and summer with the winter sample only showing a downward progression of individual supercooling ability. *C.corae* had a low supercooling point distribution in autumn and high throughout other seasons, although few data were available for winter and spring. *E.gibbofemorata* showed a low distribution of supercooling points only

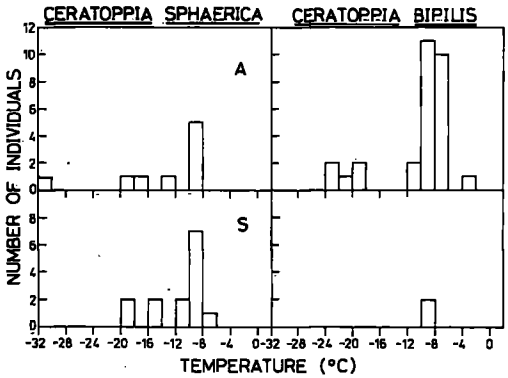


FIG. 3. Frequency distributions of supercooling points of two species of cryptostigmatid mites in autumn (A) 1974 and summer (S) 1975 from Alaskan taiga.

in autumn. It may be, of course, that some individuals tested had supercooling points below −35°C, which was the lowest temperature attainable in these tests.

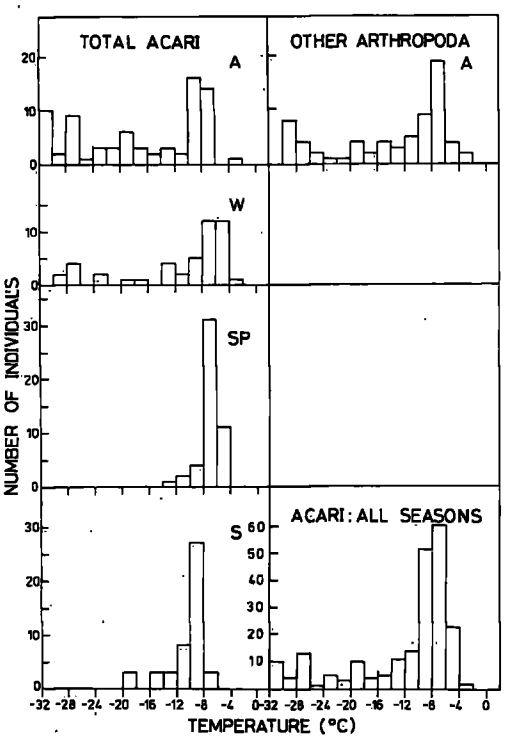


FIG. 4 Frequency distributions of supercooling points for total Acari in autumn (A) 1974, winter (W), spring (SP) and summer (S) 1975 from Alaskan taiga. Data for other soil and litter arthropods for autumn (A) 1974, and the pooled data of the Acari for the year are also shown.

Considering the individual data overal total Acari (Fig. 4), there was little chan the distribution with season except tha autumn *c.* 50% of the specimens tested supercooling points above and below −1 In winter there was a tendency for the maj of supercooling points to occur from − −16°C, which was continued in the s and summer. A comparable distributio supercooling points was shown by the c arthropods examined in the autumn pe Pooling the Acari data from all sea demonstrates that mites in this Alaskan f floor habitat have a wide range of cold t ance from −2 to −32°C with a peak in region of −8°C. Also the ability to supe is present throughout the entire year.

Discussion

Information on the supercooling abilit free-living Acari is limited. Macphee (1 1963, 1964), working in Nova Scotia, reco a variation from −20.5 to −37.2°C in su cooling points of twenty-four species of n and insects, the latter being the lethal tem ture for winter eggs of the phytophagous *Panonychus ulmi* (Koch). Large seas variations in supercooling ability were fo for a collembolan and two cryptostigm mites inhabiting mountain ridges in Nor by Sømme & Conradi-Larsen (1977). Glyc was accumulated in all three species at − Block *et al.* (1978) found supercooling po of −25 to −30°C for an Antarctic mite a springtail with small quantities (*c.* 1% of f weight) of glycerol present in the mite, w Sømme (1978a) measured supercooling po between −20 and −30°C for prostig mites susceptible to freezing in Antarc The range of supercooling data reported for Alaskan soil and litter mites are com able to these earlier observations, but Alaskan species do not achieve the very values recorded for the Norwegian and N Scotian animals. Furthermore, the avail data suggest that mites in general are susc ible to freezing, and that glycerol may or not be a constituent of their body fl during winter. Similarly with the lim information on the Collembola, it app that relatively depressed supercooling po

be achieved by individuals in winter
mme, 1976; Block *et al.*, 1978; Sømme,
'8b), and that significant quantities of
cerol may also be accumulated. Tanno
75) concluded that ten species of tundra
ngtails at Point Barrow were susceptible
freezing and that survival at −18 and
3°C after 18 h was due to supercooling,
demonstrated that smaller individuals of
somia quadrioculata (Tullberg) survived
ter than larger animals. The factors control-
supercooling potential and the mechanisms
synthesis and action of cryoprotective
stances such as glycerol in micro-arthropods
ain largely unknown.

The effects of even gentle heat extraction
niques on the supercooling process in
ro-arthropods should not be overlooked.
the present study it was necessary to
ract the fauna in this way to obtain suffi-
nt animals for experimentation, and clearly
specimens experienced large thermal
nges especially for the winter samples. To
uce these effects, field samples were
rosted in a standard fashion, the time for
raction was minimized, the fauna was
ntained at *c.* 0°C prior to the determination
supercooling points, and the overall time
m field to freezing was kept as short as
sible. As a result, comparison of mean
ercooling points obtained on a range of
es in autumn 1974 with widely different
es from field to freezing (2–32 h) showed
significant effects. However, controlled
eriments throughout the year in which
t extracted and hand sorted specimens are
npared would be necessary to substantiate
fully.

It has been assumed in most arthropod
dies that a cooling rate of 1°C min^{-1} is an
quate test of cold tolerance (Salt, 1966).
h adults of the tenebrionid beetle *Upis*
mboides (L.) Miller (1978a) showed that
unusually low cooling rate of 0.17°C min^{-1}
eased cold tolerance and depressed the
er lethal temperature. It may be that the
ure to observe freezing survival in the
sent study was due to a lethal cooling rate.
wever, evidence from other studies on
ri and work in progress on Antarctic
estrial mites confirm that susceptibility to
zing is the rule rather than the exception.
Some evidence has accrued (Sømme & Conradi-Larsen, 1977; Block *et al.*, 1978; etc.) which indicates that material in the guts of supercooled arthropods may be important in lowering their cold tolerance by acting as nucleators for ice formation in the supercooled state. It was not possible to examine the gut contents of most of the mites used in the present study, as the alimentary systems of heavily sclerotized specimens could not be observed after clearing for microscopy, and direct dissection proved impossible due to the small size of many of the species. In general, there appeared to be few specimens possessing material in their guts.

It has been suggested by several workers that glycerol may act in at least two cryoprotective ways, either by aiding supercooling ability in freeze susceptible forms (Salt, 1959), or by reducing damage during the freezing process in freeze tolerant species (Asahina, 1969). In the latter strategy some species may produce their own nucleating bodies which ensure that freezing occurs at relatively high subzero temperatures (Zachariassen & Hammel, 1976). However, some arctic insects have supercooling points below −25°C and do not fit this hypothesis (Miller, 1978b). Evidence from the present study indicates that free-living mites in Alaskan taiga avoid freezing by supercooling, but it is not clear whether this process is enhanced by glycerol or other substances. It is interesting to note the widespread occurrence of supercooling as a cold tolerance strategy among both northern and Antarctic terrestrial arthropods which inhabit low temperature but seasonally variable environments.

Acknowledgments

I am indebted to the Institute of Arctic Biology, University of Alaska at Fairbanks, for a Visiting Research Fellowship, and to Dr P. R. Morrison and Dr G. C. West, respectively Director and Acting Director of the Institute, for provision of research facilities. I thank the University of Leicester for study leave and the Royal Society for a travel grant to enable me to undertake this research. Finally, I thank Dr L. K. Miller and Dr S. F. MacLean for their helpful forbearance in the work, and the former for criticism of the manuscript. The technical assistance of Ward Testa is gratefully acknowledged.

References

Asahina, E. (1969) Frost resistance in insects. *Advances in Insect Physiology*, 6, 1–49.

Baust, J.G. & Miller, L.K. (1970) Variations in glycerol content and its influence on cold hardiness in the Alaskan carabid beetle, *Pterostichus brevicornis*. *Journal of Insect Physiology*, 16, 979–990.

Block, W., Young, S.R., Conradi-Larsen, E.M. & Sømme, L. (1978) Cold tolerance of two Antarctic terrestrial arthropods. *Experientia*, 34, 1166–1167.

Crawford, C.S. & Riddle, W.A. (1974) Cold hardiness in centipedes and scorpions in New Mexico. *Oikos*, 25, 86–92.

Hammer, M. (1952) Investigations on the microfauna of northern Canada. Part I. Oribatidae. *Acta Arctica*, 4, 1–108.

Hammer, M. (1955) Alaskan oribatids. *Acta Arctica*, 7, 1–36.

Macphee, A.W. (1961) Mortality of winter eggs of the European red mite *Panonychus ulmi* Koch, at low temperatures, and its ecological significance. *Canadian Journal of Zoology*, 39, 229–243.

Macphee, A.W. (1963) The effect of low temperatures on some predacious phytoseiid mites, and on the brown mite, *Bryobia arborea* M. & A. *Canadian Entomologist*, 95, 41–44.

Macphee, A.W. (1964) Cold hardiness, habitat and winter survival of some orchard arthropods in Nova Scotia. *Canadian Entomologist*, 96, 617–625.

Miller, L.K. (1969) Freezing tolerance in an adult insect. *Science*, 166, 105–106.

Miller, L.K. (1978a) Freezing tolerance in relation to cooling rate in an adult insect. *Cryobiology*, 15, 345–349.

Miller, L.K. (1978b) Physiological studies of Arctic animals. *Comparative Biochemistry and Physiology*, 59A, 327–334.

Salt, R.W. (1958) Role of glycerol in produ abnormally low supercooling and freezing pc in an insect, *Bracon cephi* (Gabon). *Nature*, 1281.

Salt, R.W. (1959) Role of glycerol in the cold har ing of *Bracon cephi* (Gabon). *Canadian Jou of Zoology*, 37, 56–69.

Salt, R.W. (1961) Principles of cold-hardi *Annual Review of Entomology*, 6, 55–74.

Salt, R.W. (1966) Effect of cooling rate on the fi ing temperatures of supercooled insects. *Cana Journal of Zoology*, 44, 655–659.

Sømme, L. (1965) Changes in sorbitol content supercooling points in overwintering eggs of European red mite (*Panonychus ulmi* (Ko *Canadian Journal of Zoology*, 43, 881–884.

Sømme, L. (1974) The overwintering of *Pelop borealis* Payk. III. Freezing tolerance. *wegian Journal of Entomology*, 21, 131–134

Sømme, L. (1976) Cold hardiness of winter-a Collembola. *Norwegian Journal of Entomol* 23, 149–153.

Sømme, L. (1978a) Notes on the cold-hardine prostigmate mites from Vestfjella, Dron Maud Land. *Norwegian Journal of Entomol* 25, 51–55.

Sømme, L. (1978b) Cold hardiness of *Cryptop antarcticus* (Collembola) from Bouvetøya. *O* 31, 94–97.

Sømme, L. & Conradi-Larsen, E.M. (1977) hardiness of collembolans and oribatid m from windswept mountain ridges. *Oikos*, 118–126.

Tanno, K. (1975) Supercooling in Arctic Collem in early summer. *Low Temperature Science* 33, 39–43.

Zachariassen, K.E. & Hammel, H.T. (1976) Nuc ing agents in the haemolymph of insects tole to freezing. *Nature*, 262, 285–287.

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ev. Écol. Biol. Sol, 1979, 16 (2) : 227-233.

Oxygen consumption of the Antarctic Springtail *Parisotoma octooculata* (Willem) (Isotomidae)

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INTRODUCTION

Parisotoma octooculata (Willem) occurs throughout the sub-Antarctic and ıe maritime Antarctic zones. It is widespread on South Georgia, and has een recorded from Kerguelen, Heard, Macquarie, Auckland and Campbell ılands (WISE, 1967; 1970). In addition, it has been found in the South rkney Islands, the South Shetland Islands, the Argentine Islands and at ıany sites on the Antarctic Peninsula including the offshore islands. The ɔringtail is grey-white in colour, slightly smaller in size than the ubiquitous otomid *Cryptopygus antarcticus* Willem, and is usually found under stones nd rocks. Little is known of its biology and ecology in Antarctic habitats.

During a research programme on the environmental physiology of ter- ɛstrial micro-arthropods at Signy Island, South Orkney Islands, during the ıstral summer 1971-2, an opportunity was taken to determine rates of ĸygen uptake of individuals of *P. octooculata* representing the full size range f the species. The data from these experiments are reported here for ɔmparison with other Antarctic forms: *Isotoma klovstadi* Carpenter (STRONG, UNKLE & DUNN, 1970), *C. antarcticus* (TILBROOK & BLOCK, 1972; DUNKLE : STRONG, 1972; BLOCK & TILBROOK, 1975; BLOCK & TILBROOK, 1978), and ith temperate species (HEALEY, 1966; ZINKLER, 1966). Additionally, these ata comprise the first information on the metabolism of field fresh *P. ctooculata* in the Antarctic.

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At Signy Island, *P. octooculata* is one of four springtail species, but rarely occurs in high densities although it is the most common form aft *C. antarcticus*. Although like the latter species it is intolerant of relative low relative humidities, *P. octooculata* is found in largest numbers in miner soil material associated with mosses, in the alga *Prasiola crispa* Ligh *Menegh.*, and in a variety of bird's nest material including Dominican Gu (*Larus dominicanus* Lichtenstein), Wilson's Petrel (*Oceanites oceanic* (Kulhl)) and Giant Petrel (*Macronectes giganteus* (Gmelin)) (TILBROOK, 197

I. — METHODS

Animals for respirometry were obtained fresh from the field on the day of the exp riment. Specimens were collected by aspirator from under stones along the edge of sm moss banks close to the British Antarctic Survey's station on Signy Island. Deter nations of oxygen consumption were made in the austral summer from 13 December 19 to 16 March 1972. The respiratory rates of individual springtails were determined with Cartesian Diver micro-respirometer (ZEUTHEN, 1964) using stoppered divers of 1.90 - 14.15 gas volume. The experimental technique was as described by BLOCK & TILBROOK (1975) wi an equilibration period of 30-45 min in the divers before readings commenced. Expe ments continued for 4-6 h. All determinations were made at 5° C, which is close to t summer mean field temperature experienced by this species.

The body length of each experimental animal was measured after respirometry, a converted to live weight using the equation derived for *C. antarcticus* (TILBROOK & BLO 1972):

$$\log_e W = 4.202 + 3.119 \ (\log_e L - 7.407)$$

where W : live weight (µg) and L : body length (µm). As *P. octooculata* is only sligh smaller than *C. antarcticus* (750-1680 µm) with individuals ranging from 626-1596 µm in bo length, and probably with a similar growth pattern, this conversion was considered ac quate. Further, live weight estimates and respiration data were grouped into size class for comparison with *C. antarcticus* (BLOCK & TILBROOK, *loc. cit.*).

II. — RESULTS & DISCUSSION

A total of 47 measurements were obtained distributed over size classes IV. Individual live weights ranged from 3.27 to 60.56 µg, whilst oxygen co sumption at 5° C varied from 0.583 to 13.694 nl 0_2 ind^{-1} h^{-1}. The results f individual respiration rates plotted against live weights are shown in Fig. together with the fitted regression line. There is a linear relationship be ween the two variables on a double log scale. Comparison of the weig exponent (regression coefficient b) of the results for *P. octooculata* with tho for *C. antarcticus* at 5° C from Signy Island (BLOCK & TILBROOK, 1975) sho there to be no significant difference in the relationship of individual oxyg uptake with live weight over the weight range of the two species. T metabolism results for *P. octooculata* (Fig. 2) ranged from 85.72 to 869.45 0_2 g^{-1} h^{-1}, and they suggest a decline in rate with increasing weight, but t slope of the regression is not significant from zero. Again, comparison of t

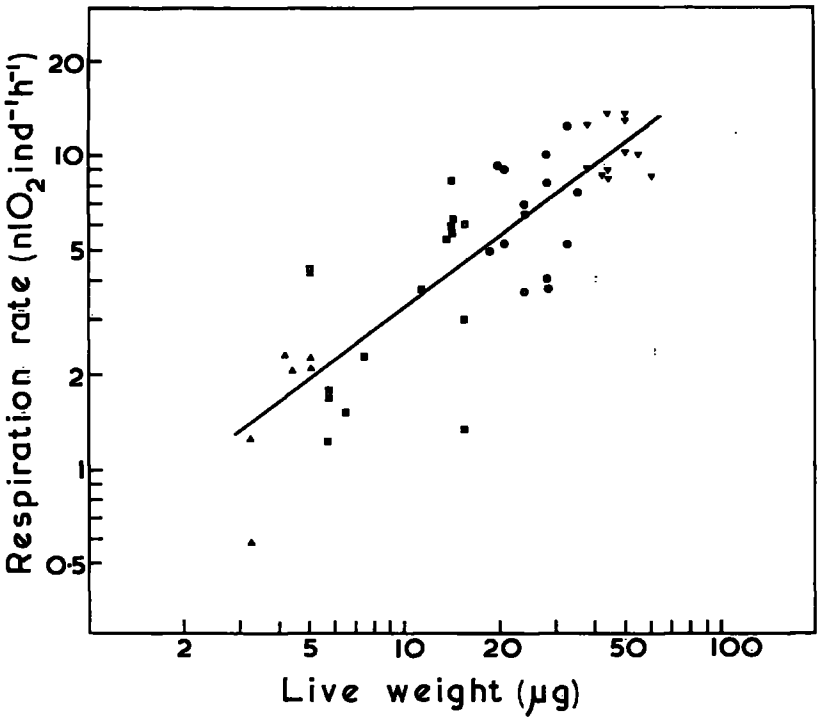

FIG. 1. — Relationship of individual respiration rate at 5° C to live weight in *Parisotoma octooculata*. The fitted linear regression is $\log_{10} R = 0.5756 + 0.7548 \log_{10} W$, where R: respiration rate (nl O_2 ind^{-1} h^{-1}) and W: live weight (µg). Size classes are shown as I: ▲, II: ■, III: ●, IV: ▼.

etabolism-weight relationship for *P. octooculata* and *C. antarcticus* shows at the slopes are similar to each other.

The mean values of oxygen consumption at 5° C of each size class of th collembolans are compared in Table I in both individual and weight ecific terms. Data are given for *C. antarcticus* from Signy Island and from uth Georgia. For size classes I - IV it is clear that there is little difference both individual respiration and metabolism between species at Signy land. Similar levels of oxygen uptake were measured for both forms with significant difference between the mean values for size classes I - IV. rther comparison with the data (Tab. I) for *C. antarcticus* at South Georgia LOCK & TILBROOK, 1978) for which determinations were made only for the st three size classes, suggests that the similarity is continued.

Information on collembolan respiration is accumulating and it is relevant review in a comparative way the data available for both polar (Tab. II) and mperate forms. Metabolic rates have been used for comparison to partly minate the effects of differences in live weight between species. It can be en that *P. octooculata* falls within the range reported for the Antarctic ringtail *C. antarcticus* in terms of metabolism, but neither species achieve

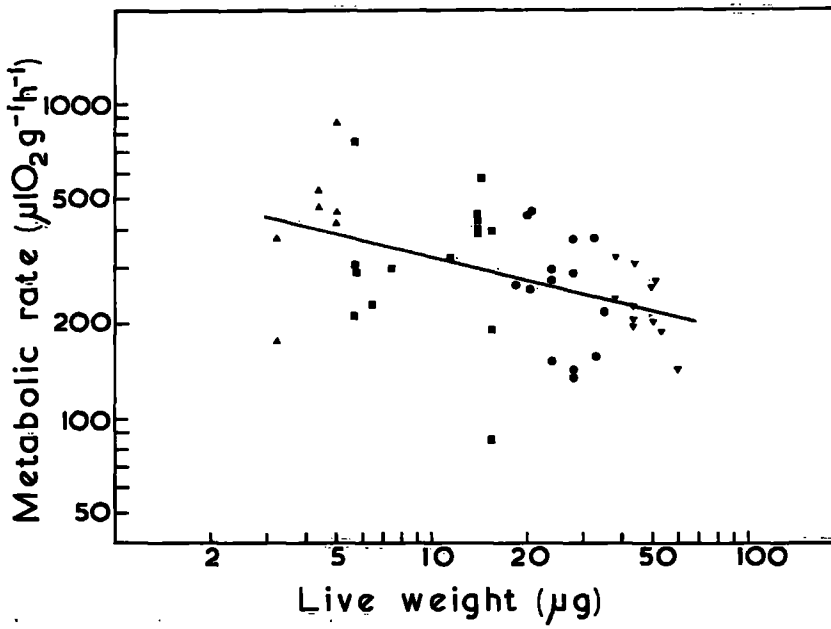

FIG. 2. — Relationship of metabolic rate at 5° C to live weight in *Parisotoma octooculata*. The fitted linear regression is $\log_{10} M = 575.6998 - 0.2452 \log_{10} W$, where M: metabolic rate (µl 0_2 g^{-1} h^{-1}) and W: live weight (µg). Size classes are shown as I: ▲, II: ■, III: ●, IV: ▼.

TAB. I

Mean (± SE) live weight, respiration and metabolic rates for size classes I - IV of *Parisotoma octooculata* at 5° C at Signy Island compared to data for *Cryptopygus antarcticus* from Signy Island and South Georgia
n : number of determinations

Size class	n	Live weight µg	Respiration rate nl O_2 ind^{-1} h^{-1}	Metabolic rate µl O_2 g^{-1} h^{-1}
Parisoloma octooculata — *Signy Island*				
I	7	4.36±0.30	2.144±0.446	471.09±78.56
II	15	11.07±1.10	3.917±0.589	356.52±42.60
III	14	26.27±1.42	7.006±0.719	273.67±28.65
IV	11	46.94±2.02	10.750±0.621	233.37±16.75
I-III mean	36	13.90	4.355	367.09
I-IV mean	47	22.16	5.954	333.66
Cryptopygus antarcticus — Signy Island				
I	12	3.04	1.410	469.23
II	10	10.26	3.197	313.25
III	10	25.72	5.934	230.71
IV	13	52.57	9.572	182.24
V	29	92.81	14.010	150.96

Size class	n	Live weight µg	Respiration rate nl O_2 ind^{-1} h^{-1}	Metabolic rate µl O_2 g^{-1} h^{-1}
I-III	32	13.01	3.513	337.73
I-IV mean	45	22.90	5.028	298.85
I-V mean	74	36.88	6.834	269.28
Cryptopygus antarcticus — South Georgia				
I	2	3.83	1.024	260.83
II	11	11.09	2.554	240.39
III	8	23.12	5.509	239.32
I-III mean	21	12.68	3.029	246.85

TAB. II

Comparison of mean live weights and metabolic rates of polar Collembola at 5°C Data derived from plots of metabolic rate on temperature

Species	Location	Live weight µg	Metabolic rate µl O_2 g^{-1} h^{-1}	Reference
risoloma ooculata	Signy Island, maritime Antarctic	22.2	334	Present study
yptopygus larcticus	Signy Island, maritime Antarctic	22.8	269	BLOCK & TILBROOK, 1975
yptopygus larcticus	Palmer Station, Antarctic Peninsula	26.0	462	DUNKLE & STRONG, 1972
yptopygus larcticus	Palmer Station, Antarctic Peninsula	29.0	246	MARSH, 1973
loma wstadi	Cape Hallett, Victoria Land, Antarctica	100*	1075	STRONG *et al.*, 1970
pogastrura sp. *trybomi*	Truelove Lowland, Devon Island, Arctic	85**	474	PROCTER, 1977
lsomia relli	Truelove Lowland, Devon Island, Arctic	10***	314	PROCTER, 1977

* estimated on basis of comparison of body size with other Antarctic springtails.
** derived from dry weight (25.5 µg) being 30 % of live weight.
*** derived from dry weight (3.4 µg) being 35 % of live weight.

the high level measured by STRONG, *et al.*, 1970 for *Isotoma klovstadi* Carpe ter. Few data exist for northern polar Collembola, but two species studi at Devon Island in the Canadian Arctic (PROCTER, 1977) suggest that levels metabolism comparable to those found in Antarctic species occur in the forms.

For temperate Collembola few measurements have been made in t temperature zone 0° to 10° C. The results of ZINKLER (1966) are the mo comprehensive and relevant to the present work. He recorded a range respiratory levels from which metabolic rates can be calculated. For eig species metabolism at 5° C varied from 48 µl O_2 g^{-1} h^{-1} (*Tetradontopho bielanensis* (Waga)) to 204 µl O_2 g^{-1} h^{-1} (*Sminthurus viridis L.*). Howev relatively higher metabolic rates were derived for two cold adapted forn *Isotoma hiemalis* Schött and *Isotoma saltans* (Nic.) from the Harz Mountai and the Austrian Alps, which ranged from 263 - 288 µl O_2 g^{-1} h^{-1}. These lat values approach the metabolic rates for *C. antarcticus* measured in t Antarctic. This poses the problem of whether elevation of metabolism is widespread feature of cold adapted terrestrial arthropods as has already be found in the Acari (BLOCK & YOUNG, 1978).

SUMMARY

Respiration rates of 0.583 - 13.694 nl O_2 ind^{-1} h^{-1} and metabolic rates 85.7 869.45 µl O_2 g^{-1} h^{-1} were recorded at 5° C for *Parisotoma octooculata* (Wille at Signy Island in the maritime Antarctic. The data are similar to those fou for *Cryptopygus antarcticus* Willem and are comparable to other polar Colle bola. In general, cold adapted Collembola have elevated metabolism compar to temperate species.

RÉSUMÉ

A Signy Island dans l'Antarctique maritime, la vitesse de respiration mesu à 5° C chez les individus du Collembole *Parisotoma octooculata* (Willem) s'éc lonne de 0.583 à 13.694 nl O_2 ind^{-1} h^{-1} et le flux respiratoire de 85.72 à 869.45 O_2 g^{-1} h^{-1}. Ces données sont similaires à celles enregistrées chez *Cryptopyg antarcticus* Willem, et sont comparables à d'autres Collemboles polaires. En gé ral, les Collemboles adaptés au froid ont un métabolisme plus élevé que ce des espèces tempérées.

ACKNOWLEDGEMENTS

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REFERENCES

LOCK (W.) TILBROOK (P. J.), 1975. — Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos*, **26**: 15-25.

LOCK (W.) & TILBROOK (P. J.), 1978. — Oxygen uptake by *Cryptopygus antarcticus* (Collembola) at South Georgia. *Oikos*, **30**: 61-67.

LOCK (W.) & YOUNG (S. R.), 1978. — Metabolic adaptations of Antarctic terrestrial micro-arthropods. *Comp. Biochem. Physiol.*, 61A : 363-368.

UNKLE (R.) & STRONG (F.), 1972. — A digital electrolytic micro-respirometer. *Ann. ent. Soc. Am.*, **65**: 705-710.

EALEY (I. N.), 1966. — The population metabolism of *Onychiurus procampatus* Gisin (Collembola). *In* : Graff, O. & Satchell, J. (ed.) *Progress in Soil Biology* : 127-134. North-Holland Publishing Company, Amsterdam.

ARSH (J. B.), 1973. — *Radioisotopic determination of the ingestion rates of three species of Antarctic arthropods : Cryptopygus antarcticus Willem (Collembola : Isotomidae), Belgica antarctica Jacobs (Diptera : Chironomidae),* and *Alaskozetes antarcticus* (Michael), (Cryptostigmata : Podacaridae). M. Sc. thesis, University of California, Davis.

OCTER (D. L. C.), 1977. — Invertebrate respiration on Truelove Lowland. *In* : Bliss, L. C. (ed.) *Truelove Lowland, Devon Island, Canada : A High Arctic Ecosystem* : 383-393. University of Alberta Press, Edmonton.

RONG (F. E.), DUNKLE (R. L.) & DUNN (R. L.), 1970. — Low temperature physiology of Antarctic arthropods. *Antarct. J. US.*, **5**: 123.

LBROOK (P. J.), 1973. — *Terrestrial arthropod ecology at Signy Island, South Orkney Islands.* Ph. D. thesis, University of London.

LBROOK (P. J.) & BLOCK (W.), 1972. — Oxygen uptake in an Antarctic collembole *Cryptopygus antarcticus. Oikos,* **23**: 313-317.

ISE (K. A. J.), 1967. — Collembola (Springtails). *In* : Gressitt, J. L. (ed.) *Entomology of Antarctica.* American Geophysical Union, Washington. *Antarctic Research Series,* **10**: 123-148.

ISE (K. A. J.), 1970. — Collembola of South Georgia. *Pac. Insects Monogr.*, **23**: 183-208.

UTHEN (E.), 1964. — Microgasometric methods : Cartesian Divers. *In* : Schiebler, T. H., Pearse, A. G. E. & Wolff, H. H. (ed.) *2nd. International Congress of Histo- and Cyto-Chemistry* : 70-80. Wiley, New York.

NKLER (D.), 1966. — Vergleichende untersuchungen zur atmungsphysiologie von Collembolen (Apterygota) und anderen Bodenkleinarthropoden. *Z. vergl. Physiol.*, **52**: 99-144.

Terrestrial Invertebrates

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pendix in "Elephant Island - An Antarctic Expedition"
C. Furse, pp. 226-229 (1979). Anthony Nelson, Shrewsbury.

outh Shetland Islands and in particular the Elephant Island group within them an important link in the terrestrial biology chain from the southern Andes to the ctic continent. In addition to their location being offset from the main axis of the ctic Peninsula and separated from it by the Bransfield Strait, it has been suggested hey represent the biologically richest and the most ecologically favoured of the ctic areas for terrestrial organisms (Holdgate, 1977).
he absence of information on the microbial components of the terrestrial unities of the Elephant Island group, the free-living invertebrates which have been led to date belong to the following groups: Protozoa (unicellular animals), toda (round worms), Tardigrada ('bear animals'), Annelida-Enchytraeidae (small nted worms), Crustacea-Copepoda (small crustaceans), Insecta-Collembola gtails), Insecta-Diptera-Chironomidae (midges) and Arachnida-Acari (mites). llowing is a brief account of their distribution and ecology in the Elephant Island , much of which has resulted from material collected by the two Joint Services litions (JSE) of 1970-71 and 1976-77.

zoa

arliest record is that of Sandon and Cutler (1924) for five species of flagellates and species of amoebae in a single sample of moraine material collected from Elephant l by the *Quest* Expedition in 1922. Smith (1972) analysed 23 samples collected in ary-March 1971 from Elephant Island by Walshaw, and recorded 54 species (18 s; 17 flagellates, 15 testate amoebae and 4 naked amoebae). The commonest oans were the flagellates *Oikomonas termo* (in 23 samples), *Cercomonas longicauda* ples) and *Cercobodo vibrans* (8 samples) with the ciliates *Urotricha agilis* (11 samples) *chelys* sp. (8 samples) together with the amoeba *Pseudodifflugia gracilis* (7 samples). reatest species diversity occurred in moss carpet peats, and in soil under the grass *mpsia antarctica*. All these species achieved their greatest numbers in one of these bitats, whilst the moraine clays were poor in species with only a few small ates present. The population density of testate amoebae varied from 0 in moraine ean of 7700±1200 individuals per g fresh weight of peat under moss carpet. The oa in the moss dominated habitats of Elephant Island show much similarity both ies and numbers with such habitats on Signy Island, South Orkney Islands.

toda

(1973) extracted worms from 11 samples collected in five habitats by Walshaw corded the dominant genera as being *Amphidelus*, *Plectus* and *Teratocephalus*. ally, the nematode fauna of Elephant Island is similar in content to Deception further south west. A re-examination of this material by Maslen (in press), d that 29 species were collected in the 1970-71 samples, distributed among the hida (5 species), Araeolaimida (6 species), Teratocephalida (2 species), ysterida (4 species), Rhabditida (2 species) and Dorylaimida (10 species). This ts that the nematode fauna of Elephant Island is comparable in species diversity to and Coronation Islands, in the South Orkney Islands, and more diverse than the arctic Peninsula sites examined (Maslen, in press). By comparison only 13 species

of worms were identified from Deception Island but these samples were mainly volcanic ash, very different from those on Elephant Island.

Tardigrada
Five samples (four from the grass *Deschampsia antarctica* and one from the moss *Drepanocladus uncinatus)* collected on the 1970-71 JSE were examined by Jennings (1976) for tardigrades. He found 316 individuals in the moss sample, and a range of 17-115 individuals in the grass samples. *Macrobiotus furciger** occurred in all the samples, whilst *Hypsibius (Diphascon) alpinus+H. (D.) pinguis** and *H. (D.) scoticus* were found in four samples. *H. (D.) chilenensis* and *Hypsibius (Hypsibius) dujardini** were also identified. (The forms marked thus * are very widespread in the Antarctic Peninsula and Scotia Arc.)

Enchytraeidae
These small, segmented worms have been collected from Elephant Island on both JSE, and preserved specimens are being identified. They were extracted from *Drepanocladus, Chorisodontium* and *Deschampsia* samples, and occurred in populations approaching 850,000 per square m in *Deschampsia* soil at a site *c.* 30 m a.s.l. and several metres inland (Spaull, personal communication). Enchytraeids were also collected from the undersides of rocks on polygonised areas (at 130 m a.s.l. on Cape Lindsey), on rocks encrusted with lichens (mainly *Usnea antarctica)* (on moraine at 80 m a.s.l. south of Stinker Point, and on a 15° slope at 180 m a.s.l. on the north side of Walker Point), and from wet moss *(Drepanocladus uncinatus)* (on a 10° slope at 135 m a.s.l. on 'Saddleback Point', 3 km west of Point Wild) during January-March 1971 by Walshaw. In addition, worms have been collected by Chuter and Baylis in moss turf and on the undersides of stones, rocks and slabs on Clarence Island, in scree on O'Brien Island and in moss turf on Aspland Island during the 1976-77 JSE. The occurrence of enchytraeids in terrestrial habitats of the Elephant Island group is of interest not only as it is the furthest south record to date for enchytraeids, but also because of the lack of ecological information on such worms in the Antarctic.

Copepoda
Several small Crustacea identified as copepods were found in terrestrial habitats on Elephant Island by Walshaw in January 1971. The sites ranged from rock surfaces encrusted with lichens, rocks near sheathbill and Wilsons Storm Petrel nests and under stones in a Chinstrap Penguin rookery south-east of Stinker Point, to a rocky outcrop almost 2 km from the nearest sea at 230 m a.s.l. north-east of Stinker Point. These specimens are being studied by specialists to confirm that they are terrestrial, creeping forms of harpacticoid copepods. If so, it may well be the first record of such terrestrial Crustacea in the Antarctic Region.

The remaining arthropods from the Collembola, Diptera and Acari groups, which have been identified from the two JSE, are listed in Table 1.

Collembola (Table 1)
Only two species have been collected, *Friesea grisea* and the ubiquitous *Cryptopygus antarcticus*. This is somewhat surprising, as the richest collembolan fauna has been reported for the South Shetland Islands (Wise, 1967).

Diptera (Table 1)
A single species of chironomid midge, *Belgica antarctica,* has been found in several locations in the Elephant Island group as adults, but mainly as larvae and pupae in soil by the JSE. It has previously been recorded on Gibbs 'Narrow Island' and on Elephant Island at 'Cape Belsham', 1 km west of Point Wild. Elephant Island is the northern limit of this species' distribution, which extends south to Cape Tuxen on the mainland of the Antarctic Peninsula (65° 27'S) and neighbouring offshore islands.

1. Records of Collembola, Diptera and Acari for the Elephant Island group.

pecies recorded.
\dults, larvae, pupae collected.
pers are total of each species recorded per habitat.

	Collembola: *Friesea grisea*	Collembola: *Cryptopygus antarcticus*	Diptera: *Belgica antarctica*	Acari, Mesostigmata: *Gamasellus racovitzai*	Acari, Cryptostigmata (oribatid mites): *Alaskozetes antarcticus*	Acari, Cryptostigmata (oribatid mites): *Halozetes belgicae*	Acari, Cryptostigmata (oribatid mites): *Magellozetes antarcticus*	Acari, Prostigmata: *Nanorchestes antarcticus*	Acari, Prostigmata: *Rhagidia gerlachei*	Acari, Prostigmata: *Stereotydeus villosus*	Acari, Metastigmata (ticks): *Ixodes uriae*
s											
carpet		+							+		
nd											
turf			L	+	+						
ntified moss			L		+						
en											
			ALP	+	+				+		
ice											
nest material		+		+						+	
peat		+								+	
rock slabs											+
revices			L	+	+				+	+	
sides of s and stones			L	+	+		+		+	+	
urf				+						+	
ater pool		+									
nt											
urf											
ichum sp.	+	+									
grass *tarctica*	+	+									
rocks near uin rookery		572								1	8
ides of rocks		26	63A	18	45	8	13	2	77	20	
encrusted rocks		2		9			54		37	90	

Acari (Table I)

Seven species of mites and a single tick *(Ixodes uriae)* have been found on the Elephant Island group. The predatory mesostigmatid mite, *Gamasellus racovitzai,* was recorded together with three species of oribatid (or cryptostigmatid) mites and 3 species of Prostigmata. Of the last, only *Nanorchestes antarcticus* appears to be restricted to Elephant Island itself, the others being found elsewhere in the group.

Six oribatid mites were listed by Wallwork (1973) from previous collections in the South Shetland Islands, including two of the three recorded here. *Magellozetes antarcticus,* previously found in Tierra del Fuego, South Georgia, the Antarctic Peninsula (Hope Bay and Base Gonzales Videla), Anvers Island (Arthur Harbour) and Adelaide Island, is a new record for the South Shetland Islands, being found on Elephant and Clarence Islands. This species has been thought of as part of the South American element in the Antarctic Cryptostigmata fauna (Wallwork, 1967) with a discontinuous distribution in the maritime Antarctic zone and with records from the southern portion only. The present record continues its distribution north from the Antarctic Peninsula area.

Other Groups

In addition to the above groups, it is very likely that representatives of the Rotifera ('wheel animals') and the Platyhelminthes (flatworms) will be found in wet moss and freshwater pools of the Elephant Island group in the future.

There is much scope for further terrestrial study not only of the Elephant Island group in particular, but also of the ecology of the South Shetland Islands as a whole.

In conclusion, the South Shetland Islands and especially the northern Elephant Island group possess a rather richer than expected fauna in number and diversity of invertebrate groups in comparison with the Antarctic Peninsula and the South Orkney Islands. The area is well worthy of further detailed investigation as regards enchytraeid worms, nematodes, mites and the probably terrestrial harpacticoid copepods. Present information therefore suggests that the South Shetland Islands are biologically rich in terms of terrestrial invertebrates, and are clearly of considerable importance in establishing links between the South American and Antarctic land faunas.

References

Holdgate, M. W. 1977. Terrestrial ecosystems in the Antarctic. *Phil. Trans. R. Soc., B, 279,* 5-25

Jennings, P. G. 1976. Tardigrada from the Antarctic Peninsula and Scotia Ridge region. *BAS Bulletin No. 44,* 77-95.

Maslen, N. R. (in press). Additions to the nematode fauna of the Antarctic Region with keys to taxa. *BAS Bulletin No. 51.*

Sandon, H. and D. W. Cutler, 1924. Some Protozoa from the soils collected by the 'Quest' Expedition (1921-22). *J. Linn. Soc. Zool., 36,* 1-12.

Smith, H. G. 1972. The terrestrial Protozoa of Elephant Island, South Shetland Islands. *BAS Bulletin No. 31,* 55-62.

Spaull, V. W. 1973. Distribution of soil nematodes in the maritime Antarctic. *BAS Bulletin No. 37,* 1-6.

Wallwork, J. A. 1967. Cryptostigmata (oribatid mites). *Antarctic Research Series, Vol. 10,* 105-122.

Wallwork, J. A. 1973. Zoogeography of some terrestrial micro-Arthropoda in Antarctica. *Biological Reviews, 48,* 233-259.

Wise, K. A. J. 1967. Collembola (springtails). *Antarctic Research Series, Vol. 10,* 123-148.

NANORCHESTES ANTARCTICUS STRANDTMANN (PROSTIGMATA) FROM ANTARCTIC ICE

BY

William BLOCK *

ABSTRACT

Nanorchestes antarcticus Strandtmann 1967 (Prostigmata : Pachygnathidae) is reported in ice samples rom the MacLeod Glacier on Signy Island in the maritime Antarctic. Its occurrence in glacier ice is iscussed in relation to features of its biology.

RÉSUMÉ

Nanorchestes antarcticus Strandtmann 1967 (Prostigmata : Pachygnathidae) a été récolté dans des chantillons de glace du Glacier MacLeod à Signy Island dans l'Antarctique Maritime. Sa présence dans glace du glacier est discuté en fonction de sa biologie.

INTRODUCTION

There have been no reports of mites or other micro-arthropods from Antarctic ice samples. considerable variety of insects were collected by EDWARDS (1970) as fallout fauna on the Gulana Glacier in Alaska as well as on snow patches (KAISILA, 1952, EDWARDS, 1972, EDWARDS & ANKO, 1976), but the Acari content of these samples was negligible. This note reports the ccurrence of a single species of prostigmatid mite in ice cores taken from the MacLeod Glacier n Signy Island, South Orkney Islands in the Antarctic. No Acari or other arthropods were found ice samples collected at two other Antarctic sites.

METHODS

Three glacier sites were sampled, two being located at Signy Island (60°44' S, 45°36' W) the maritime Antarctic, and the third on sub-Antarctic South Georgia (54°16' S, 46°30' W). n Signy Island 17 samples were collected from an area of the Orwell Glacier on 27 March 1972,

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and 17 samples from the MacLeod Glacier on 29 March 1972. At South Georgia, six samples were obtained from the Hodges Glacier above Grytviken, Cumberland East Bay on 12 April 1972. Details of the samples and collection sites are given in Table 1.

TABLE I. — Details of collection sites and ice samples for micro-arthropods.

Location	Signy Island	Signy Island	South Georgia
Glacier	Orwell	MacLeod	Hodges
Altitude (m)	60	200	495
Weight of ice (kg)	10.20	10.57	5.91
Yield of siliceous dust (mg l^{-1})	8.0	2.6	6.7
Spherules	Absent	Present	Absent
Acari	Absent	Present (30 specimens)	Absent

Samples were collected on each site within an aera of 5 m^{-2}. Surface ice was removed to a depth of 20 cm on the Signy Island glaciers, and surface slush to a depth of 65 cm on the Hodges Glacier. Ice blocks *ca.* 25 cm deep and 10 × 10 cm section were cut by ice axe from both Signy Island sites, and circular cores 10 cm diameter and 25 cm deep were removed with an ice drill from the South Georgia site. Surface contamination of the samples was reduced as much as possible by handling with sterilized gloves. Each sample was sealed into a stout, sterile polythene bag, individually wrapped with aluminium foil, and rapidly transported to the nearby British Antarctic Survey station, where they were placed in a refrigerator at — 15°C. The samples were transported by ship to the U.K. in sterile polythene containers at a temperature of — 18°C.

At Leicester University a technique for the recovery of dust and other particles from such samples was utilized, which also detected micro-arthropods. In the laboratory each sample was weighed, washed in warm distilled water, and placed in a sterile polythene tent to melt at room temperature. The washings were discarded, but the meltwater was allowed to pass through a 0.45 μ pore filter, each filter being stored in a sterile, dust-proof box for later examination. A clean filter exposed in the tent during melting as a control for each sample showed no contamination. Each filter was examined separately for arthropod material using × 100 magnification. Mites were removed from the filters with a fine needle, and mounted in Hoyers on a microscope slide to allow recovery to their natural form.

RESULTS AND DISCUSSION

Arthropods, all Acari, were detected only on filters of the MacLeod Glacier samples, seven samples yielding mites. The specimens were either transparent pale green in colour or opaque red, the latter often staining the filter. A total of 30 mites were recovered. The maximum number of mites per filter was 12 with a mean of 4.3 per filter, and an overall mean for the MacLeod Glacier site of 1.8 individuals per sample. The latter figure allows an estimate of 180 individuals per m^2 to be derived. All the specimens were *Nanorchestes antarcticus* Strandtmann and all were juveniles. Both larvae (3) and nymphae (1 protonymph, 4 deutonymphs and 6 tritonymphs) were identified using LINDSAY (1972), the remainder could not be determined to life stage.

It is interesting that mites were found only on one glacier site of the three sampled, that on the MacLeod Glacier on Signy Island. The MacLeod Glacier samples (Table 1) had a relatively

low yield of siliceous dust (2.6 mg l^{-1} being rich in chlorite and mica and poor in quartz) compared with the other sites, but they were the only samples to contain spherules (SEARS, 1975). The coincidence of mites and small (2-100 μ) black, magnetic spherules probably of terrestrial (i.e. non-cosmic) origin in the same ice samples suggests a wind borne transport of both materials. The liklihood of surface contamination during field collection was very low. Of the three glaciers sampled the MacLeod site is the most exposed to winds, which are mainly westerly throughout the year, and which pass over the northern tip of the Antarctic Peninsula and southern South America.

GODDARD (1979 *a*) working on the terrestrial Acari of Signy Island did not sample ice habitats, but found *N. antarcticus* regularly in monthly samples from moss turf and carpet communities. Its annual mean density ranged from 1,278 (1973) to 3,376 (1972) individuals m^{-2} with an overall mean for 27 months of 2,200 individuals m^{-2}. The species lived mainly in the surface layer (0-3 cm) of such habitats with larvae occurring in the austral summer when higher numbers of nymphae were also recorded. The ice population (180 individuals m^{-2}) for the MacLeod Glacier samples is very low compared to bryophyte areas. However, *N. antarcticus* has been observed in large numbers in barren scree and glacial drift at Signy Island, and it is widely distributed occurring from sea level to rocks on the Island's summit at 279 m (GODDARD, 1979 *b*).

In continental Antarctica, MATSUDA (1977) working at Syowa station, Enderby Land, found a range of 100-800 individuals m^{-2} for *N. antarcticus* in algae and soil habitats, whereas in mosses its density varied from 1,000-1,200 individuals m^{-2}. The comprehensive ecological study of *N. antarcticus* in sandy barren situations in the Vestfold Hills near Davis Station (68°34′ S, 77°83′ E) by ROUNSEVELL (1977) revealed much higher population densities of 12,700-158,600 individuals m^{-2}. There *N. antarcticus* was the only arthropod present.

It is likely that the mites or the original colonizers were blown onto the ice surface at Signy Island either from nearby rock outcrops or from a greater distance. In terms of the former possibility, the nearest rock to the MacLeod Glacier site is Garnet Hill (226 m altitude), approximately 250 m south of the collection area. Several species of arthropods occur under rocks on Garnet Hill (GODDARD, *pers. comm.*) including the prostigmatids *Tydeus tilbrooki* Strandtmann, *Halotydeus signiensis* Strandtmann, *N. antarcticus*, the mesostigmatid (*Gamasellus racovitzai* (Trouessart) and the collembolan *Cryptopygus antarcticus* Willem. If the specimens of mites frozen into the MacLoed Glacier originated from the Garnet Hill outcrop, it is surprising that only *N. antarcticus* was found in abundance. It is known that this species feeds on the gelatinous red snow alga (*Ochromonas* sp.), and being a very cold tolerant form (FITZSIMONS, 1971, ROUNSEVELL 1977), the mites trapped in such glacier ice may be the remnants of an ear lier thriving popula tion in a depression on the glacier surface.

N. antarcticus is the most southerly occurring arthropod, having been found in the Horlick Mountains of continental Antarctica at latitude 85°32′ S. It is distributed over the whole of the Antarctic region and much of the sub-Antarctic, and appears to have a circum-polar distribution. It is a moderately active species, and when disturbed it can jump many times its own length. GODDARD (1979 *b*) observed a jump of 8 cm. Other Antarctic Prostigmata are also saltatorial, e.g. *Eupodes wisei* Womersley and Strandtmann (GLESS, 1972), and this may be a contributory factor in the dispersal of such species. FITZSIMONS (1971) concluded that *N. antarcticus* could tolerate a very wide range of environmental temperatures and was active from — 23° to + 31°C. Metabolically, individual *N. antarcticus* have higher levels of activity at their normal environmental temperatures than temperate foms (BLOCK, 1976), which are comparable to other Antarctic prostigmatids (GODDARD, 1977).

It seems that *N. antarcticus* has the physiological capacity to tolerate and remain active

at low temperatures, which, combined with its small size (length : 147 μ (larva)-280 μ (adult ♂ enables it to colonize, albeit temporarily, glacier areas with suitable food resources as suggeste by samples from the MacLeod Glacier on Signy Island. Although mites as small as *N. antarc ticus* are likely to be transported considerable distances by wind, just as are similar sized sphe rules of volcanic or industrial origin, there is scant evidence to date of such aerial transport. I nets flown from aircraft and ships en route to and from the Antarctic the number of Acari trappe are very few compared to insects and other arthropods (GRESSITT, *et al.*, 1961). Nevertheless terrestrial Acari may be a significant component of the passive fallout fauna of ice and snov in Antarctic areas.

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REFERENCES

BLOCK (W.), 1976. — Oxygen uptake by *Nanorchestes antarcticus* (Acari). — Oikos **27** (2) : 320-323.

EDWARDS (J. S.), 1970. — Insect fallout on the Gulkana Glacier, Alaska Range. — Can. Ent. **89** : 389 395.

EDWARDS (J. S.), 1972. — Arthropod fallout on Alaskan snow. — Arctic Alpine Res. **4** (2) : 167-176.

EDWARDS (J. S.) & BANKO (P. C.), 1976. — Arthropod fallout and nutrient transport : a quantitativ study of Alaskan snowpatches. — Arctic Alpine Res. **8** (3) : 237-245.

FITZSIMONS (J. M.), 1971. — Temperature and three species of Antarctic arthropods. Pacif. Ins. Monogr **25** : 127-135.

GLESS (E. E.), 1972. — Life cycle studies of some Antarctic mites and description of a new species, *Pro toereunetes paulinae* (Acari : Eupodidae). — (*In* LLANO, G. A., *ed. Antarctic terrestrial biology* Washington, D. C., American Geophysical Union : 289-306). [Antarctic Research Series, Vol. **20**

GODDARD (D. G.), 1977. — The Signy Island terrestrial reference sites VIII. Oxygen uptake of som Antarctic prostigmatid mites (Acari : Prostigmata). — Bull. Br. Antarct. Surv. No. **45**, 101-115

GODDARD (D. G.), 1979 *a*. — The Signy Island terrestrial reference sites XI. Population studies on th Acari. — Bull. Br. Antarct. Surv. No. **48** : 71-92.

GODDARD (D. G.), 1979 *b*. — Biological observations on the freeliving mites of Signy Island in the mari time Antarctic. — Bull. Br. Antarct. Surv. No. **49** : 181-205.

GRESSITT (J. L.), LEECH (R. E.), LEECH (T. S.), SEDLACEK (J.) & WISE (K. A. J.), 1961. — Trappin of air-borne insects in the Antarctic area (Part 2). — Pacif. Insects **3** (4) : 559-562.

KAISILA (J.), 1952. — Insects from arctic mountain snows. — Ann. Ent. Fennici, **18** : 8-25.

LINDSAY (K. L.), 1972. — *Nanorchestes antarcticus* Strandtmann ; a taxonomic description of the instars — Acarologia **13** (4) : 593-606.

MATSUDA (T.), 1977. — Ecological investigations on free-living mites near Syowa station, Antarctica. — (*In* LLANO, G. A., *ed. Adaptations within Antarctic ecosystems*. Houston, Texas, Gulf Publishing Co 1015-1021).

ROUNSEVELL (D. E.), 1977. — The ecology of the pan-Antarctic mite *Nanorchestes antarcticus* (Strandt mann). — (*In* LLANO, G. A. *ed. Adaptations within Antarctic ecosystems*. Houston, Texas, Gu Publishing Co : 1023-1033).

SEARS (D. W.), 1975. — Interplanetary dust on the earth's surface. — J. Br. astr. Ass. **85** (2) : 115-11

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ld hardiness of some Alpine Collembola

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ABSTRACT. 1. Individual supercooling points ranged from −2 to −44°C for six species of springtails, five species from the Swiss Alps and one from lowland Britain. Individuals of *Isotomurus alticola* (Carl) and *Isotoma viridis* Bourlet without gut contents had substantially lower supercooling points than those containing food material.

2. Juveniles were more cold resistant than adults in both *I.alticola* and *Isotoma hiemalis* Schött, both with respect to supercooling point and to their survival at prolonged subzero temperatures.

3. Temperature and acclimation time affected the degree of supercooling of four of the Alpine species especially *I.hiemalis.*

4. Duration of culture period had no consistent influence on the supercooling potential of all the species.

5. Tests for glycerol in the body fluids of the five Alpine springtails were negative, but the presence of a sugar, probably glucose, together with a five carbon polyhydric alcohol was indicated by chromatography.

oduction

) principal strategies are employed by cts and other terrestrial arthropods to ive low environmental temperatures. A ies may be tolerant to freezing in that viduals survive freezing of the body tissues, st others are susceptible to freezing in individuals are killed by the freezing ess. Freezing of arthropod tissue can ır at 0°C or a lower temperature depen- on the powers of supercooling and the ence of anti-freeze compounds such as hydric alcohols.

lost research in this field has been con- rated on large insects: Coleoptera (Baust Miller, 1970, 1972; Baust & Morrissey, 5; Miller, 1969; Sømme, 1974; Zacharias- sen, 1977), Lepidoptera (Frankos & Platt, 1976) and Hymenoptera (Ohyama & Asahina, 1972; Salt, 1958, 1961). Little attention has been paid to the lower insects and particularly to the abundant and widespread Collembola, many species of which inhabit soil and litter in extreme Alpine and polar communities. Recent work by Tanno (1975), Sømme (1976, 1978b), Sømme & Conradi-Larsen (1977) and Block *et al.* (1978) has demonstrated levels of cold hardiness in springtails from such habitats comparable to those found in higher insects.

The present work was concerned with the survival of Alpine Collembola at low temperatures and entailed experiments with field fresh and cultured animals. Two techniques were utilized to assess the cold tolerance of individuals of a range of species: the measurement of individual supercooling points (lowest body temperature reached before spontaneous

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freezing), and testing for glycerol as a possible cryoprotectant in their body fluids. The objectives of the research were to determine the effects of acclimation temperature, the presence of food in the alimentary canal, developmental stage and time in culture on the cold tolerance of five species collected from a variety of habitats in the Swiss Alps in the Canton of Bern, and to compare these results with data obtained from a lowland form from the U.K. The results permit a comparison of the selected species and enable the extent of their cold hardiness to be defined.

Materials and Methods

Five species were studied from the Family Isotomidae and one from the Family Poduridae, all Alpine forms with the exception of *Isotoma viridis* Bourlet which was collected in Cambridge, U.K. The following is a brief description of the four field habitats from which the animals were collected:

(1) *Isotoma hiemalis* Schött is a litter and surface dwelling species of open montane woodlands, often very conspicuous in winter when it is active on the snow surface during daytime at temperatures down to −6°C. The sample was collected in January 1978 at Dürrbachgraben, 13 km west of Thun, altitude 830 m, on snow and ice beside a stream.

(2) *Isotomurus alticola* (Carl) and *Isotomurus schaefferi* (Krausbauer) both live on wet surfaces of stones, wooden debris, etc., in small rivers and waterfalls, or where meltwater flows over rocks and stones. Both species occur in woodland and open areas, the former being recorded up to 3000 m. *I.alticola* was collected at two sites: (a) wet rocks at the edge of the Kanderfirn, 8 km east of Kandersteg, altitude 2500 m, in September 1976; (b) on the undersides of rocks near a small stream in open spruce forest at Gurnigel, 15 km west of Thun, altitude 1500 m, in November 1977. *I.schaefferi* was collected at the same site and date as the sample of *I.hiemalis*, but from the wet undersides of bare stones and in frozen leaf litter accumulated between stones.

(3) *Vertagopus montanus* Stach and *Hypogastrura sahlbergi* (Reuter) were both found on glaciers, living in a thin layer of moraine gravel or on the undersides of l stones in direct contact with ice. Both sp are known from Alpine grassland soils, bu from glaciers. *V.montanus* was collected a side moraine of Unterer Grindelw gletscher, 4 km south of Grindelwald, alti 1620 m, in September 1976. *H.sahlbergi* found together with *Onychiurus alborufes* (Vogler), which is an Alpine glacier spe under stones and partly in contact wit or perennial snow at the edge of the Tie gligletscher, 3 km south-west of Susten at 2800 m altitude, in August 1976. It found also on the Steinlimmigletscher ne and at a lower altitude together with *I.alti*

(4) *Isotoma viridis* Bourlet occurs variety of habitats: the individuals used i present experiments derived from a cu started in September 1977 with ani collected from a gravel path in Cambri U.K.

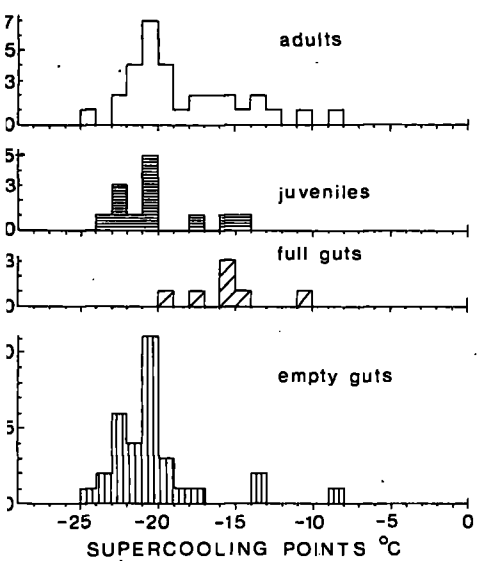
All animals were cultured from the da their field collection in 60 ml glass jars tight lids and at a relative humidity of *c.* 1 which was maintained by a base laye plaster of Paris–charcoal mixture moist with distilled water: *I.viridis* was kept at and the other cultures maintained at except for the acclimation experiments *I.hiemalis*. The cultures were exposed 12 h light: 12 h dark photoperiod and with Tetramin fishfood, except for *I.hie* which was fed on lichen (*Parmelia* sp.), *I.viridis* on algae (*Pleurococcus* sp.), which they flourished. The Collembola maintained in separate species cultures varying periods of time prior to the ex ments: *H.sahlbergi* 17 months, *V.mont* 16 months, *I.alticola* (a) 16 months, (b) months, *I.schaefferi* 1 month and *I.hie* < 1 month. Individuals of *I.viridis* second generation animals bred in culture 4 months.

The supercooling points of indivi springtails were measured by monitoring body temperatures using fine (36 swg) cop constantan thermocouples whilst they subjected to a linear cooling gradien $1°C\ min^{-1}$. The insect was attached to sensor in the thorax region by means spot of vaseline to ensure good contact. thermocouple, placed in a small glass t

s suspended in a methanol bath which was
oled by a Cryocool CC-100 immersion
it. The cooling gradient was produced using
heater in conjunction with the cooler
ntrolled by an Exatrol-30 unit interfaced
th an ETP-3 temperature programmer
eslab Inc, Portsmouth, New Hampshire,
S.A.). It was found that this system could
intain cooling rates of up to $2°C\ min^{-1}$
wn to $-70°C$ dependent on the cryostat
lume. A triple-pen recorder (Mitsui
chinery Sales, Chessington, U.K.) with
tomatic cold junction compensation over
temperature range -80 to $+20°C$ was
d to monitor body temperatures con-
uously throughout each experiment. Three
cimens were measured simultaneously. The
ercooling point was detected by a
nporary, but significant, increase in body
nperature of the insect due to latent heat
eased during freezing in the supercooled
te.

Analyses of the gut contents of individual
llembola were made after the supercooling
eriments. The springtails were degreased
initially cleared with chloroform for
10 min, followed by lactic acid at gentle
it (*c.* 40°C), the time being dependent upon the species. *I.viridis*, *I.alticola* and *I.schaefferi* required 30 min clearing in lactic acid, whereas the other species took between 3 and 6 h dependent upon the degree of pigmentation. Guts were assessed as being empty (without food or with only very small traces present in them) or full (with large amounts of food in them) using up to x 100 magnification. Individuals were classified as adults or juveniles on the basis of body length (juveniles being one-third to three-quarters the size of mature adults).

Paper chromatographic techniques were used to test for glycerol (Metzenburg & Mitchell, 1954), and to differentiate between sugars and polyhydric alcohols (Bean & Porter, 1959) in extracts of the body fluids of four of the Alpine species. Three replicates each of 2 mg fresh weight were utilized for each species.



. 1. Frequency distributions of individual super-
ling points of *Isotomurus alticola* for adults,
niles, and animals with full and empty guts from
culture.

Results

Effect of gut content on supercooling

In the six species investigated, individuals with empty guts had generally lower supercooling points than those with food present in their alimentary tracts. This was particularly well shown in *I.alticola*, culture b (Fig. 1). The mean (± 1 SE) supercooling point of those individuals ($n = 31$) with empty guts was $-20.0 \pm 0.6°C$ compared to $-15.5 \pm 1.1°C$ of those ($n = 7$) with gut contents, the difference in supercooling ability being significant at $P < 0.001$. In *I.viridis* the mean supercooling point for animals with gut contents ($n = 40$) was $-15.8 \pm 1.9°C$, whilst for those with empty guts ($n = 7$) it was $-22.6 \pm 1.8°C$ (significant at $P < 0.001$). This confirms earlier observations on microarthropods from Norway (Sømme, 1976; Sømme & Conradi-Larsen, 1977) and from the maritime Antarctic (Block *et al.*, 1978), and supports Salt's (1953) original recognition of the importance of food in the gut as nucleators for ice formation in supercooled insects. Field evidence of the role of food in collembolan cold hardiness has been found for *I.hiemalis*. In a collection of seventy-three adults of this species from Dürrbachgraben on 18 January 1978, sixty-seven had empty guts, five had food traces in the mid-gut whilst only one specimen had a full mid-gut.

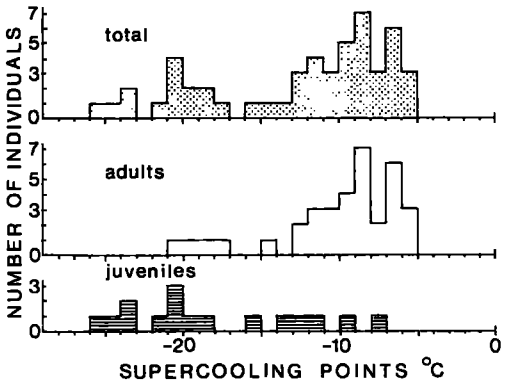


FIG. 2. Frequency distributions of individual supercooling points for adults and juveniles of *Isotoma hiemalis* after 1 week acclimation at 0°C.

Adult and juvenile supercooling ability

As both juvenile and mature Collembola are found in overwintering populations, the supercooling points of these two groups were examined in four species to determine if there was differential survival at low temperatures. Data are presented for *I.alticola* (Fig. 1), *I.hiemalis* (Figs. 2 and 3), *I.schaefferi* and *I.viridis* (Fig. 3). For both *I.alticola* and *I.hiemalis* the frequency distributions of individual supercooling points show clearly that immature forms generally have greater c tolerance than adults, and juveniles forr large proportion of those animals supercoo to temperatures > −15°C. This may have b partly an effect of differences in gut cont in *I.hiemalis* as 57% of the adults and 19% the juveniles contained identifiable f materials. In both species, the differenc mean supercooling point of adults juveniles was significant. For *I.alticola* (Fig the mean (±1 SE) supercooling points v −18.4±0.7°C ($n = 29$ adults) and −20 0.8°C ($n = 13$ juveniles), $0.1 > P > 0.05$; wl for *I.hiemalis* (Fig. 2) the values were −9 0.7°C ($n = 35$ adults) and −17.9±1. ($n = 16$ juveniles), $P < 0.001$. A sim significant difference between adults juveniles of *I.hiemalis* was apparent afte month at 0°C (Fig. 3). The differences mean supercooling points of adults juveniles of both *I.schaefferi* and *I.viridis* (3) were not significant. It can be seen th fore that the juvenile forms are more c tolerant than adults in two of the four Alp species investigated, which may be an imp tant factor in their overwintering survival.

These data are the first reported differer in cold tolerance related to life stage maturity within a collembolan species.

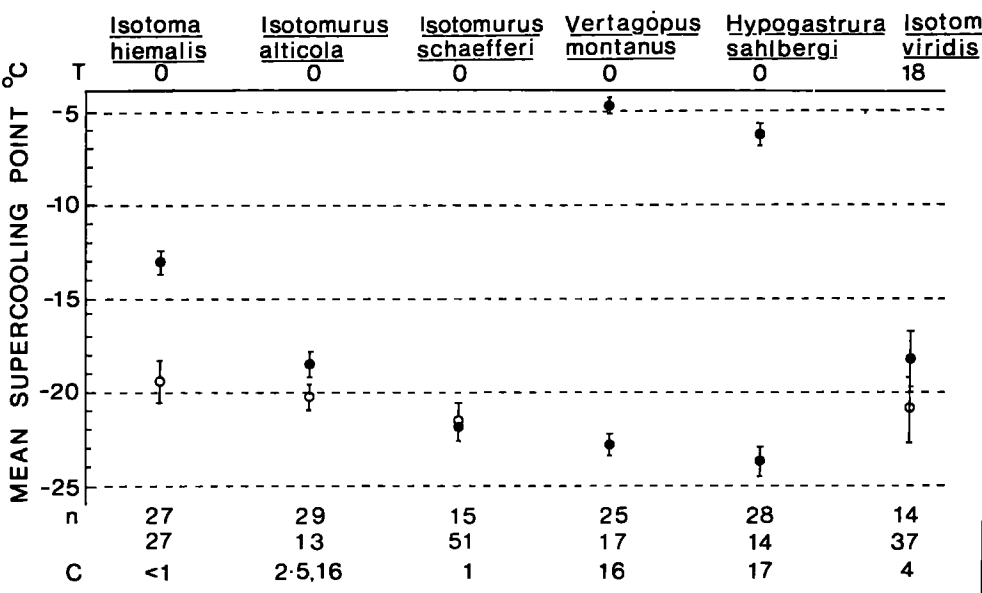


FIG. 3. Mean (± 1 SE) supercooling points for adults (●) and juveniles (○) of six species of Collembola *T*: culture temperature (°C); *n*: number of determinations; *C*: culture period (months).

e prostigmate mite, *Tetranychus urticae* ch, Stenseth (1965), working in Norway, corded similar substantial increases (up to °C) in cold tolerance of larvae compared diapausing female mites. Also, Almquist 970) reported considerable lowering of the hal temperature during winter of both adult nales and subadults of a dune living spider southern Sweden, the change (11.7°C) ing greatest in the juveniles, which probably resented a change in the supercooling lity.

climation temperature and supercooling

The effects of prior temperature acclimaon on supercooling ability were investigated *I.hiemalis*, although the mean supercooling ints of −18.7 and −20.9°C for adults and eniles of *I.viridis* (Fig. 3), which were limated to 18°C are comparable to the jority of the Alpine species cultured at . In *I.hiemalis*, the mean supercooling ints of groups of individuals acclimated to were calculated for each of the following atments: (i) 0→−5→−10°C with 1 ek at each temperature; (ii) 0°C for 1 nth; and (iii) 0→−5°C for 1 week and 1 nth respectively. Fig. 4 presents the results, ich demonstrate that both lowering of the acclimation temperature from 0°C and increasing the period of acclimation to 0 and −5°C overall results in a depression of the mean levels of cold tolerance for both adults and juveniles. The mean adult supercooling point is depressed by *c.* 8°C by the change from 0 to −5°C, whereas continued exposure to −5°C for 1 month or transfer to −10°C for 1 week does not decrease the supercooling point significantly. The juveniles show a less distinct pattern in *I.hiemalis*, but again lowering the temperature from 0 to −5°C brings about a marked increase in cold tolerance (*c.* 6°C supercooling point depression). Such acclimatory responses of Alpine Collembola may have considerable survival advantages in the field either at the onset of, or during, winter.

Sømme & Conradi-Larsen (1977) working with the collembolan *Tetracanthella wahlgreni* Linnaniemi from the Hardangervidda mountains in south Norway found increased supercooling ability in individuals acclimated for between 14 and 32 days at −5 and −10°C compared to 0 and +12°C. The decrease in mean supercooling point was *c.* 4.7°C, which is less than that for *I.hiemalis* for similar times and temperatures in the present study. The Antarctic springtail, *Cryptopygus antarcticus* Willem, showed no significant changes in its

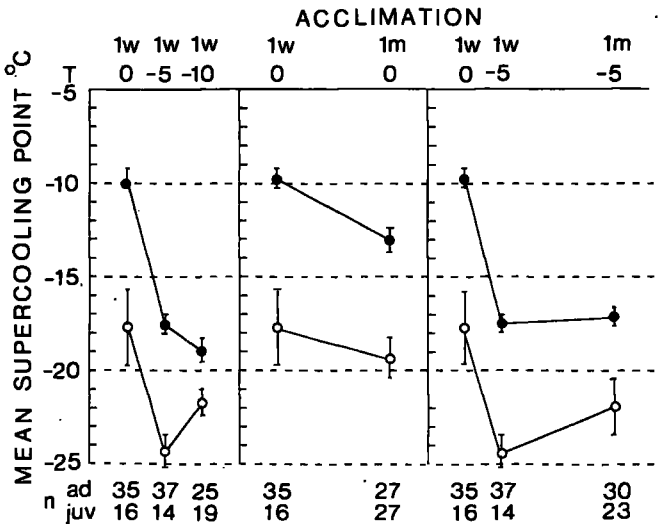


FIG. 4. Mean (± 1 SE) supercooling points for adults (•) and juveniles (○) of *Isotoma hiemalis* after acclimation at various temperatures and time periods. *T*: temperature (°C); *n*: number of determinations; w: week; m: month.

ability to supercool to *c.* −25°C when acclimated at −5, 0 and +12°C for times ranging from 17 to 79 days (Sømme, 1978b).

Culture time and supercooling

The effects of culture time on the cold hardiness of micro-arthropods are largely unknown. In the present study Collembola were maintained in culture for periods of time varying from 1 to 17 months before measurement of their supercooling points (Fig. 3). In *I.hiemalis* comparison of the mean supercooling points of adults after 1 week and 1 month at 0°C (Figs. 2 and 3) suggests a significant increase in cold tolerance with time ($P < 0.001$), whilst the juveniles remained relatively unchanged. In adults of *I.alticola* no differences in supercooling were detected between cultures of 2.5 months and 16 months but the values for the older culture showed a greater individual deviation from −2.8 to −36.0°C (mean: -19.7 ± 2.8°C, $n = 15$). Values for the 2.5 month culture are shown in Fig. 1. For adults of both *H.sahlbergi* and *V.montanus* similar culture periods at 0°C resulted in two distinct groups (Fig. 3) with a separation of individual supercooling points at −15°C and no correlation with gut content. The mean values were 17 and 18°C respectively apart ($P < 0.001$). The group with low supercooling ability probably contained senescing individuals as they had been collected as adults and were at least 28 months old.

Overall, no pattern of change in mean supercooling points with time in culture at 0°C for the five Alpine species can be discerned. Species which experienced only 1 month in culture had comparable levels of supercooling to those of 16–17 months culture. Clearly this aspect requires further investigation.

Cryoprotectant tests

Ethanol extracts were made of animals cultured at 0°C from *I.alticola* (2.5 months), *V.montanus* (17 months) and *H.sahlbergi* (18 months) and these were tested for glycerol and other possible cryoprotectant compounds. Tests for glycerol were also undertaken on extracts of *I.hiemalis* after culture for 1 week at each of the following temperatures sequ tially: 0, −5, −10 and −15°C. Glycerol not detected in any of these test, but sp representative of either sugars or sugar alcoh were observed on chromatograms of e species. Subsequent tests have shown presence of a hexose sugar of similar Rf va to glucose in both *I.hiemalis* and *I.altic* the latter species appearing to possess sligh less than *I.hiemalis*. In addition both th species contained polyols other than glyce and erythritol. By contrast the *V.monta* samples showed no traces of sugars but th was clear evidence of a five carbon poly possibly either arabitol or ribitol.

Few reports of cryoprotective compou in Collembola have been made; Sømme Conradi-Larsen (1977) found that glyce accumulated in *T.wahlgreni* both in the fi in winter and at low temperatures in laboratory. This is the only report of presence of glycerol in a collembolan. Glyce has not been detected in the Antarctic colle bolan *C.antarcticus* either from habitats Signy Island in the South Orkney Isla (Block *et al.*, 1978) or from Bouvet (Sømme, 1978b), when acclimated to 0°C, a 0 and −5°C respectively. However, Block *al.* (1978) reported that another substa with lower Rf values than glycerol appea on the chromatograms which was probal a sugar, and this has been confirmed in t species by Sømme (1978b). Four species Collembola from habitats at 2700 m a. in the Austrian Alps also did not cont glycerol (Sømme, 1979). It appears that Antarctic form may possess similar cryop tective compounds in their body fluids as four Alpine species tested in this study, further experiments are required to clar the role of these compounds.

Discussion

Individual supercooling points of five Alpi Collembola range from −2 to −40°C, and are freezing susceptible. In general, anim with empty guts are more cold tolerant th those containing food material, whi probably provide centres for ice nucleation the supercooled insect. Juveniles possess

ter degree of cold hardiness than adults of same species. Whilst both low temperature duration of exposure are important imatory factors in cold hardening of these nals, no consistent effect of culture time heir supercooling ability can be discerned. re is evidence of a lowered supercooling ity in senescing adults of two species. omatographic tests indicate that although erol is absent from samples of body fluids our of the Alpine species, several sugars at least one other polyhydric alcohol are ent.

hiemalis, which is often termed 'snow ', is essentially a surface species and in the ent experiments did not exhibit the levels cold hardiness achieved by the lower ips of *V.montanus* and *H.sahlbergi* (Fig. *I.hiemalis* is active on the snow surface at peratures above −6°C, colder periods g spent below the snow layer, where peratures normally range between −4 and . The temperatures in the microhabitats of *ontanus* and *H.sahlbergi* are relatively stant throughout the year, fluctuating veen +2 and −5°C (Ambach, 1961), so e is no explanation at present for the low n supercooling points of −23 and −24°C ectively. Further experiments are required determine the cold hardiness of freshly ected individuals.

Both species of *Isotomurus* are exposed to eme temperature fluctuations. During spells in the absence of snow cover, they unable to retreat into protected parts of habitat, and have to survive temperatures −10°C for several days. Consequently, ts of *Isotomurus* spp. have low mean ercooling points (−21.9 ± 0.7°C for *aefferi*, and −18.4 ± 0.7°C for *I.alticola*) pared with *I.hiemalis* (0°C for 1 month, .1 ± 0.8°C). The generally cold-hardier niles show comparable mean super- ing points (*I.schaefferi*, −21.6 ± 1.0°C; *icola*, −20.2 ± 0.8°C; *I.hiemalis*, −19.6 ± C).

The cold hardiness of *I.viridis*, a species id both in the lowlands and up to the Alpine region and which often occurs on , is comparable to two of the Alpine ies (*I.hiemalis* and *I.alticola*) showing the st individual supercooling points (−40.9, .2, −43.9°C). This raises the interesting question as to whether such temperate micro-arthropods have the potential to survive lower environmental temperatures than they normally experience. Alternatively, have cold adapted, freezing susceptible, species merely extended and developed mechanisms which had already been evolved?

During longer acclimation to subzero temperatures, *I.hiemalis* showed decreasing supercooling ability, this being especially evident in the juveniles (Fig. 4). The treatment of 1 week at −5°C with a further week at −10°C was survived by only 49% of the juveniles and 14% of the adults (total $n = 429$; difference significant at $P < 0.001$). During a further week at −15°C all animals ($n = 597$) except a single juvenile died. One week at −5°C showed a mortality comparable to the control culture at 0°C. A long period at subzero temperatures may be physiologically stressful, which may affect the supercooling powers, this being more evident in the juveniles. Further experiments are being conducted to clarify this point.

Within the Collembola, data for supercooling points of both temperate and cold adapted species are few. A total of eleven species have been examined. Minimum values range from −24 to −38°C. A mean supercooling point range of −8.9 to −20.0°C was recorded for *I.hiemalis* collected from snow surfaces in several localities near Oslo in winter (Sømme, 1976). The lowest individual supercooling point was *c.* −24°C for this species which is comparable to that of the present study. The lowest supercooling point (−38°C) has been measured for *T.wahlgreni* from mountain ridges in Norway (Sømme & Conradi-Larsen, 1977), whilst −33°C was recorded for *Tetracanthella afurcata* Handschin from 2700 m a.s.l. in Austria (Sømme, 1979), and −29°C for *C.antarcticus* from the maritime Antarctic (Block *et al.*, 1978). All Collembola tested have been found to be freezing susceptible, and whilst glycerol has been demonstrated in one species (Sømme & Conradi-Larsen, 1977) and sugars suspected in an Antarctic species, the compounds responsible for the enhancement of supercooling have not been elucidated.

The situation in the Acari, ecologically a closely related micro-arthropod group in which about thirty species have been studied,

shows similar supercooling levels and freezing susceptibility, but different antifreeze compounds. The lowest supercooling point (−38°C) has been found in adults of two species of cryptostigmatid mites from the Norwegian Hardangervidda by Sømme & Conradi-Larsen (1977), which is lower than those recorded for Antarctic mites: *Nanorchestes* spp. −31°C; *Eupodes tottanfjella* Strandtmann −30°C (Sømme, 1978a), and *Alaskozetes antarcticus* (Michael) −31°C (Block *et al.*, 1978). Minimum supercooling points of phytophagous prostigmatid mites are −33.2°C (eggs of *Panonychus ulmi* (Koch); Sømme, 1965), and −32.2°C (eggs of *Bryobia arborea* M. & A.; Macphee, 1963, 1964). For the generally predacious mesostigmatid mites, few data on supercooling are available: −31.4°C for adult *Typhlodromus* spp. (Macphee, 1964) and −7.8°C for adult *Arctoseius ornatus* Evans (Block, 1979). In terms of possible cryoprotectants, whilst sorbitol has been shown to accumulate in overwintering eggs of *P.ulmi* (Sømme, 1965), the only compound frequently recorded has been glycerol. Concentrations of glycerol range from 8.6 to 50 $\mu g\ mg^{-1}$ fresh weight.

In general it seems that whilst freezing is lethal to both groups of micro-arthropods and survival at low temperatures is by supercooling, the latter process is aided in Collembola by sugars and possibly polyols other than glycerol and in the Acari mainly by polyols especially glycerol. The degree of supercooling point depression and the precise mechanism of cold hardening in both groups have yet to be investigated.

Acknowledgments

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References

Almquist, S. (1970) Thermal tolerances preferences of some dune living spiders. *O* 21, 230–236.

Ambach, W. (1961) Die Bedeutung des a frorenen Eises (superimposed ice) für den Ma und Energiehaushalt eines Gletschers. *Zeitsc für Gletscherkunde und Glazialgeologie*, 4, 1 189.

Baust, J.G. & Miller, L.K. (1970) Variatio glycerol content and its influence on cold h ness in the Alaskan carabid beetle, *Pterosti brevicornis*. *Journal of Insect Physiology*, 979–990.

Baust, J.G. & Miller, L.K. (1972) Influence of temperature acclimation on cold hardiness i beetle, *Pterostichus brevicornis*. *Journal Insect Physiology*, 18, 1935–1947.

Baust, J.G. & Morrissey, R.E. (1975) Supercoo phenomenon and water content independen the overwintering beetle, *Coleomegilla macu Journal of Insect Physiology*, 21, 1751–1754

Bean, R.C. & Porter, G.G. (1959) Detection differentiation of sugars and polyols on si paper chromatograms. *Analytical Chemistry*, 1929–1930.

Block, W. (1979) Cold tolerance of micro-art pods from Alaskan taiga. *Ecological Entomol* 4, 103–110.

Block, W., Young, S.R., Conradi-Larsen, E.M Sømme, L. (1978) Cold tolerance of Antarctic terrestrial arthropods. *Experientia*, 1166–1167.

Frankos, V.H. & Platt, A.P. (1976) Glycerol accu lation and water content in larvae of *Lime archippus*: their importance to winter surv *Journal of Insect Physiology*, 22, 623–628.

Macphee, A.W. (1963) The effect of low temp tures on some predacious phytoseiid mites, on the brown mite, *Bryobia arborea* M. & *Canadian Entomologist*, 95, 41–44.

Macphee, A.W. (1964) Cold hardiness, habitat winter survival of some orchard arthropod Novia Scotia. *Canadian Entomologist*, 96, 6 625.

Metzenburg, R.L. & Mitchell, H.K. (1954) Detec of periodate oxidisable compounds on p chromatograms. *Journal of the American Ch cal Society*, 76, 41–87.

Miller, L.K. (1969) Freezing tolerance in an a insect. *Science*, 166, 105–106.

Ohyama, Y. & Asahina, E. (1972) Frost resistanc adult insects. *Journal of Insect Physiology*, 267–282.

Salt, R.W. (1953) The influence of food on c hardiness of insects. *Canadian Entomologist*, 261–269.

Salt, R.W. (1958) Role of glycerol in produ abnormally low supercooling and freezing po in an insect, *Bracon cephi* (Gahan). *Nature*, 1281.

Salt, R.W. (1961) Principles of cold-hardi *Annual Review of Entomology*, 6, 55–74.

ıme, L. (1965) Changes in sorbitol content and ıupercooling points in overwintering eggs of the European red mite (*Panonychus ulmi* (Koch)). *Canadian Journal of Zoology*, 43, 881–884.

ıme, L. (1974) The overwintering of *Pelophila ɔorealis* Payk. III. Freezing tolerance. *Norwegian Journal of Entomology*, 21, 131–134.

ıme, L. (1976) Cold hardiness of winter-active Collembola. *Norwegian Journal of Entomology*, 23, 149–153.

ıme, L. (1978a) Notes on the cold hardiness of ɔrostigmate mites from Vestfjella, Dronning Maud Land. *Norwegian Journal of Entomology*, 25, 51–55.

ıme, L. (1978b) Cold hardiness of *Cryptopygus antarcticus* (Collembola) from Bouvetøya. *Oikos*, 31, 94–97.

me, L. (1979) Overwintering ecology of Alpine Collembola and oribatid mites from the Austrian Alps. *Ecological Entomology*, 4, 175–180.

Sømme, L. & Conradi-Larsen, E.M. (1977) Cold hardiness of collembolans and oribatid mites from windswept mountain ridges. *Oikos*, 29, 118–126.

Stenseth, C. (1965) Cold hardiness in the two-spotted spider mite (*Tetranychus urticae* Koch). *Entomologia Experimentalis et Applicata*, 8, 33–38.

Tanno, K. (1975) Supercooling in Arctic Collembola in early summer. *Low Temperature Science* (B), 33, 39–43.

Zachariassen, K.E. (1977) Effects of glycerol in freeze tolerant *Pytho depressus* L. (Col., Pythidae). *Norwegian Journal of Entomology*, 24, 25–29.

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LOW TEMPERATURE EFFECTS ON MICRO-ARTHROPODS

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ABSTRACT

main features of the cold hardiness strategies adopted by Antarctic terrestrial arthro-
s (principally Acari and Collembola) are reviewed. These include lethal low temperatures,
ll-coma temperature, supercooling ability, cryoprotectants and survival in anoxic condit-
s.

KEYWORDS

arctic arthropods; cold hardiness; supercooling; cryoprotection.

INTRODUCTION

mechanisms, both physiological and biochemical, by which arthropods survive sub-zero
peratures is of fundamental importance to their biology and ecology. The success of arth-
od groups such as the terrestrial Acari and Collembola is due, in no small measure, to
ir ability to resist cold conditions and to remain active at low environmental temperat-
s (Block, 1981). Such animals have been enabled thereby to colonize habitats as varied
as extreme as polar and alpine tundra. This short review considers the effects of low
peratures, especially in the sub-zero range, on Antarctic micro-arthropods, and summarizes
main features of the cold hardiness strategies that have been found.

REVIEW

d hardiness may be defined as the ability of an organism to resist temperatures which
ld normally be lethal. An invertebrate poikilotherm has two options in this respect:
ıer to avoid freezing or to minimize damage to cells and tissues during the freezing pro-
s. The former species are termed "freezing-susceptible" and avoid freezing, which is al-
s lethal, by supercooling, i.e. the maintenance of their body fluids in a liquid state
ow the solution freezing point. Supercooling in such animals may be enhanced by solutes
luding polyhydric alcohols and sugars, and body temperatures of c. -40°C may be reached
ore freezing occurs. The other group of species are termed "freezing-tolerant", and sur-
e extra-cellular freezing in the supercooled condition. Freezing in such animals occurs
relatively high sub-zero temperatures (-5° to -12°C) and ice nucleators may promote it.
ols such as glycerol may afford freezing tolerant species protection by reducing cell
age. Early work on arthropod cold hardiness is reviewed by Salt (1961) and Asahina
59), whilst Meryman (1966) reviews biological freezing. Excellent reviews of recent in-
t work are provided by Ring (1980) and Baust (1981).

ly research was concentrated on insects, and examined species from the Arctic, sub-Arctic
Canada. Preliminary studies on Antarctic arthropods were concerned with upper and lower
ıal temperatures. Studies of the survival mechanisms in these animals have been under-
en only recently, and Block, et al., (1978) and Sømme (1978a, b) working on micro-
ıropods were the first to examine supercooling potential and cryoprotectants. Supercool-
ability is normally assessed by measurement of the individual's supercooling point
west body temperature reached at which spontaneous freezing occurs) using standard cooling
ımes (usually 1°C min^{-1}). Cryoprotectants are assayed by various chromatographic methods
luding ascending paper, thin layer (TLC) and gas-liquid (GLC) techniques.

liminary observations indicated that the cryptostigmatid mite Maudheimia wilsoni could
rive temperatures as low as -30°C, and Dalenius (1965) suggested that locomotion and

possibly breeding occurred in sub-zero conditions. Pryor (1962) demonstrated that the let cold temperature for adults of the collembolan Isotoma klovstadi from north Victoria Land between -50° and -60°C. Another springtail, Gomphiocephalus hodgsoni from the McMurdo are is less cold hardy and dies between -20° and -28°C (Janetschek, 1967). Fitzsimons (1971) found no evidence in G. hodgsoni and the prostigmatid mite Stereotydeus mollis that the pr sence of food in the gut inhibits cold hardiness, but conversely that starved specimens su cumbed to cold more quickly than well-fed animals. When supercooled to -11°C G. hodgsoni froze when touched with ice, while animals in ice-free containers survived for longer at this temperature. Using adult Stereotydeus villosus and cooling rates of c. 3°C h^{-1}, Grah (1974) examined their survival after 12h exposure to a range of sub-zero temperatures. Mortality increased below -8°C and at -16°C all were dead. Activity of Nanorchestes antarcticus at low temperatures was observed by Rounsevell (1977).

Working with two species of Antarctic micro-arthropods (Alaskozetes antarcticus and Cryptopygus antarcticus), Block, et al., (1978) showed that both were able to supercool to -30°C, but full realisation of this potential was dependent on starvation. Additionally, the mite, A. antarcticus contained glycerol in a concentration of c. 1% (c. 10µg mg^{-1}) of fresh weight, when acclimated at 0°C for one week. No glycerol was detected in the collem bolan. Field-fresh specimens of the mites Eupodes tottanfjella and Nanorchestes spp. in t Vestfjella, Dronning Maud Land had supercooling points between -20° and -30°C, and were freezing-susceptible (Sømme, 1978a). Extending the work on C. antarcticus, Sømme (1978b) found that Bouvetøya specimens supercooled to c. -25°C, and acclimation to -5°, 0° and 12° for various times had no affect. Glycerol was not found and all specimens were freezing-susceptible. The only freezing-tolerant Antarctic species, the chironomid Belgica antarct has been studied at Palmer Station, Antarctic Peninsula, by Baust (1980) and Baust & Edwa (1979). Only larvae are freezing-tolerant during the austral summer and possess several cryoprotectants including erythritol, glucose, sucrose and trehalose. Adults are freezing-susceptible and contain only trace quantities of these substances. Larval feeding experi ments using artificial diets suggested that cryoprotectant profiles were directly dependen on food source and temperature. Adults and larvae had mean supercooling points of -5.3° -5.7°C respectively. Thus both freezing-susceptible and freezing-tolerant strategies hav been adopted by Antarctic land arthropods.

Using cultured Alaskozetes antarcticus from Signy Island, maritime Antarctic, the mechani of cold tolerance has been investigated (Young, 1979; Young & Block, 1980), and freezing found to be fatal for all life stages. Glycerol was the major compound involved in its c hardiness, where it occurred in average concentrations of up to 50µg mg^{-1} water (=0.55g m cules kg^{-1} water). Individual supercooling points were as low as -31°C, but feeding detr ted from this ability by providing ice nucleators in the gut which initiated freezing at relatively high sub-zero temperatures (-2° to -20°C). This degree of cold hardiness woul be insufficient at times in winter and in a climatically severe autumn. Supercooling is enhanced by glycerol, and an inverse, linear relationship between its concentration and m supercooling point was demonstrated. Low temperature acclimation increased glycerol conc rations and suppressed feeding, whilst desiccation appeared to stimulate glycerol synthes This was the first report of such an effect on poikilotherm cold hardiness. Differences photoperiod had no effect on cold tolerance. Much of the additional cold hardiness of A. antarcticus is built up during two phases in the autumn period. First, when mean dail ground surface temperatures are close to 0°C for c. one month and oscillations are minima (Walton, 1977), and secondly, when mean daily temperatures occur between 0° and -10°C at onset of winter (although daily minima may be lower). During this period feeding suppres and gut evacuation is more important than supercooling point depression, but, as sub-zero conditions continue in early winter, glycerol production enhances survival. Low relative atmospheric humidities may occur in its habitats before a snow cover develops, and the gl cerol accumulation that accompanies desiccation will play a crucial role in overwintering The nymphal stages of A. antarcticus possess a greater degree of low temperature toleranc than the adults. Although glycerol is the main polyol, ribitol, arabitol, xylitol, manni inositol, rhamnitol and fucitol are found also. Juvenile Collembola of several Alpine sp ies are more cold hardy than the adults and sugars such as glucose may aid supercooling (Block & Zettel, 1980). Juvenile micro-arthropods appear to have a greater safety margin than adults, but why this should occur in A. antarcticus, where all stages overwinter, ca be explained at present.

Micro-arthropods acclimatized to Antarctic summer conditions have been investigated at Si Island, maritime Antarctic (Block & Sømme, 1981; Sømme & Block, 1981). Four species of A (two prostigmatids, one each of mesostigmatid and cryptostigmatid) and two Collembola (bo species of Isotomidae) were studied by means of field samples and long-term acclimation e periments. Mean supercooling points ranged from -6° to -29°C (Acari) and from -5° to -21 (Collembola), and individual supercooling points of field samples were bimodally distribu on the basis of gut contents, the division occurring between -15° and -20°C. In most spe ies, starvation and/or low temperature exposure lowered the mean supercooling point, whi was related to an increase in concentration of glycerol in the body. However, other poly and sugars (mannitol, ribitol, glucose and trehalose) were detected in what clearly is a multicomponent cryoprotectant system. In Collembola particularly, the type of food mate

s critical in terms of its nucleating capacity. Chill-coma temperatures (level at which comotion ceases) varied between species from -4° to -8°C, and survival in anoxic conditions N_2 differed considerably with two species being much more resistant than the others. Seanal changes in cold hardiness of such animals is likely to be of major importance to their rvival, and current Antarctic research is aimed at correlation of the physiological and ochemical parameters underlying this with micro-climatic and other environmental changes their terrestrial habitats.

ycerol and other solutes lower the homogeneous nucleating temperature of water, but in imals, nucleation is mainly heterogeneous, i.e. foreign particles act as centres for ice ystal formation (Salt, 1961). Comparison of the effect of glycerol on the heterogeneous cleation temperature of individual A. antarcticus and small distilled water droplets lock & Young, 1979) suggests that a given quantity of glycerol depresses the supercooling int more than it does the melting point. The effect is more marked in the mites, where e supercooling point is lowered by more than twice the melting point depression at any ven glycerol concentration. This is of considerable adaptive significance in cold-tolerant cro-arthropods. Supercooling in aqueous solutions in the absence of anti-freeze compounds limited, and synthesis of these compounds may be metabolically costly. If temperatures uctuate around 0°C for long periods of time, it will be advantageous to avoid repeated eezing and thawing of the body, and supercooling would be the optimal strategy. However, ring exposure to positive temperatures, feeding will occur, and food in the gut will prote nucleation when the temperature declines below zero. The balance resulting from the ed, on the one hand, to avoid freezing, and on the other, to ingest food to provide energy r growth, etc. may be crucial in such poikilotherms.

e distribution of the two strategies of cold hardiness in the Antarctic land fauna is interting, in that the majority of the arthropods investigated have adopted the freezing-sceptible-supercooling approach in common with many northern species. It is significant at the only Antarctic form which is freezing-tolerant is also the largest, and only its rvae possess this ability. In the Arctic, adult insects may be freezing-tolerant, e.g. an askan carabid beetle (Miller, 1969). Investigations of other polar soil invertebrates may eld other freezing-tolerant forms, and there is a need for a wider study of both the mechisms themselves and their biochemical bases (Baust, 1981). Cold hardiness is not limited ly to species inhabiting low temperature environments (Sømme, 1979) and cold resistance has en reported in desert centipedes and scorpions (Crawford & Riddle, 1974), in a temperate te (Young, 1980) and in tropical arthropods (Cloudsley-Thompson, 1973).

REFERENCES

ahina, E. (1969). Frost resistance in insects. Adv. Insect Physiol., 6, 1-49.

ust, J. G. (1980). Low temperature tolerance in an Antarctic insect: a relict adaptation? Cryo-Letters, 1, 360-371.

ust, J. G. (1981). Biochemical correlates to cold hardening in insects. Cryobiology, 18, 186-198.

ust, J. G. and J. S. Edwards (1979). Mechanisms of freezing tolerance in an Antarctic midge, Belgica antarctica. Physiol. Entomol., 4, 1-5.

ock, W. (1981). Terrestrial arthropods and low temperature. Cryobiology, 18, 1-9.

ock, W. and L. Sømme (1981). Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. Oikos, in press.

ock, W. and S. R. Young (1979). Measurement of supercooling in small arthropods and water droplets. Cryo-Letters, 1, 85-91.

ock, W., S. R. Young, E. M. Conradi-Larsen and L. Sømme (1978). Cold tolerance of two Antarctic terrestrial arthropods. Experientia, 34, 1166-1167.

ock, W. and J. Zettel (1980). Cold hardiness of some Alpine Collumbola. Ecol. Entomol., 5, 1-9.

awford, C. S. and W. A. Riddle (1974). Cold hardiness in centipedes and scorpions in New Mexico. Oikos, 25, 86-92.

lenius, P. (1965). The acarology of the Antarctic regions. Monographiae biol., 15, 414-430.

tzsimons, J. M. (1971). Temperature and three species of Antarctic arthropods. Pacif. Insects Monogr., 25, 127-135.

aham, W. L. (1974). Arthropods near Palmer Station, Anvers Island. Antarct. J. U.S., 9, 306-307.

netschek, H. (1967). Arthropod ecology of South Victoria Land. Antarct. Res. Ser. (Am. Geophys. U.), 10, 205-293.

ryman, H. T. (1966). Review of biological freezing. In H. T. Meryman (Ed.), Cryobiology, Academic Press, London and New York. pp. 1-114.

ller, L. K. (1969). Freezing tolerance in an adult insect. Science, N. Y., 166, 105-106.

yor, M. E. (1962). Some environmental features of Hallet Station, Antarctica, with special reference to soil arthropods. Pacif. Insects, 4, 681-728.

Ring, R. A. (1980). Insects and their cells. In M. J. Ashwood-Smith and J. Farrant (Eds.
Low temperature preservation in Medicine and Biology, Pitman Medical, Tunbridge Wells.
pp. 187-217.
Rounsevell, D. E. (1977). The ecology of the pan-Antarctic mite Nanorchestes antarcticus
(Strandtmann). In G. A. Llano (Ed.), Adaptations within Antarctic ecosystems, Gulf Pu
Co., Houston. pp. 1023-1033.
Salt, R. W. (1961). Principles of insect cold-hardiness. A. Rev. Ent., 6, 55-74.
Sømme, L. (1978a). Cold hardiness of Cryptopygus antarcticus (Collembola) from Bouvetøya.
Oikos, 31, 94-97.
Sømme, L. (1978b). Notes on the cold-hardiness of prostigmate mites from Vestfjella, Dron
ing Maud Land. Norw. J. Entomol., 25, 51-55.
Sømme, L. (1979). Overwintering ecology of alpine Collembola and oribatid mites from the
Austrian Alps. Ecol. Entomol., 4, 175-180.
Sømme, L. and W. Block (1981). Cold hardiness of Collembola at Signy Island, maritime Ant
arctic. Oikos, in press.
Walton, D. W. H. (1977). Radiation and soil temperatures 1972-74: Signy Island terrestri
reference sites. Br. Antarct. Surv. data 1.
Young, S. R. (1979). Aspects of the environmental physiology of an Antarctic terrestrial
mite. Ph. D. thesis, University of Leicester, pp. 1-208.
Young, S. R. (1980). Cold hardiness in a temperate cryptostigmatid mite. Oikos, 35, 350-
352.
Young, S. R. and W. Block (1980). Experimental studies on the cold tolerance of Alaskozet
antarcticus. J. Insect Physiol., 26, 189-200.

ew Trends in Soil Biology

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Low temperature tolerance of soil arthropods — Some recent advances

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mmary :

Information on the effects of cold and freezing on soil arthropods and on their cold resistance mecha- ms is reviewed. Recent studies on selected Arctic and Antarctic species is summarised comparatively. The urrence of two survival strategies (freezing susceptible and freezing tolerant) is discussed, and the impor- ce of an ecophysiological approach in such studies is emphasized.

y words : freezing tolerance, freezing susceptibility, supercooling.

I. Introduction

The thermal tolerances of soil invertebrates have received increasing attention the past decade, and adaptations to low temperature have been particularly investig ted. Most attention has been given to terrestrial arthropods, and especially to t Insecta and Acari, which are major components of soil ecosystems throughout t world. Low temperature affects soil arthropods in a variety of ways, influencing th development and life cycles, their colonisation and survival of extreme environmen and their population and community dynamics. This paper summarises current info mation on low temperature tolerances of soil arthropods and focuses on the ecoph siological approach to problems in this field.

II. Effects of cold and freezing

Low environmental temperatures create two major stresses for soil arthropods (i) reduction of activity, feeding and growth through cold, and (ii) increasing the pr bability of tissue freezing.

Cold shock results in a general metabolic deceleration as well as having reversib effects on cell membranes. Locomotory activity is reduced by cold (non-freezing te peratures) and results, eventually, in chill-coma, at which temperature mobility ce ses. This is usually in the region of 5 to *ca* 15° C for temperate soil species, and may as low as -8 to -11° C for polar forms. Although soil arthropods are immobilis during chill-coma, internal changes may occur which are normally completely rever ble.

However, irreversible disturbances (cold injury) may occur above the freezi point (FPt) of the body fluids due to disruption of weak chemical bonds, damage membrane lipids, etc. Such changes are likely to be brought about by desynchroni tion of physiological processes arising from a lack of, or incomplete, acclimati (laboratory) or acclimatisation (field).

The body fluids (haemolymph, etc.) often remain in the liquid phase to tempe tures well below their FPt, already depressed by dissolved solutes, a phenomenon t med supercooling (or undercooling). Many soil arthropods are able to supercool

ɔund -30° C to avoid freezing in nature. The temperature at which freezing occurs by ıpid ice nucleation in the supercooled body is the supercooling point (SCP), and may e detected by a transitory increase in body temperature due to the latent heat of ısion during freezing.

The site of freezing is critical to soil invertebrates; extracellular ice being sustained 'hereas intracellular ice is usually lethal. Tissue ice brings about mechanical damage ɔ cell membranes and reduces gaseous diffusion in and out of cells. The minimum cri- cal cell volume is exceeded through dehydration and cell shrinkage, with membrane ıpture and protein denaturation occurring. Concomitant with such effects, an ıcrease in solute concentration may cause electrolyte imbalance leading to osmotic isruption and denaturation of membranes, enzymes, etc. Finally, there is the additio- al stress of ice recrystallisation during thawing from the frozen state.

II. Mechanisms of cold resistance

Ice nucleation may be homogeneous, involving only water molecules, or hetero- :neous, when ice crystals form around a foreign body. Heterogeneous nucleation :curs in invertebrates down to *ca* -40° C, and many potential sources of nuclei occur soil arthropods to promote freezing during supercooling. Two main strategies of ɔld resistance are utilized by poikilotherms : that of freezing susceptibility and free- ng tolerance. Species using the former, resist tissue ice formation by supercooling ıd FPt depression, whilst those in the latter group freeze at relatively high sub-zero mperatures, often employing nucleators synthesized for the purpose.

The FPt and melting point (MPt) of haemolymph may occur at the same tempe- ture (for arthropods in the zone 0 to *ca* -2° C) or the FPt may be depressed down to -10° C relative to the MPt. The latter situation is termed thermal hysteresis, and it ıs been shown that it is brought about by proteins (termed thermal hysteresis pro- ins or THP) (DUMAN, 1979a, b). THP may vary seasonally, thereby affording the thropod protection during low temperature periods. THP may also act to stabilize percooling over a wide temperature range in freezing susceptible animals (ZACHA- [ASSEN & HUSBY, 1982). The deepest extent of supercooling has been recorded as 3° C in a willow gall dipteran (MILLER & WERNER, 1980). It is generally recogni- d that supercooling is enhanced by polyhydric or sugar alcohols (polyols) in arthro- ɔds and other invertebrates, and glycerol is common in the species which have been vestigated. In some freezing tolerant insects, ice nucleating proteins (INP) promote :ezing by heterogeneous nucleation (ZACHARIASSEN & HAMMEL, 1976).

V. Antarctic and Arctic studies

Freeze avoidance by extensive supercooling is a widespread survival strategy of ılar terrestrial arthropods, especially in species which have a slower rate of develop-

ment due to the constraints of a low temperature environment (BLOCK, 1980). In t
Antarctic, individual SCP distributions of six species of micro-arthropod showed
bimodality in that a high group (HG) at –10 to –15° C, and a low group (LG) at abo
–25 to –30° occurred in most species during the year (BLOCK *et al.*, 1982).
small number of individuals in these populations die during winter, especially duri
rapid freeze-thaw cycles, which induce feeding and hence nucleation via gut conten
All the species showed a lowering of the mean LG SCP during winter associated wi
strong seasonal shifts in the SCP distributions. Five potential cryoprotectants we
elaborated in these animals with glycerol being the most frequent in occurrence and
the highest concentration. In the cryptostigmatid mite, *Alaskozetes antarctic*
increasing glycerol levels up to *ca* 20 μg mg^{-1} fresh weight were correlated with depre
sion of the mean LG SCP from –25 to –35° C, and this in turn was reflected in cha
ging glucose levels. All the species investigated at Signy Island, maritime Antarcti
except the collembolan *Parisotoma octooculata*, possess a high capacity for superco
ling and thereby ensuring that large proportions of their populations survive t
extreme low winter temperatures (–20 to –28° C) in their soil habitats.

A survey of terrestrial arthropods shows supercooling to be a common form
cold tolerance, and SØMME (1982) concluded that insect eggs supercool slightly be
ter than other life stages and other groups. Larval Diptera are amongst the high supe
cooling capacity arthropods, whilst some of the Araneida exhibit least supercoolin

By contrast, in nine species of Arctic insects, including Coleoptera, Dipter
Lepidoptera and Hymenoptera, six species proved to be freezing tolerant, the remai
der were freezing susceptible (RING, 1981). Most insects showed the expected pro
les of overwintering response during low temperature acclimation, although only o
polyol appeared to be synthesized in any one species. In the freezing tolerant bee
larvae, *Pytho deplanatus*, from an alpine habitat, moderate glycerol levels and de
supercooling (to –54° C) were demonstrated. Whether this species is physiological
and biochemically incapable of synthesizing INP and natural nucleators are abse
from the body in winter remains to be tested. Marked differences in the cold hardine
of phylogenetically closely related forms suggest that the mechanisms of cold resi
tance have evolved independently on several different occasions. This contention
supported by the results of Antarctic micro-arthropod studies (BLOCK & SØMM
1982; SØMME & BLOCK, 1982; BLOCK *et al.*, 1982).

Examination of the distribution of the two survival strategies throughout the te
restrial invertebrates (BLOCK, 1982) reveals that in 17 taxonomic groups, seven a
freezing susceptible, four are freezing tolerant whilst six taxa contain representativ
from both types. In the arthropods, the higher insect orders Lepidoptera, Dipte
Hymenoptera and Coleoptera contain species which have adopted either strategy.

V. Conclusions

Soil insects are the highest taxon and also the largest invertebrates to survive freeing in their natural habitats. Many of them survive freezing temperatures over long periods of time, and as their cellular organisation is as complex as any other metazoan, the study of such adaptations is of considerable theoretical and practical importance. In the union of ecological and physiological studies, there is a powerful tool for the solution of the more important problems in the field of poikilotherm cold tolerance. The adaptations of soil animals may be viewed as biological solutions to problems posed by their environment. In ecophysiology we are unravelling the answers which have been fashioned by natural selection during evolution.

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References

LOCK (W.), 1980. — Survival strategies in polar terrestrial arthropods. — *Biological Journal of the Linnean Society*, **14** : 29-38.
LOCK (W.), 1982. — Cold hardiness in invertebrate poikilotherms. — *Comparative Biochemistry and Physiology*, **73A** : 581-593.
LOCK (W.) & SØMME (L.), 1982. — Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. — *Oikos*, **38** : 157-167.
LOCK (W.), WORLAND (M.R.) & RICHARD (K.J.), 1982. — Seasonal variation in cold resistance of Antarctic land arthropods. — *Cryo-Letters*, **3** : 308.
UMAN (J.G.), 1979a. — Sub-zero temperature tolerance in spiders. The role of thermal hysteresis factors. — *Journal of Comparative Physiology*, **131** : 347-352.
UMAN (J.G.), 1979b. – Thermal hysteresis-factors in overwintering insects. – *Journal of Insect Physiology*, **25** : 805-810.
ILLER (L.K.) & WERNER (R.), 1980. — Supercooling to –60° C : an extreme example of freezing avoidance in northern willow gall insects. — *Cryobiology*, **17** : 621-622.
ING (R.A.), 1981. — The physiology and biochemistry of cold tolerance in Arctic insects. — *Journal of Thermal Biology*, **6** : 219-229.
ØMME (L.), 1982. — Supercooling and winter survival in terrestrial arthropods. — *Comparative Biochemistry and Physiology*, **73A** : 519-543.
ØMME (L.) & BLOCK (W.), 1982. — Cold hardiness of Collembola at Signy Island, maritime Antarctic. — *Oikos*, **38** : 168-176.
ACHARIASSEN (K.E.) & HAMMEL (H.T.), 1976. — Freeze-tolerance in adult tenebrionid beetles. — *Norwegian Journal of Zoology*, **24** : 349-352.
ACHARIASSEN (K.E.) & HUSBY (J.A.), 1982. — Antifreeze effect of thermal hysteresis agents protects highly supercooled insects. — *Nature* (London), **298** : 865-867.

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HYADESIA MAXIMA sp. n. (Acari, Hyadesiidae) FROM SOUTH GEORGIA*

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The new species of *Hyadesia, H. maxima* sp. n., that we describe here occurs abundantly in the inter-tidal zone of South Georgia, in the sub-Antarctic. Mites of the family Hyadesiidae (Astigmata) have not previously been recorded from South Georgia. These mites, however, are well represented in several other islands of the sub-Antarctic region. Five species, all belonging to the genus *Hyadesia,* have been described from three of these islands. Among them three species (*H. kerguelenensis* (LOHMANN), *H. subantarctica* FAIN and *H. halophila* FAIN) are known from Iles Kerguelen ; one (*H. paulensis* FAIN) from St. Paul Is. and one (*H. travei* FAIN) from St. Paul Is. and Nouvelle-Amsterdam.

It is to be noted that Hughes (1970) described a new species of mite from South Georgia (*Neocalvolia claggi*) belonging also to the Astigmata but to the family Saproglyphidae.

HYADESIIDAE

Hyadesia MEGNIN, 1891

Hyadesia maxima sp. n.

FEMALE (fig. 1-5) : Holotype 870 μ long (idiosoma) and 620 μ maximum width (non gravid). Measurements in four non gravid

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paratypes : 810 × 600 μ ; 840 × 580 μ ; 900 × 600 μ ; 990 × 690 μ ; in five larvigerous paratypes 915 × 630 μ (containing 1 larva) ; 960 × 690 (containing 2 larvae) ; 978 × 690 μ (with 2 larvae) ; 1110 × 840 μ (with 7 larvae) : 1164 × 750 μ (with 2 larvae). *Dorsum* : Cuticle soft except in anterior part of

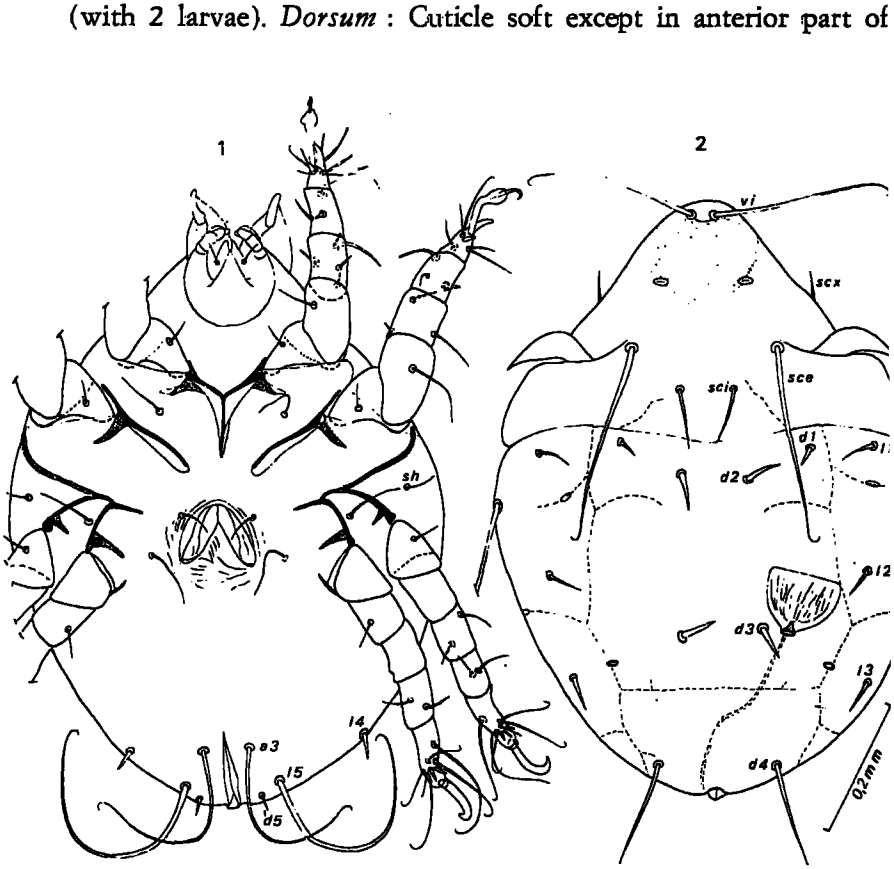

FIG. 1-2. — *Hyadesia maxima* sp. n. Holotype female in ventral (1) and dorsal (2) view.

propodosoma bearing a punctate shield slightly wider (165 μ) than long (124 μ). In two paratypes the measurements (length × width) of this shield are : 105 μ × 135 μ ; 120 μ × 150 μ. Copulatory pore situated not far from the posterior extremity (in a paratype at 60 μ). *Venter* : Sternum 90 μ long. Epimeres II free. Epimeres III-IV fused. Anus vetro-terminal. *Legs* : Tarsi I-IV 53 μ - 61 μ - 89 μ - 100 μ long (pretarsi and spines not included). Claws I-II

25 μ, pretarsi 90 μ ; claws III-IV 75 μ, pretarsi 39 μ. Gnathosoma 158 μ long, 130 μ maximum width (palps included). Grandjean's organ curved, relatively short with bifid apex.

Chaetotaxy : Setae *vi* 255 μ, *sc x* thin, 45-55 μ ; *sc i* relatively thin and attenuated apically, incomplete in holotype, in paratypes 90 μ ;

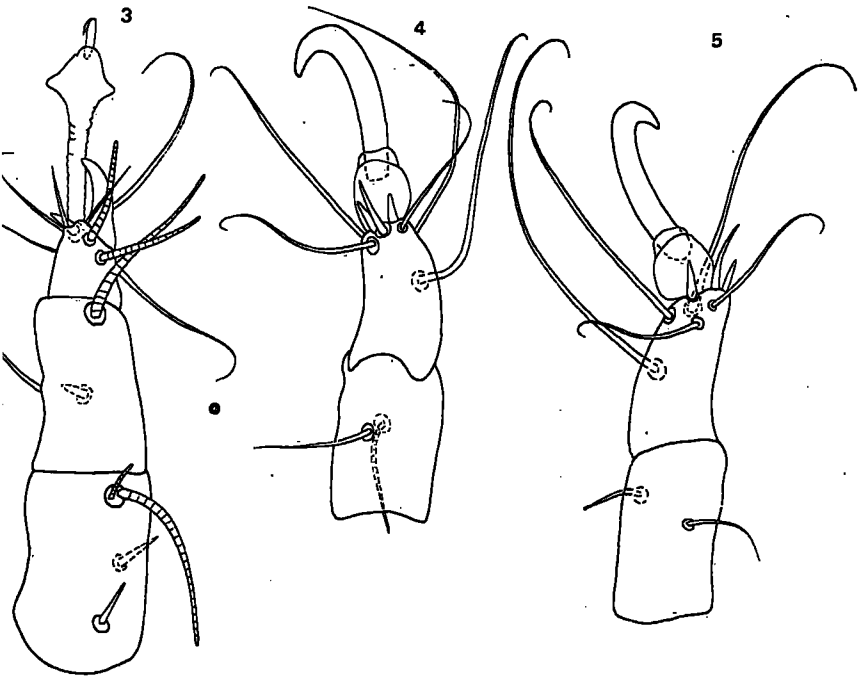

FIG. 3-5. — *Hyadesia maxima* sp. n. Holotype and paratype female : Tarsus, tibia and genu I dorsally (3) ; tarsus and tibia III (4) and IV (5).

sc e 300 μ ; *d 1* a thin spine, 30 μ ; *d 2* and *d 3* spinous, 45 μ ; *d 4* strongly attenuated at apex, 130 - 160 μ ; *d 5* is a thin spine, 30 μ ; *l 1, l 2, l 3* and *l 4* spinous and 45-60 μ long ; *l 5* 420 μ ; *a 3* 330-350 μ ; *h* 280 μ ; *sh* 27 μ. There are two pairs of thin genital setae (40 μ and 66 μ). The setae *vi, sc e, h, l 5* and *a 3* end in a hook.

Leg chaetotaxy : Tarsi I-II with a strong apical and a small subipicoventral spine, 5 thin setae. Tarsi III-IV with 3 subapico-ventral spines and 5 thin setae. Ventral seta of tibiae III-IV, thin and flexible. *Solenidiotaxy* : Tarsus I : *ω 1* 53 μ, *ω 3* 46 μ. Genu I with two solenidia (21 μ and 90 μ long respectively).

MALE (fig. 6-7) : A paratype is 920 μ long (idiosoma) and 625 μ wide. In two other paratypes : 840 × 600 μ and 978 × 660 μ. Dorsum as in female. Propodonotal shield 120 μ long and 150 μ wide. *Venter* : Sternum fused with epimeres II. Genital organ

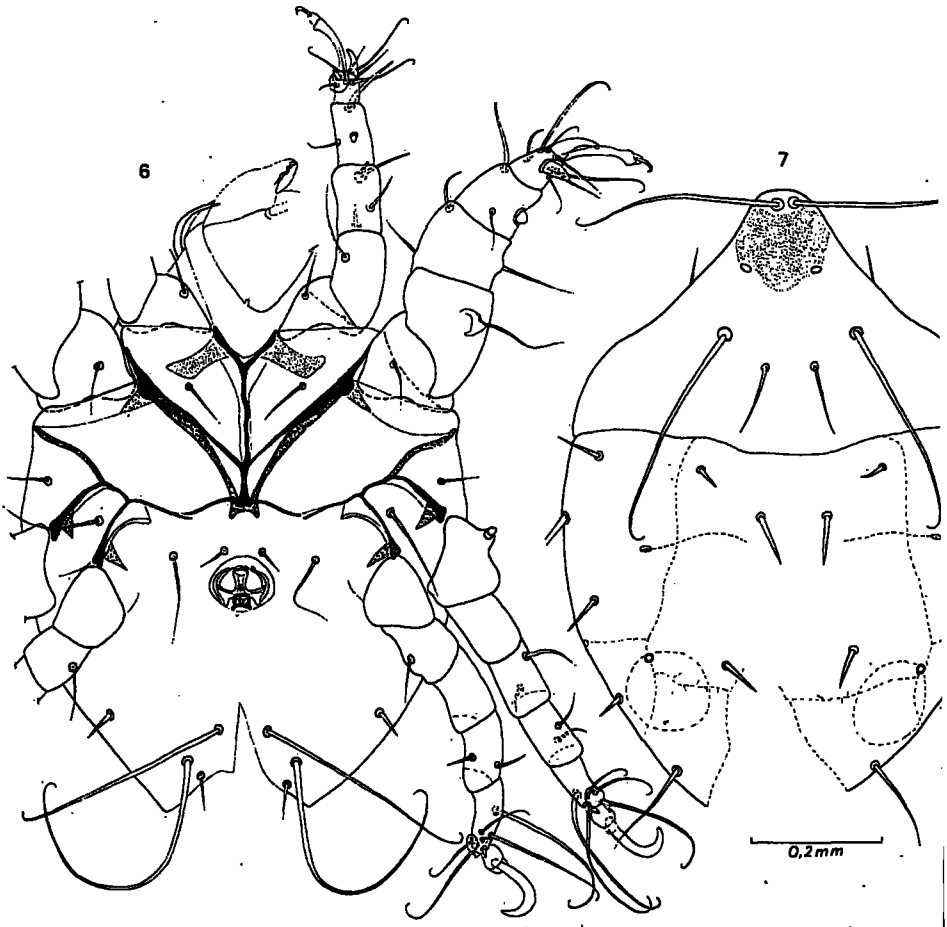

FIG. 6-7. — *Hyadesia maxima* sp. n. Male in ventral (6) and dorsal (7) view.

strongly rounded laterally, 90 μ wide. Genital setae thin, 35 μ and 120 μ respectively. *Legs* : The legs II are very strongly inflated and slightly modified : the tibia bears a short and a thick rounded spine, femur with a ventral rounded process bearing a thin seta.

Tarsi I-IV 66 μ - 84 μ 117 μ - 120 μ long (pretarsi and spines not included). The trochanter III is produced ventrally where it bears a short thick rounded seta. Tarsi I-III and IV with a ventro-apical sucker (copulatory suckers). Gnatosoma as in the female.
TRITONYMPH : 595 μ long and 420 μ wide. General characters as in female. Vulva lacking. Dorsal and ventral setae shorter than in female.

REMARK :

H. maxima is the largest species of the family Hyadesiidae. It is closest to *Hyadesia travei* Fain, 1975, described from St. Paul Is. and New-Amsterdam Is. It is however distinguished from that species by the following characters (in both sexes) :

1. Much larger size of the body.
2. Propodonotal shield shorter and narrower. The shield is always distinctly wider than long. In *H. travei* this shield is always longer than wide (in both sexes).
3. Grandjean's organ distinctly longer.
4. Setae *sc i* thinner and longer (90 μ). In *H. travei* this seta is a spine 40 μ long.
5. Setae *d 4* is much longer (130 to 160 μ) and progressively attenuated apically. In *H. travei* this seta is a short spine 45 μ long.
6. Setae *a 3* and *l 5* longer.
7. Posterior claws more curved.
8. Male : leg II more inflated and with the ventral spine of tibia modified (very short and rounded). In *H. travei* this leg is much less inflated and the ventral spine of tibia II is normal.

LOCATION :

Holotype and 25 paratypes female, 15 paratypes males and 30 paratypes nymph all from the Sub-Antarctic island of South Georgia. The mites were collected at Maiviken and Sooty Bluff, February 1982.

ECOLOGY :

The mites are found in small rock crevices in the upper part of the inter-tidal zone, where they presumably feed on green marine algae. With the changing tides the species is exposed to a variety of unfavourable conditions. At low tide they must tolerate heat and desiccation during summer, and enclosure by ice in winter. At all seasons they are submerged in sea water at high tide, which may result in an oxygen deficiency. During the winter the mites are exposed to subzero temperatures when the water is low. From laboratory studies (Block & Sømme, in prep.) it appears that nymphs and adults of *H. maxima* are well adapted to survive all these adverse conditions.

In the laboratory 90 percent of nymphs and adults survived 12 hr in a dry atmosphere, and 50 percent survived 24 hr in a saturated atmosphere at 35° C. About 60 percent of the mites survived submergence in sea water for three weeks at room temperature, while higher mortalities were recorded in fresh water.

The mites are susceptible to freezing, but have individual supercooling points in the range of — 9° to — 29 ° C even in summer. More than half of them survived 8 days in contact with frozen sea water at — 5° C, indicating that freezing by inoculation may occur at a slow rate.

To simulate the possible oxygen deficiencies during submergence in water and ice enclosure, the mites were stored at 0° C in sealed tubes filled with nitrogen. About 35 percent survived 8 days and 65 percent 16 days under these conditions.

Bibliography

BLOCK W. & SØMME L. (in prep.). Ecophysiology of two inter-tidal mites at South Georgia.

FAIN A., 1975. — Acariens récoltés par le Dr. J. Travé aux îles subantarctiques. I. Familles Saproglyphidae et Hyadesidae (Astigmates). *Acarologia,* XVI (4) : 684-708.

FAIN A., 1975. — Deux nouvelles espèces du genre *Hyadesia* récoltées par le Dr. J. Travé aux îles Saint-Paul et Nouvelle-Amsterdam (Astigmates : Hyadesidae). *Acarologia,* XVII (1) : 153-159.

FAIN A., 1981. — Notes on the Hyadesiidae Halbert, 1915 and Algophagidae Fain, 1974, nov. tax. (Acari, Astigmata) with a redescription of *Hyadesia curassaviensis* VIETS, 1936 and H. *sellai* VIETS, 1937. *Acarologia,* XXII (1) : 47-61.

HUGHES A.M., 1970. — Acarina : Astigmata : Saproglyphidae of South Georgia. *Pacific Insects Monograph,* 23 : 153-160.

arctica

urvival on land

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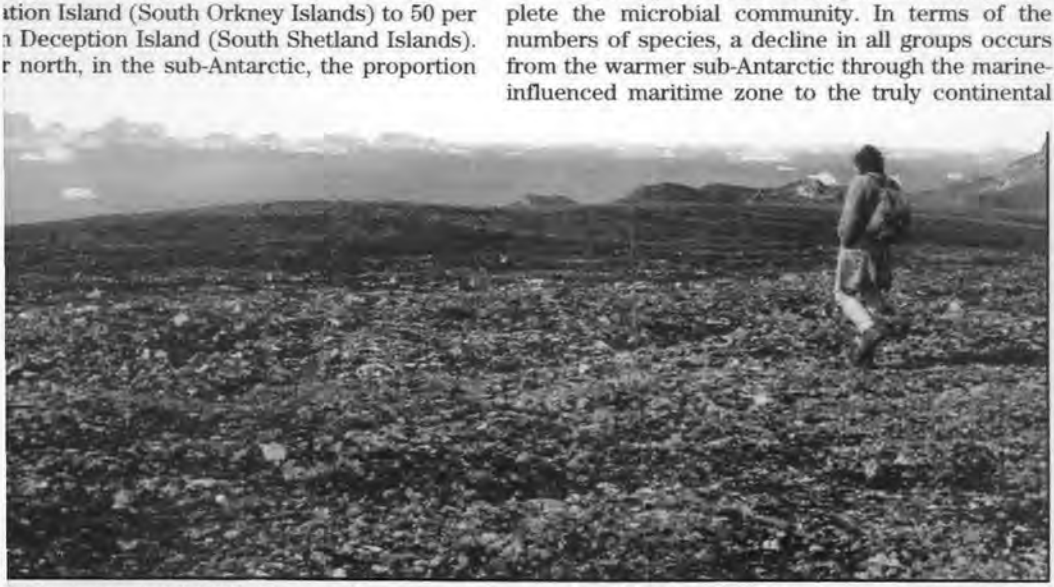
ıtrial life in Antarctica (area of 13.9 million s confined to only about 2 per cent of the vast ent, which is not covered by permanent ice now. The extent of snow-free land varies y between years, and is at a maximum in er (December-February). On the Antarctic ent there are three main types of ice-free d (Walton, 1984): (1) permanent snow-free with little or no precipitation, such as the Dry s in Victoria Land; (2) areas experiencing snow that melts in summer, thereby provid- ential water for a variety of organisms, such Bunger Oasis (Wilkes Land) and the locality rmachervatna (Enderby Land); (3) exposed aces on isolated mountains that are sur- ed by ice, such as nunataks of the Vestfjella efront Range) in Dronning Maud Land. On the ne Antarctic islands, snow- and ice-free land mer varies greatly in area between locations, ample from 5 per cent of the total area of ation Island (South Orkney Islands) to 50 per n Deception Island (South Shetland Islands). r north, in the sub-Antarctic, the proportion of snow-free land ranges from about 15 per cent (Heard Island) to complete exposure in summer (Macquarie Island). Thus although the area of terrestrial habitats is very small for the size of the southern continent, the diversity of habitats is relatively high and an amazing range of organisms has colonized them.

Such snow- and ice-free areas may be considered as oases because they not only provide suitable substrata for life, but liquid water becomes available for at least part of the summer. This factor, linked to thermal microclimates that allow biological activity, largely controls the distribution and development of populations and communities on land in Antarctica.

There are no true land vertebrates in Antarctica. The terrestrial fauna consists entirely of invertebrates, ranging from protozoans to arthropods (mites, springtails, and a dipteran). Mosses and lichens dominate the macroflora, whereas microalgae, fungi, and yeasts comprise the microflora. Bacteria, many of them cosmopolitan forms, complete the microbial community. In terms of the numbers of species, a decline in all groups occurs from the warmer sub-Antarctic through the marine-influenced maritime zone to the truly continental



l. The Antarctic fellfield habitat – a discontinuous community of lichens and mosses on a stony substrate. sland, South Orkney Islands.

Antarctic. Table 1 is a collation of information on the numbers of plants and invertebrates in the three ecological zones (after Block, 1984; after Smith, 1984). Restricting ourselves to the maritime and continental zones the importance of lichens (125–150 species) and mosses (30–75 species) in the plant communities can be appreciated, whereas among free-living arthropods the mites (29–32 species) and springtails (8–10 species) are dominant – at least in terms of numbers of species. Of the lower invertebrates, the nematode worms, tardigrades, rotifers, and protozoans are comparatively abundant although not so well known.

Table 1 Number of species in the major groups of terrestrial invertebrates and plants relative to the three zones of the Antarctic. Parentheses indicate number uncertain.

Taxon	Sub-Antarctic	Maritime Antarctic	Continental Antarctic
Invertebrates:			
Protozoa	(124)		(68)
Rotifera	–	–	13
Tardigrada	–	17	6
Nematoda	22	40	10
Annelida	4	(2)	0
Mollusca	3	0	0
Arthropoda	358	(68)	(78)
Insecta	210	35	49
Collembola	37	8	10
Diptera	44	2	0
Coleoptera	40	0	0
Arachnida	144	(32)	(29)
Araneida	14	0	0
Acarina	128	(32)	(29)
Myriapoda	3	0	0
Total (excluding Protozoa	387	(127)	(107)
Plants:			
Mosses	250	75	30
Liverworts	150	25	1
Lichens	300+	150	125
Macro-fungi	70+	22+	2
Macro-algae	(10)	(3)	(2)
Grasses, rushes, sedges	24	1	0
Forbs	32	1	0
Ferns and clubmosses	16	0	0
Total	852	(277)	(160)

The vegetation of Antarctica falls into two broad categories: tundra-like communities and fellfields of various types. The former, mainly limited to sub-Antarctic islands, are similar to their northern counterparts but without woody shrubs. The fellfields are typical of semi-desert (maritime Antarctic) and polar desert (continental Antarctic) areas, and their vegetation comprises a sparse cryptogram cover with vascular plants found only rarely in some maritime localities (figure 1). Fellfield soils are low in organic matter, often underlain by permafrost and subject to frost heave processes. Their microclimates are influenced by many physical and biological processes. The effect of plant cover, be it composed of discrete and discontinuous units such as cushion mosses and lichen stands, or conti ground cover such as is provided by moss c and turves, is to ameliorate the climatic ext Thus, the microclimates within vegetation e buffering and insulation characteristics relat the macroclimate, and provide shelter and su micro-environments for the development of bial and invertebrate populations. As a relatively simple communities are a featu Antarctic land habitats (Davis, 1981).

Two major environmental factors have a dor influence on the survival of terrestrial organi Antarctica – temperature and water. Of a potential stressors, these two, to a large control the life and death of most living things polar landscape. They are inextricably linl their action on biological systems, and may determine the survival not only of individua also of their populations, communities, and s in the polar ecosystem.

Temperature

Although the total annual solar radiation rece the South Pole is almost equal to the input Equator, despite the six-month-long polar much of it is reflected back into space fro permanent ice cap. So, despite its consid radiation receipt, Antartica is the coldest of continents. This is evident in the mean air tem tures and the extremes. In summer (January) temperatures range from just below 0 °C alo coasts to below −30 °C on the polar plateau, winter (July) means are about −20 °C and les −65 °C, respectively. The world's recor temperature of −89 °C was recorded in July Vostock Station in the Antarctic. Highest tem tures occur along the northern fringes continent and the Antarctic Peninsula, rem above freezing for between one and four mo summer with winter minima occasionally re below −30 °C. Thermal microclimates ne ground are generally less variable, both di and seasonally. Many short-term records hav made making generalization difficult. Coasta tions, in the main, have warmer microclimate inland sites. Surface temperatures on soil o and stones may achieve 16 to 20 °C in cont habitats with maxima higher than 42 °C, and surface of moss communities in the maritim temperatures of 25 to 36 °C are not uncommo brief maxima exceeding 45 °C! Minima of (continent) and −21 to −27 °C (maritime been measured in winter. Equable tempe suitable for biological activity in summer ar found in soil or organic material such as depths of between 3 and 6 cm.

ddition to the extremes of temperature, the physiologically stressful temperature zone for organisms is around the freezing point of . During such a temperature transition, known reeze–thaw cycle, biological systems have to tand the physically and osmotically disruptive ss of ice formation and thawing. Many plants oikilothermic animals do not survive this ally induced trauma and they die. Numerous -thaw cycles occur in soils and moss com- ies during the growing season. From 84 to 123 cycles per year have been found in the me Antarctic, and many species have evolved ations that overcome the problems caused by versible phase change from water to ice. The of heating or cooling is important. Surface g may reach 6.4 deg. h^{-1} whereas cooling at of about 1.4 deg. h^{-1} or less are common on the rface. Short-term heating rates for lichens and s may be up to 2 deg. min^{-1}, whereas short cooling rates of 10-14 deg. h^{-1} are not mon in summer in the maritime Antarctic.

econd major environmental factor is water. dependent upon free water. Although over 70 nt of the world's store of fresh water is found arctic ice, much of it is locked out from ical processes even during the austral sum- recipitation, mostly in the form of snow, is n the polar plateau, the annual snow fall is lent to less than 5 cm of rain, whereas in the umid coastal areas it may be equivalent to as as 50 cm per year. In some cases, radiative g causes melting to form local ponds and, in areas, glacial meltwater forms rivers (for le, the Onyx, which flows inland for over 30 the Wright Valley of Victoria Land). At higher es, thermal radiation and dry katabatic winds ne to cause water loss from the ground and by sublimation, and snow melt is much d.

vater and water contained in vegetation and re important reservoirs which contribute to rvival of many Antarctic plants and animals. rozen silt and organic soils contain significant ts of unfrozen water down to −10 °C, which utilized by a variety of organisms. Continen- s are usually very dry (water contents being er cent of dry weight) and, in the absence of a over, invertebrate life is often concentrated h stones where the soil remains moist due to condensation. Maritime Antarctic fellfield ontain more water (about 20–30 per cent of ight), whilst some moss peats remain satu- through the year with water contents of 250–2600 per cent dry weight being the range. In biological terms, therefore, the availability of water during the summer growing season is crucial not only to organism survival but also for growth, reproduction, and behaviour.

Where free water occurs in the Antarctic, it is important to distinguish between substrate moisture and the relative humidity (RH) of the atmosphere above and within the substrate, be it vegetation, soil, or rocks. Very low RH (7–14 per cent at temperatures in the range 10–22 °C) have been measured on the surface of moss patches and stone 'pavements' in the Dry Valleys of Victoria Land in summer. These levels will restrict the locomotion and activity of air-breathing invertebrates, as well as reducing respiration and photosynthesis of plants. Atmospheric moisture from mist and cloud is an important source of water for cryptogams elsewhere in the Antarctic.

Stress or stimulus

The term 'stress' has crept into current usage, whereas 'stimulus' (describing a change in the environment) is the classical expression in biology. Stress in biological terms may be considered to occur when there is a deviation from the optimum of a particular parameter in response to a stimulus. In other words, a continuum of response exists along which the organism functions. Stress, although tarred with emotive overtones, is a useful term particularly for zoological studies. In respect of cold and hot, dry and wet conditions, an organism may alter its level of activity of a particular physiological process, such as respiration, in response to deviations about the optimum condition. Inhibition of an activity or process may well occur through changes in environmental variables such as moisture and temperature.

It is most likely that significant physical and biochemical changes in membranes take place before extremes of temperature and moisture are reached. In the prime example of freezing and thawing, biological stress and damage occur at the water phase changes, and are not necessarily determined by the maximum or minimum temperatures experienced. In cold-adapted animals and plants there is an increase in the degree of unsaturation of certain lipids, which in turn is linked to the fluidity of their membranes. At low temperatures lipid bilayers are formed, which maintain the membranes in an active state. Slow cooling rates are usually necessary for these changes to occur.

Freezing is a major stress of polar plants and invertebrates. Their response is either to avoid ice formation in their cells and tissues by ecological and/or physiological strategies, or to tolerate the

presence of ice by restricting it to the extra-cellular compartment, or when it occurs intra-cellularly, by limiting the amount of cell damage. Heat stress is unlikely to be quite so acute for the Antarctic biota, because of the relatively short duration of exposure to extremes of high temperature. It is possible that inhibitory responses will play a greater role in combating heat stress in such organisms. Antarctic desert environments test the ability of terrestrial organisms to survive both extreme dryness and, on occasion, extreme wetness. In the maritime Antarctic, localized waterlogging and inundation can occur from meltwater in summer creating anaerobic conditions. Arid environments are characteristic of many continental areas and in most terrestrial habitats much of the water will be frozen as ice for long periods in winter. There is little doubt that such a shortage of water will prevent invertebrate activity, especially that of nematodes, tardigrades, and protozoans, which live in moisture films, and air-breathing arthropods because of the dry atmosphere.

The interactive effects of temperature and water on the survival of Antarctic terrestrial life forms are best discussed with reference to two abundant taxa, about which most is known – the arthropods and the lichens.

Arthropods

Cold hardiness is a widespread phenomenon amongst arthropods, especially in polar and alpine regions, and is the ability of the individual to resist low (often sub-zero) temperatures, which would normally be lethal. One of two strategies is adopted by such species: either the avoidance of freezing by

Figure 2. The oribatid mite Alaskozetes antarcticus *– about the size of a large pin-head and weighing only 200 µg when adult, it is one of the largest terrestrial animals in the Antarctic. SEM photograph.*

Figure 3. Reading the supercooling points of indi mites from the chart record after a freezing expe at the BAS station at Signy Island in the maritim Antarctic.

the physical process of supercooling (the tenance of their body fluids in the liquid below the solution freezing point), or the rest of internal ice to the extracellular spaces dur freezing process. In the former strategy, f kills the animal – it is 'freezing susceptible'. latter it does not kill – it is 'freezing toler freezing-susceptible species (which comprise Antarctic micro-arthropods investigated), cooling may extend to about −40 °C in indi acclimatized for winter. In freezing-tolerant (only a single Antarctic species – the larv chironomid midge), nucleators are thought to ote body freezing at relatively high sub-zero t atures (around −10 °C), and much lower te tures may then be tolerated. In both options, solutes including polyhydric alcohols and may act as antifreezes and help to m cytoplasm and membrane damage.

In the Antarctic oribatid mite *Alaskozetes ticus* (figure 2) and the springtail *Crypt antarcticus*, both of which have been stu detail, supercooling is extensive (to below but its full realization is dependent on gut cle (figure 3). Nucleators present in food mater water in the gut system readily act as centres formation, and cold hardiness can be im experimentally by starvation. The full super potential is aided by glycerol (a common and synthesized antifreeze) which is found in cor tions between 1 and 5 per cent of fresh body Its synthesis is dependent on low temperatu to 0 °C) acclimation and body-water cont

d amounts of glycerol are found in animals ave been slowly dehydrated over several , thereby confirming that a low atmospheric luces increased glycerol production over and any concentration effect. Where sub-zero ·atures are experienced in the field for long s in summer, such species will have to strike nce between the necessity to feed (and y reduce their individual supercooling ability crease the possibility of lethal freezing) and quirement to survive. Field studies have that much of the additional cold hardiness of species is built up in two phases: firstly, a when mean ground temperatures are close to r between 4 and 6 weeks in the autumn and ature fluctuations are minimal and, secondly, mean daily temperatures between 0 and occur at the onset of winter. During the first feeding cessation is more important than the ement of supercooling but, as freezing condi- ontinue in the second period, glycerol pro- ı becomes essential for survival, especially temperatures decline to below −20 °C in Low RHs are likely to occur in terrestrial s before a snow cover develops, thereby ing glycerol synthesis at a critical time. The stages of both species appear to have slightly levels of cold hardiness than mature indi- , thus having an increased 'safety margin' for rerwintering survival.

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oup of lower plants has proliferated in the ic primarily because of the low levels of ition, both between lichens and by the absence of flowering plants and the rela- ew mosses (table 1), and also by their high ce of drought and cold. Lichens are able to nutrient-poor substrates, which are often ble for higher plants, and colonise stones ·ks rather than unstable soils. Their tolerance emes of both temperature and moisture may ed in part to their morphology and their being sed of algal and fungal components.

e lichens such as *Umbilicaria antarctica* 4) tolerate a wide temperature range (−30 to nd can withstand continuous dehydration- on cycles. During the Antarctic winter, most are inactive and their metabolism remains at low level. Some may freeze-dry, and mini- allus water contents of 20 per cent (= 0.2 g weight) have been measured (P. M. Harris- rs. comm.). Rehydration is rapid from liquid r water vapour. During summer, photosynth- l respiratory activity is resumed and maxi- tes of net photosynthesis and dark respira-

Figure 4. A large foliose lichen – Umbilicaria antarctica – *which may survive for 1-2 thousand years in the maritime Antarctic.*

tion occur around 13 °C, when the thallus is saturated with water. Above a thallus temperature of 20 °C, respiration continues at a high rate, but as the plant loses water rapidly, metabolism is considerably reduced. The water content of the thallus can therefore limit metabolic activity of such lichens during the summer. Freeze-thaw cycles may be less damaging to lichens in that ice forms primarily in the air spaces of the thallus with less damage to cells. Although several compounds with potential cryoprotectant functions are known to occur in Antarctic lichens, their role in drought and cold survival is not established. 'Lichen substances', which are peculiar to lichens, may be associated with the sugar alcohols in these high-resistance-capacity plants. Mannitol is probably universal to lichens. In the Antarctic, *Usnea* spp. and *Himantormia lugubris* are known to have mannitol contents of between 7 to 10 per cent of the total sugars, but these are exceeded by arabitol (80 to 85 per cent of all sugars). Arabitol comprises 7 to 65 mg g^{-1} fresh weight of these lichens (P. V. Tearle, pers. comm.).

That lichens are successful in the Antarctic environment is evidenced by estimates of their age. Individual thalli of *Umbilicaria antarctica* reach 30 cm in diameter and may be at least 1000 years old, on the basis of their size and growth rates. Growth

rates of other species, for example *Rhizocarpon geographicum*, may average only 4 mm per century. In general, from what is known of the ecology and physiology of Antarctic lichens, their metabolic strategy of being able to 'sit it out' in terms of their resistance to physical conditions, clearly is successful. In terms of reproduction, although some species require between 10 and 20 years to reach sexual maturity, asexual reproduction by means of soredia, isidia, and so forth, occurs much earlier in life. The vegetative products are fully formed units capable of photosynthesis immediately, whereas viable spores produced in apothecia require longer to grow into lichen plants.

Survival strategies

The strategies evolved by these representatives of the Antarctic land fauna and flora are not unique to that environment. Many of the features shown by arthropods and lichens as adaptations to the harsh polar environment are found in related species of both groups elsewhere in the world. Antarctic lichens are no better adapted than species of hot deserts; both utilise their inbuilt resistance to physical factors to exploit their particular environment. Their relatively slow growth rates are partly a result of such adaptations. So, the colonization of south polar habitats has not resulted in the evolution of specific physiological mechanisms by either the lichens or the micro-arthropods. The latter have developed and extended mechanisms found in tropical and temperate species of mites and springtails. Supercooling, which is widespread in the invertebrates, can be seen as an advantage in a thermally fluctuating environment, whereby repeated freezing and thawing of tissue can be avoided. Perhaps this may explain the rarity of the freezing tolerance strategy in terrestrial invertebrates in general and in Antarctic forms in particular. Both life forms appear to have elements of two complementary life styles in their makeup: the ability to 'sit it out' and that of a 'get up and go' strategy. Both groups are able to assimilate energy, store, and utilize it at low temperatures within a short space of time. Respiration of both forms proceeds at low temperatures, as does photosynthesis in the lichens, which have low light saturation levels. Dark pigments in both arthropods and lichens may aid in raising tissue temperature by heat absorption, thereby allowing physiological activity when ambient air temperatures are not optimal. Asexual reproduction confers a temporal advantage on polar lichens and, although Antarctic arthropods only reproduce sexually, there may be other features of their life cycles which overcome this (Block, 1980). In terms of cold hardiness, both groups exhibit a well-developed resistance to sub-zero conditions, helped by sugar alcohols, and their compounds ac antifreezes. The role of water in the cold re of both groups is intriguing, and the si between the processes of cold hardeni dehydration go a long way to underline the ance of water in the survival of Antarctic te organisms.

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References

Block, W. (1980) Survival strategies in polar terres arthropods. *Biological Journal of the Linnean So* **14**, 29-38.

Block, W. (1984) Terrestrial microbiology, inverteb and ecosystems. In *Antarctic ecology*, Vol. 1, ed. R.M. pp. 163-236. London and New York: Academ

Davis, R.C. (1981) Structure and function of two A terrestrial moss communities. *Ecological Monogr* **51**, 125-143.

Smith, R.I.L. (1984) Terrestrial plant biology of the sub-Antarctic and Antarctic. In *Antarctic ecology* ed. Laws, R.M. pp. 61-162. London and New York: Academic Press.

Walton, D.W.H. (1984) The terrestrial environment *Antarctic ecology*, Vol. 1, ed. Laws, R.M. pp. 1-60. and New York: Academic Press.

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ECOLOGICAL AND PHYSIOLOGICAL STUDIES OF TERRESTRIAL ARTHROPODS IN THE ROSS DEPENDENCY 1984–85

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ABSTRACT. Aspects of the ecology and physiology of terrestrial arthropods were studied at nine locations on Ross Island and South Victoria Land during the 1984–85 summer. Four species (three mites and one springtail) were identified from a range of terrestrial habitats. Physiological work was concentrated on the cold resistance of two of these species (*Gomphiocephalus hodgsoni* (Collembola) and *Stereotydeus mollis* (Acarina). Supercooling of cold adapted individuals was extensive (range of −24 to −30°C) before freezing, which was lethal in both forms. Thus, freezing avoidance by supercooling is the strategy adopted by these invertebrates, which appear well able to resist the thermal minima experienced during summer. Experiments demonstrated that moisture, ingested or absorbed, caused nucleation at higher sub-zero temperatures, thereby reducing cold resistance. Levels of potential anti-freezes in sample extracts are being assayed by gas–liquid chromatography. The abundance and field movement of individuals in these arthropod populations was directly related not only to substrate moisture but also to the presence of vegetation (e.g. mosses, lichens, algae). A special study of the microclimates of terrestrial habitats was undertaken to define the environmental conditions experienced in summer by both arthropods and discrete plant patches. Temperature and relative humidity readings at 5-min intervals were logged for periods up to 25 days in soil, vegetation, under stones and rocks, and in air at the ground surface. Minimum temperatures reached −8 to −11°C in such micro-sites, and maxima of *c.* 26°C were recorded on vegetation surfaces. Atmospheric humidity at the surface of soil and vegetation patches was also variable (minima 8–11%; maxima 90–97%). An opportunity was taken to collect 40 small soil and plant samples from eight of the locations for protozoological and nematological studies.

INTRODUCTION

Research on the terrestrial arthropods (Acarina and Collembola) of South Victoria Land and Ross Island has been mainly confined to taxonomic studies (e.g. Wise, 1967; Strandtmann, 1982) and ecology (e.g. Janetschek, 1967*a*, *b*; Peterson, 1971). Much ecological work had been undertaken on the springtail *Gomphiocephalus hodgsoni* at Cape Bird, Ross Island (Smith, 1970; Duncan, 1979). No data exist on the physiological characteristics of such populations, nor on their field activity, and information on their field microclimates was limited. An attempt was made to fill this gap utilizing experience and techniques developed through field studies in the maritime Antarctic the Antarctic Peninsula, and Signy Island, South Orkney Islands).

The specific aims of the project were:

(*a*) To investigate the ecophysiology of terrestrial arthropods at locations on Ross Island and the Dry Valley region of South Victoria Land.

(*b*) To examine experimentally the cold resistance of field populations of mites (Acarina) and springtails (Collembola) in order to evaluate their survival characteristics.

(*c*) To assess the field movement and activity of species representative of extreme cellfield communities.

(*d*) To provide environmental data for the above experiments, microclimate monitoring (temperature and relative humidity (RH)) was undertaken in a range of terrestrial habitats.

(*e*) To collect small soil and vegetation samples from a variety of terrestrial habitats for subsequent analyses of the nematode and protozoan fauna.

Methods

As far as possible, the methods for this project were simple, enabling them to be used under field (camp) conditions, and most had been tested previously.

(*1*) *Arthropod cold resistance*

Individual supercooling points (= whole body freezing points) of mites and springtails were measured using a Cu-con thermocouple and a battery-driven Grant recorder. Body temperatures were monitored in air with a cooling rate of *c.* 1 deg min^{-1}. This was achieved by lowering the animal on the thermocouple inside an air-filled tube into a freezing mixture of granular snow and $Ca\ Cl_2 . 6H_2O$ (1.5:1 v/v) contained in a vacuum flask. Supercooling points were read as the point of origin of the small temperature rise that accompanied the emission of latent heat during freezing. Supercooling is the maintenance of the animal's body fluid in the liquid phase below its freezing point. Full experimental details are given in Block & Sømme (1982).

The antifreezes in the body fluid were examined by making extracts of polyhydric alcohols and sugars in 70% ethanol from samples of 25–100 individual micro-arthropods. About 40 such extracts are being analysed by gas–liquid chromatography at BAS, Cambridge (see Block & Sømme (1982) for further details). Further whole animal samples were preserved for osmometry.

(*2*) *Arthropod field activity*

A measure of ground surface movement of micro-arthropods was obtained from sticky traps placed among field transects in moss patches, algal felts and lichen communities. Traps were operated also in wet and dry soils at Cape Bird and Cape Crozier with up to 20 traps being used per transect. Each trap comprised a clear perspex sheet (5 × 8 cm), coated on one surface with Sticktite, and it was exposed in either a vertical or horizontal position on the substrate. After differing exposure periods, trapped animals were identified and counted using a binocular microscope.

(*3*) *Microclimates*

Soil, rock and vegetation temperatures, together with atmospheric RH, were monitored continuously in selected terrestrial habitats using two Grant Squirrel data loggers (Fig. 1). Mini-thermistors (range −35 to 35°C) and capacitative Vaisala probes (0 to 100%) were used for sensing temperature and RH respectively. Recording was at 5-min intervals for up to six days, the loggers were then interfaced with an Epson HX-20 micro-computer and the data down-loaded for subsequent analysis. Data analysis including the calculation of means (±SD), selection of maximum and minimum values with their times of occurrence, and plots of all the data points for selected periods or for complete runs were undertaken in the field. Further analyses will be done on the field data transferred to micro-cassette tapes.

Fig. 1. Microclimate data logger (Grant Squirrel) located in a fellfield study area at Cape Bird, Ross Island. The Epson HX-20 microcomputer (in black case) is interfaced with the logger for data transmission.

Table I. Occurrence of arthropod species at locations visited in the 1984–85 field season.

	Collembola	Acarina		
Location	*Gomphiocephalus hodgsoni*	*Stereotydeus mollis*	*Nanorchestes antarcticus*	*Nanorchestes* sp.*
Ross Island				
Cape Bird (Keble Valley)	+	+	+	+
Cape Royds (Collembola Heights)	+	+	+	–
Cape Crozier (nr Post Office Hill)	+	+	+	–
Scott Base, Hut Point	+	+	–	–
South Victoria Land				
Garwood Glacier, Garwood Valley	+	+	–	–
Lake Fryxell, Taylor Valley	–	+	–	–
Lake Bonney, Taylor Valley	–	–	–	–
Lake Vanda, Wright Valley	–	–	–	–
West Beacon Mountains, Taylor Glacier	–	–	–	–

* Probably *Nanorchestes bellus* or *Nanorchestes lalae*, but subject to confirmation.

Table II. Mean (±SD) supercooling points (SCP) of field samples of two species of arthropods from locations on Ross Island and South Victoria Land. (*n*): number of observations.

Location	*Date*	*SCP (°C)*	
		High group	*Low group*
Gomphiocephalus hodgsoni			
Cape Bird (Keble Valley)	27 Nov. 1984	−15.4±3.8 (3)	−30.4±1.9 (72)
(Keble Valley)	5 Dec. 1984	−11.2±3.2 (5)	−29.9±0.9 (53)
(Keble Valley)	14 Dec. 1984	−7.6±3.3 (10)	−30.6±1.8 (56)
Cape Royds (Collembola Heights)	24 Dec. 1984	−13.8±5.5 (6)	−29.5±1.7 (65)
Garwood Glacier	29 Dec. 1984	−13.6±5.3 (16)	−29.8±1.4 (54)
Cape Crozier (nr Post Office Hill)	12 Jan. 1985	−18.3±5.1 (18)	−30.4±1.5 (70)
Stereotydeus mollis			
Cape Bird (Keble Valley)	30 Nov. 1984	−18.3±2.6 (59)	−26.4±1.4 (27)
(Keble Valley)	7 Dec. 1984	−14.7±3.6 (52)	−25.0±1.8 (10)
(Keble Valley)	18 Dec. 1984	−15.4±4.1 (73)	−24.9±0.7 (8)
Cape Royds (Collembola Heights)	24 Dec. 1984	−17.9 (1)	−24.8±1.1 (8)
Garwood Glacier	30 Dec. 1984	−16.3±3.2 (40)	−25.3±1.6 (13)
Cape Crozier (nr. Post Office Hill)	16 Jan. 1985	−16.7±4.3 (59)	−27.7±1.1 (33)

(*4*) *Qualitative invertebrate samples*

A total of 40 small samples of soils and plants was collected by hand from eight locations on Ross Island and South Victoria Land for analysis of their protozoan and nematode fauna. Material was placed in small polythene bags, labelled and transported to the UK for specialist study.

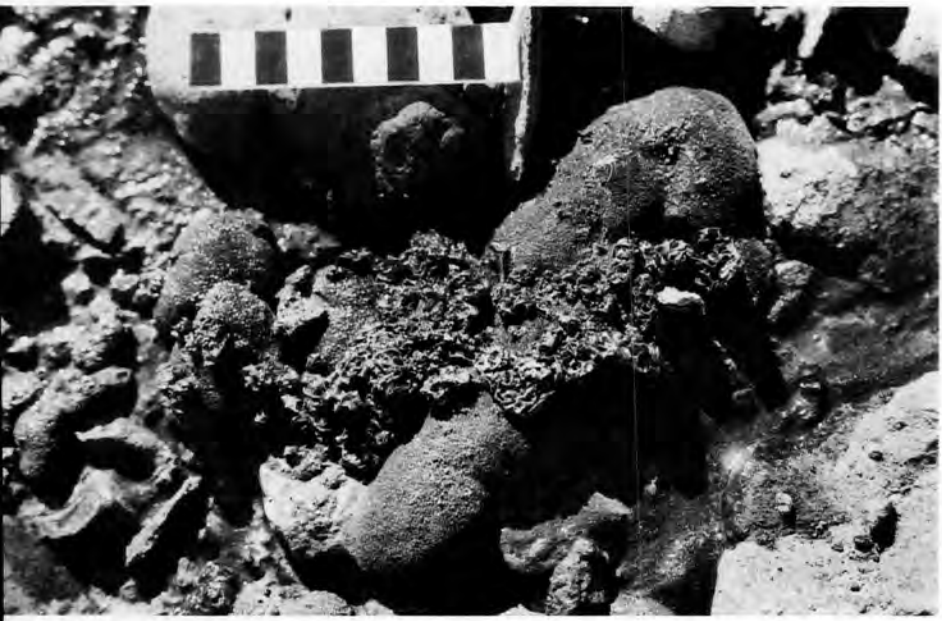
Results

(*1*) *Arthropod cold resistance*

Arthropods were found at six out of the nine locations visited (Table I). Four species (one collembolan and three mites) were found in Keble Valley, Cape Bird, the second species of *Nanorchestes* being a new record for that area. The commonest species was the collembolan *Gomphiocephalus hodgsoni*, which was particularly abundant in Keble Valley at Cape Bird (Fig. 2).

Cold resistance experiments were concentrated on *G. hodgsoni* and the prostigmatid mite *Stereotydeus mollis*. Both species were susceptible to freezing, i.e. ice formation in their bodies was lethal. Frequency distributions of the supercooling points (SCP) determined for each experiment often showed a separation into a high group (HG) (> −20°C) and a low group (LG) (< −20°C), but this was less clear for data from *S. mollis*. The HG is caused mainly by nucleation of food and water within the gut system during supercooling, whereas the LG probably represents the maximum potential cold resistance of the species under the experimental conditions. Table II shows the mean SCP for both groups for all the field samples. The HG values vary considerably, whereas the LG means do not, for both species. *C. hodgsoni* is more cold resistant than *S. mollis* under summer field conditions, with mean LG SCP around −30°C for the former and from −24 to −28°C for the latter species.

ig. 2. Continental Antarctic fellfield on Ross Island (Cape Bird). The photograph shows one of the melt-streams in Keble Valley and the area where arthropod field studies were made in December 1984.



g. 3. A clump of the moss *Bryum antarcticum* with associated algae (*Phormidium* spp.) forming a typical streamside community on Ross Island, Antarctica. The scale is in centimetres.

Experiments were conducted at Cape Bird and Cape Crozier to determine i exposure to moisture altered the extent of supercooling in the collembolan. Althoug the mean LG SCP changed little, the proportions of animals in the groups altere with the majority (68–100%) being in the HG. Thus ingestion and inhibition c moisture for growth, etc. appears to reduce the cold resistance in this species.

The levels of antifreezes and their role in the cold resistance of these micro-arthropod will be discussed later.

(2) *Arthropod field activity*

Using the total number of trapped individuals per unit time for comparison, it i clear that arthropod activity was highest at microsites where both vegetative growt (mosses, algal or lichens) and moisture were present (Fig. 3). Fewer animals wer trapped in the drier microsites along the transects, and none were found in th extremely dry areas. No significant differences were found between the catches o vertical or horizontal traps in similar microsites.

(3) *Microclimates*

Table III presents a summary of the mean values (and their ranges) for temperatur and atmospheric RH in the twelve terrestrial habitats in which recording wa undertaken. Minimum microsite temperatures (−8 to −11°C) occurred early in th summer (Nov.–Dec.) and at the mountain location (West Beacon) in January Maximum temperature records were for surfaces of mosses and lichens (26°C) at Cap Bird and Cape Crozier respectively. Lowest RH measurements were at West Beaco (8%) during a cold period, and in the Garwood Valley (11%) with a high ai temperature (*c.* 17°C). RHs up to 97% were measured at moss surfaces. For th locations where micro-arthropods occurred in sufficient numbers for cold resistanc experiments to be undertaken (Table II), it is clear that both species were well abl to avoid lethal freezing by supercooling. Summer conditions in microsites occupie by both arthropods did not appear to be thermally stressful, but alternativel atmospheric water vapour may be limiting at certain times.

Further analyses will help to define more precisely the environmental condition which are experienced by such arthropods. In addition, it is hoped that the particula characteristics of favoured microsites in such continental Antarctic habitats will b elaborated.

(4) *Qualitative invertebrate samples*

Analyses of the micro-fauna (Protozoa and Nematoda) are in progress, and th results will add to the scant knowledge of these groups in the continental Antarcti

Future Research

Work that could develop from these studies includes:

(*a*) a year-round seasonal examination of the cold resistance of *G. hodgsoni* an possibly *S. mollis* at Cape Bird;

(*b*) seasonal changes in terrestrial microclimates at selected sites (e.g. moss patche algal felts) by means of automatic recording or integration systems or remot sensing techniques;

(*c*) an in-depth examination of the life cycle of the dominant arthropod, *G. hodgson*

Table III. Summary of microclimate data from terrestrial habitats at six locations during the 1984–85 season. *n*: number of readings.

Location	*Habitat*	*Microsite**	*Record dates*	*Temp. & Rel. Humidity*		*n*
				Mean	*Range*	
Cape Bird	Algal felt	1	26 Nov.–	2.2°C	−7.6–19.6	3728
		2	9 Dec. 1984	2.0°C	−7.3–14.0	
		3		2.5°C	−2.8–12.3	
		4		68.0%	29.5–87.0	
	Moss patch (lower)	1	26 Nov.–	1.7°C	−8.4–18.8	5721
		2	20 Dec. 1984	1.4°C	−6.2–12.6	
		3		2.2°C	−5.9–12.9	
		4		73.0%	54.5–85.5	
	Moss patch (upper)	1	10–20 Dec.	6.4°C	−4.5–26.6	2965
		2	1984	5.6°C	−2.5–19.3	
		3		2.8°C	0.3–13.4	
		4		81.0%	49.0–97.0	
Cape Royds	Unvegetated dry volcanic debris	1	23–26 Dec.	11.8°C	1.7–23.0	860
		2	1984	11.5°C	3.1–18.8	
		4		39.0%	15.5–74.0	
	Moss patch	1	23–26 Dec.	6.7°C	−1.1–22.7	927
		2	1984	5.6°C	−0.3–17.4	
		3		5.3°C	−2.2–24.9	
		4		56.0%	23.0–93.0	
Garwood Valley	Unvegetated dry stone 'pavement'	1	27 Dec. 1984	6.4°C	−0.6–16.8	1482
		2	–2 Jan. 1985	7.0°C	−0.6–17.6	
		3		6.2°C	1.1–12.9	
		4		29.0%	11.5–54.0	
	Moss patch	1	27 Dec. 1984	5.6°C	−0.6–22.1	1471
		2	–2 Jan. 1985	5.9°C	0.6–15.1	
		4		63.0%	27.5–84.5	
Lake Vanda	Unvegetated dry ridge	1	2–4 Jan. 1985	6.2°C	0.6–17.6	466
		2		7.0°C	1.4–12.6	
		3		5.9°C	1.4–10.6	
		4		29.5%	10.5–53.5	
West Beacon Mountain	Valley floor	1	4–8 Jan. 1985	−4.8°C	−11.8– 5.3	987
		2		−4.5°C	−10.9– 7.6	
		3		−4.2°C	−9.5– 6.2	
		4		46.5%	8.0–91.0	
	Exposed ridge	1	5–8 Jan. 1985	−2.5°C	−9.5–10.1	809
		2		−0.3°C	−6.7–10.1	
		4		41.0%	9.0–86.5	
Cape Crozier	Lichen patch	1	10–18 Jan.	5.0°C	−3.6–26.3	2421
		2	1985	6.2°C	−1.1–21.8	
		3		5.0°C	−1.4–19.3	
		4		43.5%	14.5–84.5	
	Exposed hill	1	10–18 Jan.	4.5°C	−1.1–14.6	876
		2	1985	4.5°C	−5.3–25.5	
		4		47.0%	21.5–82.5	

* The microsites were not always comparable but in general the sensors were located as follows:

Temperature

(1) Surface of vegetation, stone, rock or soil (unshielded).
(2) Beneath stone or rock or 3 cm inside vegetation.
(3) At 3 cm depth in mineral soil.

Relative Humidity

(4) Air at ground surface.

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REFERENCES

BLOCK, W. *and* SØMME, L. 1982. Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. *Oikos*, **38**, 157–67.

DUNCAN, K. W. 1979. Distribution and abundance of *Gomphiocephalus hodgsoni* at Cape Bird, Antarctica. *Mauri Ora*, **7**, 19–24.

JANETSCHEK, H. 1967*a*. Arthropod ecology of South Victoria Land. *Antarctic Research Series*, **10**, 205–93.

JANETSCHEK, H. 1967*b*. Growth and maturity of the springtail *Gomphiocephalus hodgsoni* Carpenter from South Victoria Land and Ross Island. *Antarctic Research Series*, **10**, 295–305.

PETERSON, A. J. 1971. Population studies on the Antarctic collembolan *Gomphiocephalus hodgsoni* Carpenter. *Pacific Insects Monograph*, **25**, 75–98.

SMITH, D. J. 1970. The ecology of *Gomphiocephalus hodgsoni* Carpenter (Collembola, Hypogastruridae) at Cape Bird, Antarctica. M.Sc. thesis, University of Canterbury, Christchurch, New Zealand.

STRANDTMANN, R. W. 1982. Notes on *Nanorchestes* II. Four species from Victoria Land, Antarctica (Acari: Nanorchestidae). *Pacific Insects*, **24**, 60–8.

WISE, K. A. J. 1967. Collembola (Springtails). *Antarctic Research Series*, **10**, 123–48.

TERRESTRIAL ENCHYTRAEIDAE FROM SOUTH GEORGIA AND THE MARITIME ANTARCTIC

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ABSTRACT. Seven taxa of enchytraeid worms have been identified in soil and peat samples collected on South Georgia, and Signy Island (South Orkney Islands). They are all different from the 16 enchytraeid taxa previously recorded from the Antarctic Region. Five of the seven enchytraeids occur in the Holarctic Region, and it seems likely that their presence in the Antarctic is connected with human activity.

INTRODUCTION

Earthworms (Families Megascolecidae and Lumbricidae) have been recorded from several sub-Antarctic islands, e.g. Macquarie, South Georgia, Marion (Benham, 1905, 1922; Pickford, 1932; Burger, 1978). Smaller oligochaete worms of the Family Enchytraeidae have been found in various locations in the Antarctic, and this preliminary paper brings together the information obtained so far. It also records the finding of two taxa new to science.

Sixteen taxa of enchytraeids have been recorded from the Antarctic Region and southern cold temperate zone (Table I), and much remains to be investigated in terms of their taxonomy and distribution. Three genera (*Marionina*, *Lumbricillus* and *Enchytraeus*) are also widespread throughout Europe and North America, whilst several species are common to both Europe and the sub-Antarctic.

Little is known of the ecology of enchytraeid worms in the Antarctic, but highest numbers have been recorded in soil under species of grass in the maritime zone (Block, 1979) and in the sub-Antarctic (Smith and Stephenson, 1975).

METHODS

Live material was collected in soil and peat from five terrestrial habitats on South Georgia (54° 20′ S, 36° 40′ W) and one on Signy Island, and a few preserved worms were obtained from Signy and Lynch Islands (South Orkney Islands; 60° S, 45° W) and Deception Island (62° 57′ S, 60° 38′ W) in the South Shetland Islands. Soil and vegetation samples from South Georgia were transported to Copenhagen in small plastic bags, maintained at *c.* 5° C for most of the time. Immediately upon arrival the worms were extracted by the wet funnel technique (Whitehead and Hemmings, 1965) and inspected alive. In most cases the material was studied 3–4 months after field collection. It is believed that this procedure is satisfactory for a qualitative study of this kind, since replicate samples kept in the laboratory at 4°C for up to 2 years still contained live worms, and the species in question occurred in the expected relative numbers. Where possible the samples were subdivided into three sections (surface

Table I. Enchytraeidae previously recorded from the Antarctic Region and the southern cold temperature zone.

Taxon	*Location*
Marionina georgiana (Michaelsen)	South Georgia[1,3], Iles Crozet[3], Falkland Islands[3]
M. grisea Stephenson	Antarctic Peninsula[3]
M. aestuum Stephenson	South Georgia[3]
M. antipodum Benham	Macquarie Island[2]
M. benhami Stephenson	Macquarie Island[2]
M. exigua Michaelsen	South Georgia[1,3]
M. werthi Michaelsen	Iles Kerguelen[3], Macquarie Island[2]
Lumbricillus lineatus (Müller)	Antarctic Peninsula[3], South Orkney Islands[3], South Georgia[3], Tierra del Fuego[3]
L. maximus (Michaelsen)	South Georgia[1,3], Antarctic Peninsula[3], South Orkney Islands[3], New Amsterdam[3]
L. macquariensis Benham	South Georgia[3], Macquarie Island[2], Auckland and Campbel islands[3]
L. antarcticus Stephenson	South Georgia[3]
Enchytraeus albidus Henle	South Georgia[1,3], Iles Crozet[3], Iles Kerguelen[3], Falkland Islands[3], Tierra del Fuego[3], southern Patagonia[3], New Zealand shelf islands[3]
E. australis Stephenson	South Georgia[3], Gough Island[3]
E. colpites Stephenson	South Georgia[3]
Michaelsena monochaeta (Michaelsen)	South Georgia[1,3],
Achaeta sp. (indet.)	South Georgia[3]

Data from Michaelsen (1888, 1905)[1]; Benham (1905, 1922)[2] and Stephenson (1932)[3].

vegetation and litter, 0–3 cm and 3–6 cm depth of soil from the surface) on collection and extracted separately. There was a strong predominance of worms in the uppe (0–3 cm) soil section.

Worms were examined alive under 100–500 × magnification and identified usin Nielsen and Christensen (1959).

Samples Sites

South Georgia

1. A dry grassland community consisting of *Festuca contracta* T. Kirk growing i short tussocks up to 20 cm in diameter with an understorey of mosses and lichens. Th soil is an acid brown earth. The site was located close to a large lake at 84 m a.s. at the Maiviken end of Bore Valley to the north of King Edward Cove.

2. A moss bank composed of two principal species, *Polytrichum alpestre* Hopp and *Chlorisodontium aciphyllum* (Hook f. et Wils.) Broth. These have developed a lev moss turf overlying peat up to 2 m deep in parts. This site is closer to the sea (7 r a.s.l.), near Maiviken in Bore Valley.

3. A dwarf shrub association of *Acaena magellanica* (Lam.) Vahl with a dens understorey of the moss *Tortula robusta* Hook et Grev. on an organic soil overlyin a glacial till. It is situated on the south side of King Edward Cove at *c.* 12 m a.s.l.

4. A eutrophic mire situated between Brown Mountain and Gull Lake at 91 m a.s. to the south of King Edward Cove. The vegetation comprises a continuous carp of *Tortula robusta* and other mosses together with the short rushes *Rostkov magellanica* (Lam.) Hook. f. and *Juncus scheuchzerioides* Gaudich. The soil compris over 1 m deep waterlogged peat.

5. A tussock grassland, close to the BAS station on King Edward Point at *c.* 20 m a.s.l., dominated by large (1–2 m high) tussocks of *Poa flabellata* (Lam.) Hook. f. Areas of the site are enriched by elephant seals and *c.* 1 m of peat has developed beneath much of it.

Signy Island

6. The site at Signy Island is a small plot (*c.* 1 m²) in a moss community formed by *Polytrichum alpestre* and *Chorisodontium aciphyllum*, into which various flowering plants and grasses were transplanted from South Georgia and/or the Falklands in experiments conducted between 1967 and 1969 (Edwards, 1980; Edwards and Greene, 1973). It is in Factory Cove, *c.* 13 m a.s.l. and close to the BAS station (see Block, Burn and Richard (1984) for a description).

Results

Enchytraeidae

Unless otherwise stated, reference should be made to the descriptions in Nielsen and Christensen (1959).

Mesenchytraeus pelicensis Issel 1905

Found in *Acaena* (site 3) collected on 12 March 1981 at King Edward Cove, South Georgia.

Cognettia sphagnetorum (Vejdovsky) 1877

Common in *Polytrichum* from moss bank, *Festuca*, *Poa*, *Rostkovia* vegetation and *Acaena* (sites 1–5) collected at King Edward Cove, South Georgia on 23 February 1978 and 12 March 1981. Sexually mature individuals were not observed. The chief method of reproduction seems to be fragmentation and subsequent regeneration. Mitotic divisions in regenerative buds showed many chromosomes and, although the exact number was not established, it is obvious that these sub-Antarctic forms are polyploids like most North European strains.

Cognettia glandulosa (Michaelsen) 1888

Identified from *Rostkovia* and *Acaena* from King Edward Cove, South Georgia; 12 March 1981. Abundant in these samples. Reproduction and chromosome number are similar to *C. sphagnetorum*.

Henlea perpusilla Friend 1911 augm. Cernosvitov 1937.

Ex *Rostkovia* (as above). Analysis of mature eggs showed that the form present is what has been referred to as *cytotype 4x, MI* (Christensen, 1961). This is a tetraploid in which the chromosomes remain in the first meiotic metaphase until the eggs are laid.

Henlea ventriculosa (Udekem) 1854.

Found in *Rostkovia* and *Acaena* collected at King Edward Cove, South Georgia; 23 February and 12 March 1981.

Marionina sp.

Found only in *Rostkovia* (King Edward Cove, South Georgia; 12 March 1981). This species belongs to the '*M. argentea* complex' characterized by its small size (4–7 mm, about 25 segments), large refractile lymphocytes (intensely white in reflected light). Ectal duct of spermatheca covered with glands, ampulla spherical or pear-shaped. The two anterior pairs of septal glands merge dorsally, the last pair being free and elongate. The distinctive feature of the present species is the entire absence of setae except for the ventral bundles in segment II–VI. In segment III–VI each bundle contains two setae whereas there is usually only one seta present in segment II although this is occasionally absent.

Generis et species incerti

Peat was collected from near the BAS station on Signy Island, South Orkney Islands, on 20 November 1980 containing plant material thought to be introduced to this island from the Falkland Islands and/or South Georgia in the mid-1960s (see Block, Burn and Richard, 1984). The worms from this locality were inspected alive and are congeneric with some preserved specimens collected from Lynch Island (South Orkney Islands) and Deception Island (South Shetland Islands). As fully mature individuals were not present, a complete species description cannot be given at present. Since the taxon in question shows a combination of characters unknown in any existing genus, it is undoubtedly necessary to erect a new genus in which to include it, when it is fully described. Estimates of population density are > 3200 worms per square metre.

The main characteristics are as follows: Medium sized, *c.* 15 mm in length, rather stout, milkish white in colour, approximately 40 segments. Setae sigmoid 2,3,4,*5*,*6*–2,*3*,4:6,*7*,*8*–4,*5*,6. Gradual transition between oesophagus and intestine. Chloragogen cells form a dense layer from VII, the diameter of the cells being slightly larger than the length of the lymphocytes, the chloragogen cells filled with brown refractile globules. All three pairs of septal glands free dorsally, ventral lobes in V and VI. The brain slightly incised posteriorly. Blood colourless, dorsal vessel arising in XIII. Anteseptale portion of nephridia with coils of the nephridial canal, efferent duct arising ventrally or nearly terminally on postseptale. Small elongate, hyaline lymphocytes pointed at both ends present in abundance. No other type of lymphocytes observed. Seminal vesicle apparently well developed. Spermathacae without diverticulae, its ectal duct rather long and well demarcated and apparently with a crown of glands round the ectal orifice. Entally the spermathecae communicate with oesophagus.

In the general shape of nephridia and spermathecae and in the presence of small hyaline lymphocytes the present finding resembles members of the genera *Fridericia* and *Buchholzia*. However, it differs from the former in having sigmoid setae (*Fridericia* has straight setae and innermost setae in the bundles pairwise shorter than the outer ones), and it differs from the latter in having a straight gut and postclitellar origin of the dorsal vessel (*Buchholzia* has an abrupt expansion of the gut at VII/VIII usually with intestinal diverticula from which the dorsal vessel arises).

Miscellaneous

A few immature Aelosomatidae and Tubificidae from living *Rostkovia* (site 4) (collected on 12 March 1981 at King Edward Cove, South Georgia).

Discussion

Seven terrestrial species have been identified, and five of these (*Mesenchytraeus pelicensis*, *Cognettia sphagnetorum*, *C. glandulosa*, *Henlea perpusilla* and *H. ventriculosa*) are widely distributed also in the Holarctic region. The two *Cognettias* and the two *Henleas* are among the most common enchytraeids in a wide variety of habitats in northern Europe. It is likely that they have been introduced unintentionally by man into some of these isolated Antarctic sites.

Some of the species, particularly *Cognettia sphagnetorum* and *C. glandulosa*, occurred in such high numbers in the South Georgia habitats (the moss bank, *Festuca*, *Rostkovia* and *Acaena*) that their densities equal those reported from northern Europe (e.g. Nielsen, 1955; Peachey, 1963). Population estimates of enchytraeids up to 3110 m^{-2} have been made for sheltered *Festuca contracta* grassland above the south side of King Edward Cove, South Georgia (Smith and Stephensen, 1975).

A detailed discussion of the zoogeographical and ecological implications of these results is inappropriate here, but some comments may be made. Only 16 taxa of Enchytraeidae have been recorded previously for the Antarctic region (mostly from littoral habitats) and none of the seven species identified from the present terrestrial collections has been found previously. That five of these new records are for species widely distributed in Europe and elsewhere in the Northern Hemisphere, suggests that they may have been transported by human or other agency into the Antarctic region. Dispersal may have been as worms, worm fragments or as cocoons. If this is the case, it complicates the biogeographical interpretation of the data.

Enchytraeids have been recorded from every continent, but they reach their greatest abundance in moist temperate soils. The family is commonly supposed to be of Arctic origin (Stephenson, 1930), and it is well represented there. These worms are terrestrial, littoral or aquatic in habitat, and some taxa may be bipolar in distribution. More information on their taxonomy and distribution within the Antarctic Region, and in the Southern Hemisphere generally, is required.

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References

Benham, W. B. 1905. On the Oligochaeta from the Southern Islands of the New Zealand region. *Transactions of the New Zealand Institute*, **37**, 285–97.

Benham, W. B. 1922. Oligochaeta of Macquarie Island. *Australasian Antarctic Expedition, 1911–1914. Scientific Report*, **6**, 1–38.

Block, W. 1979. Terrestrial invertebrates. (*In* Furse, C. *Elephant Island – an Antarctic Expedition*. Anthony Nelson, Shrewsbury, 226–9. Appendix E.)

Block, W., Burn, A. J. *and* Richard, K. J. 1984. An insect introduction to the maritime Antarctic. *Biological Journal of the Linnean Society*, **23**, 33–9.

BURGER, A. E. 1978. Terrestrial invertebrates: a food resource for birds at Marion Island. *South African Journal of Antarctic Research*, **8**, 87–99.

CHRISTENSEN, B. 1961. Studies on cyto-taxonomy and reproduction in the Enchytraeidae. *Hereditas*, **47**, 387–449.

EDWARDS, J. A. 1980. An experimental introduction of vascular plants from South Georgia to the maritime Antarctic. *British Antarctic Survey Bulletin*, No. 49, 73–80.

EDWARDS, J. A. *and* GREENE, D. M. 1973. The survival of Falkland Island transplants at South Georgia and Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 33 & 34, 33–35.

MICHAELSEN, W. 1888. Die Oligochaeten von Sud-Georgien. *Jahrbuch der Hamburgischen wissenschaftlichen Anstalten*, **5**, 53–73.

MICHAELSEN, W. 1905. Die Oligochaeten der schwedischen Sudpolar-Expedition. *Wissenschaftliche Ergebnisse der schwedischen Sudpolar-Expedition 1901–1903*, Band V, Zoologie I, Lief 3, 1–12. Stockholm.

NIELSEN, C. O. 1955. Studies on Enchytraeidae 2. Field Studies. *Natura Jutlandica*, **4**, 1–58.

NIELSEN, C. O. *and* CHRISTENSEN, B. 1959. The Enchytraeidae: critical revision and taxonomy of European species. *Natura Jutlandica*, **8–9**, 1–160.

PEACHEY, J. E. 1963. Studies on the Enchytraeidae (Oligochaeta) of moorland soil. *Pedobiologia*, **2**, 81–95.

PICKFORD, G. E. 1932. Oligochaeta 2. Earthworms. *Discovery Reports* (*Cambridge*), **4**, 265–90.

SMITH, R. I. L. *and* STEPHENSON, C. 1975. Preliminary growth studies on *Festuca contracta* Kirk and *Deschampsia antarctica* Desv. on South Georgia. *British Antarctic Survey Bulletin*, Nos. 41 and 42, 59–75.

STEPHENSON, J. 1930. *The Oligochaeta*. Oxford, Oxford University Press.

STEPHENSON, J. 1932. Oligochaeta. Part I. Microdrili (mainly Enchytraeidae). *Discovery Reports* (*Cambridge*), **4**, 233–64.

WHITEHEAD, A. G. *and* HEMMINGS, J. R. 1965. A comparison of some quantitative methods of extracting small vermiform nematodes from soil. *Annals of Applied Biology*, **55**, 25–38.

SEASONAL CHANGES IN COLD RESISTANCE OF SOIL ARTHROPODS

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INTRODUCTION

The invertebrate soil fauna, and the arthropods in particular, exhibit two main strategies for surmounting freezing conditions in the field. The first is freezing tolerance in which the animal survives the formation of ice in extracellular tissue. The second strategy is freezing intolerance (or freezing susceptibility) where ice formation within the animal's body is lethal. The former may be termed a risk-free strategy whilst the latter is risk-dominated. Soil arthropods have largely adopted the second strategy, that of being freezing susceptible, and avoid ice crystallisation within their bodies by varying amounts of supercooling or undercooling (the maintenance of their body fluids in the liquid phase at temperatures below their normal freezing level). Information for other soil invertebrates is fragmentary (Block 1982), but it appears that supercooling is common and widespread incommunities ranging from temperate to polar conditions. Supercooling is a prime factor in the survival of arthropods living in extreme or low temperature habitats and a large body of data about it has been accumulated.

Compared with above ground/aerial habitats the soil environment is relatively buffered, especially with regard to temperature fluctuations. Even so, considerable powers of freezing avoidance by means of supercooling are found in those arthropod representatives of the soil community that have been investigated. If the measured supercooling point of an individual is taken as an indication of its overall cold resistance, it is apparent that large seasonal variations can occur,dependent upon species, habitat, etc. The physiological mechanisms and the biochemistry underlying such natural changes in cold resistance are currently being unravelled for a variety of arthropod systems (see Sømme (1982) and Baust (1982) for reviews). From an

ecological viewpoint, the environmental processes that trigger these changes are equally important, and overwintering survival may be crucial for many soil species, especially those living in marginal, stressful or extreme low temperature habitats. Cold survival may affect soil community structure andthe population dynamics and life histories of particular species, which in turn may influence the ways in which such communities respond to perturbations, either natural or man-made.

The scope of this paper is to review some of the information on freezing tolerance and intolerance pertinent to soil zoological studies, and to consider the conditions surrounding nucleation events as they pertain to arthropods.

FREEZING TOLERANCE

This appears to be relatively rare in the soil fauna, the majority of the examples of this adaptational strategy being found in aerial insects, mainly Coleoptera and Diptera (Zachariassen and Hammel 1976; Miller 1982; Ring 1982). The main features of such a strategy are that the organism freezes at a relatively high sub-zero temperature (-5 to -10°C), and freezing of the extra-cellular fluid occurs, which is non-lethal. Most freezing-tolerant insects possess ice nucleating agents in their body fluids, especially in the haemolymph. These inhibit supercooling and ensure ice formation in the extracellular fluids, thereby reducing the possibility of the formation of lethal intracellular ice before cell dehydration has proceeded too far. Such ice nucleating agents are heat sensitive and likely to be proteinaceous. They often act in systems containing high levels of polyols, and appear to override the supercooling potential. As few truly soil forms exhibit freezing tolerance, this will not be detailed further.

FREEZING INTOLERANCE

Supercooling occurs widely in soil arthropods (Block 1982). The degree of supercooling of an individual may be influenced by the size of the animal, the water content and physiological condition, the biochemical composition, and, of importance in terms of its biology, the life stage to which the individual belongs, i.e. whether it is an overwintering one or not. Seasonal changes (acclimatisation) in supercooling capacity occur regularly and predictably in field populations and, in some species can be induced in laboratory cultures by various acclimation regimes including temperature and moisture changes. The levels of some low molecular weight polyhydroxy compounds (e.g. sugars and sugar alcohols or polyols) have been correlated with such increases in supercooling ability. Food type and the material contained within the alimentary system, although biochemically isolated from the remainder of the arthropod body, is a prime ice nucleation site in some species, but not so in others. Many other possible nucleators are known (see below), and their activity is likely to depend on the microsite conditions prevailing at the time of exposure to potentially freezing environmental conditions. Moisture may be important during supercooling in two main ways. Firstly, it may be an initiator of whole-body freezing from surface films and droplets. Secondly, the amount of internal water and its distribution within the arthropod may regulate polyol levels and initiate ice nucleation in freezing-susceptible forms.

It is tempting to suggest that supercooling as an adaptation has been selected for during evolution, not only in arthropods living in soil, but also in a wide variety of other ectotherms. In the relatively stable conditions of the sub-surface soil environment, the ability to supercool by only a few degrees Celsius will ensure the arthropod's survival during short periods of freezing. However, near the soil surface, the frequency of such

freeze-thaw cycles will increase markedly, and the survival value of supercooling will be enhanced from a metabolic and biochemical standpoint. But the mechanisms by which supercooling is brought about may be extremely simple, especially in physical terms, and may have required little evolutionary selection. This may explain its common occurrence throughout the invertebrates. Freezing tolerance, on the other hand, requires specific physiological, and often biochemical, conditions within the animal, and selection for these may have been far more rigorous.

NUCLEATION AND THERMAL HYSTERESIS

Nucleation in biological systems is defined as the physico-chemical process by which ice forms and grows throughout an organism. Homogeneous nucleation of pure water occurs around -40°C and, in most organisms, nucleation is heterogeneous, being caused by substances or particles acting as nucleators. These are often termed ice nucleating agents and include dust particles, proteins, food fragments, etc. There are four main classes of nucleators that may operate in soil arthropods: (a) certain organic compounds, (b) bacteria, (c) plant-derived substances, which are probably polysaccharides, found in sap (Krog et al. 1979) and (d) insect substances mainly contained in haemolymph. The precise site(s) of ice nucleation within the arthropod body is unknown, but several possibilities have been suggested. The gut and its contents are important in certain species (e.g. Collembola and mites), whilst the haemolymph and other compartments appear to be significant in others. After freezing, recrystallisation may occur, which extends the damage brought about by initial ice crystal formation. By absorption of smaller, neighbouring crystals onto larger crystals their surface to volume ratio is reduced. Thus crystallisation and re-crystallisation can proceed extremely rapidly through the invertebrate body. For this reason, the measured supercooling points in both freezing

tolerant and intolerant forms are important. It is difficult, however, on current evidence to define the actual lethal temperature or state in many species.

The phenomenon of thermal hysteresis (a temperature difference between the freezing point and melting point of an isolated body fluid sample) occurs in many cold-adapted arthropods, both freezing tolerant and intolerant. It is brought about by proteins (termed thermal hysteresis proteins), which are similar to the antifreeze proteins and glycoproteins of polar marine teleosts. Such antifreezes protect the arthropod without the osmotic disruption of the accumulation of polyols and sugars. Such proteins can be accumulated during warm periods, and photo-period, as well as temperature, controls their level in the insects which have been studied (Duman 1982). In freezing tolerant species, it is likely that thermal hysteresis will have a protective role only when their level of freeze tolerance is low, i.e. spring and early autumn when sub-zero temperatures may occur.

DISCUSSION

Seasonal changes in cold resistance occur in response to a variety of environmental triggers, temperature, moisture and photo-period being paramount. The field observations and laboratory measurements made on field samples of soil arthropods suggest a complex series of interactions, which result in the overall cold resistance of a particular species or life stage. In freezing-tolerant forms, these centre on the efficiency of their ice-nucleating agents and the level of supercooling, influenced by the presence or absence of polyols and other substances. In freezing-intolerant species, the interplay of thermal hysteresis proteins (when present), cryoprotectants (including polyols such as glycerol), body water and a variety of ice nucleators contribute to cold resistance. In species that

have adopted either strategy, the physical event of ice nucleation is of fundamental and far-reaching importance. It is an event about which little is known in biological systems.

The direct importance of the study of cold resistance in soil arthropods is not always the mechanism by which it is achieved, but the result of it in terms of the numbers of individuals in a population that survive winter or a similar cold period. This aspect has considerable value in the study of soil-borne arthropod pests, where post-winter survival numbers create the pattern of pest infestation in future years. More research in this area should be directed towards economic species, whilst appreciating that all overwintering mortality may not be attributable to cold/freezing survival.

The widespread and common occurrence of freezing susceptibility in arthropods should be noted. All the UK insect pests that have been investigated, are freezing intolerant (Bale 1985), whilst some freezing-tolerant forms are plant parasites. It may be that selection pressure has been exerted, in evolutionary terms, on ice-nucleating agents (Duman 1985), and that the present distribution of freezing-tolerant and intolerant forms in the arthropods reflects such adaptations.

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REFERENCES

Bale, J. 1985. Applied aspects of insect cold hardiness. Cryo-Letters (in press).

Baust, J.G. 1982. Environmental triggers to cold hardening. Comparative Biochemistry and Physiology 73A: 563-570.

Block, W. 1982. Cold hardiness in invertebrate poikilotherms. Comparative Biochemistry and Physiology 73A: 581-593.

Duman, J.G. 1982. Insect antifreezes and ice-nucleating agents. Cryobiology 19: 613-627.

Duman, J.G. 1985. Ice nucleating agents in insects. Cryo-Letters (in press).

Krog, J.O., Zachariassen, K.E., Larsen, B. & Smidsrod, O. 1979. Thermal buffering in Afro-alpine plants due to nucleating agent induced water freezing. Nature (London) 282: 300-301.

Miller, K. 1982. Cold-hardiness strategies of adult and immature insects overwintering in interior Alaska. Comparative Biochemistry and Physiology 73A: 595-604.

Ring, R.A. 1982. Freezing-tolerant insects with low supercooling points. Comparative Biochemistry and Physiology 73A: 605-612.

Sømme, L. 1982. Supercooling and winter survival in terrestrial arthropods. Comparative Biochemistry and Physiology 73A: 519-543.

Zachariassen, K.E. & Hammel, H.T. 1976. Nucleating agents in the haemolymph of insects tolerant to freezing. Nature (London) 262: 285-287.