FEEDING STUDIES ON THE COLLEMBOLAN *Cryptopygus antarcticus* Willem AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS

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Abstract. The gut contents and faecal pellet constituents of individuals of *C. antarcticus* collected from 11 sites are described. Freshly collected material was examined microscopically and categories of food intake were assessed on a 0–5 scale of abundance. In addition, microbiological culture techniques were used to detect the presence of viable bacteria, fungi, and algae in the gut contents and faeces. *C. antarcticus* exhibits a degree of selectivity in its food intake, and filamentous fungi and algae are the most important food materials at Signy Island. The feeding behaviour and importance of *C. antarcticus* in soil processes are discussed.

Cryptopygus antarcticus Willem is a common Antarctic collembolan which also has a circumpolar distribution in the sub-Antarctic. Research on this species, including data from a study at Signy Island, was reviewed by Tilbrook (1970). Within its geographical range, this small arthropod, varying from 400 to 2,000 μm. in length for all its life stages, is found in almost all terrestrial habitats which are free from permanent ice and snow. On Signy Island this species is usually numerically dominant in the arthropod communities especially in the wetter habitats.

Information on the feeding habits of *C. antarcticus* is limited and Tilbrook (1970) concluded that it is impossible to assess the true role of this species within the ecosystem until its food intake in the field has been evaluated. The present study was undertaken to provide this information.

Several studies have been made on the feeding of other Collembola in temperate climates. In most of these the gut contents were scored for presence or absence, or frequency of different materials (Agrell, 1940; Poole, 1959; Knight and Angel, 1967; Bödvarssen, 1970; Gilmore and Raffensperger, 1970). A quantitative approach was used by McMillan and Healey (1971) and Anderson and Healey (1972). In the present study the former technique was employed.

The feeding of Antarctic species of Collembola has not been examined in detail. Fitzsimons (1971) examined gut contents of *Gomphiocephalus hodgsoni* Carpenter and made culture studies for detecting the presence of viable micro-organisms; this technique is used more extensively in the present work.

The majority of the results obtained by other workers indicate that the Collembola are largely unselective feeders ingesting what is available (Christiansen, 1964; Hale, 1967; Wallwork, 1970). Christiansen (1964) suggested that exhaustive analyses of the different categories of food eaten by a single species under widely varying conditions were required. By direct microscopic examination and microbiological culture techniques of gut contents and faeces of individuals of *C. antarcticus* from several habitats on Signy Island, it is hoped that the present study partly fulfils that need.

Materials and Methods

Collection of animals

Animals were collected from 11 sites on Signy Island during the 1972–73 summer as follows (map references taken from the Directorate of Overseas Surveys, map 210, Signy Island, 2nd edition, with 1 km. grid, 1975):

1. Signy Island reference site 1 (see Tilbrook, 1973), in a moss turf dominated by *Polytrichum alpestre* Hoppe and *Chorisodontium aciphyllum* (Hook. f. et Wils.) Broth. (103^{8} 045^{3}).
2. Signy Island reference site 2 (see Tilbrook, 1973), in a wet moss carpet dominated by *Calliergon sarmentosum* (Wahlenb.) Kindb., *Calliergidium austrostramineum* (C. Muell.) Bartr. and *Drepanocladus uncinatus* (Hedw.) Warnst. (103^{7} 034^{1}).
3. Moss turf dominated by *P. alpestre* with some *C. aciphyllum* (103^{9} 045^{2}).

4. Under stones at the margin of a stone stripe caused by solifluction; no macroscopic vegetation (104^{1} 045^{1}).
5. Beneath *Prasiola crispa* (Lightf.) Menegh. in a water-flushed rock gully below a cape pigeon (*Daption capensis* L.) nesting area (103^{9} 045^{1}).
6. In a wet moss carpet dominated by *D. uncinatus* (104^{1} 045^{1}).
7. Under large stones surrounded by a wet stand of *D. uncinatus* (104^{0} 045^{2}).
8. In a wet organic soil consisting of elephant seal (*Mirounga leonina* L.) faeces, moulted skin and hair. Surface overgrown by thalli of *P. crispa* and filamentous blue-green algae (103^{5} 045^{5}).
9. In dry moss cushions of *Tortula* sp. on slopes below a marble outcrop (103^{0} 045^{9}).
10. In *D. uncinatus* at the top of a water-flushed rock gully (103^{8} 045^{3}).
11. Under a felt of filamentous Cyanophyceae overgrowing a very wet *D. uncinatus* carpet (103^{7} 043^{1}).

Most collecting was undertaken at the two Signy Island reference sites (SIRS 1 and 2), where long-term ecosystem studies are in progress (Tilbrook, 1973).

Portions of vegetation and soil were removed from each site and transported to the laboratory in clean containers. Immediately prior to treatment the material was teased apart on a sterile surface, and the live Collembola which emerged were collected by sterile aspirator and placed in sterile Petri dishes containing slightly moistened filter paper for temporary storage until treatment. Treatment was always within a few hours of sample collection.

Microscopic examination of gut and faecal pellet contents

The complete gut was obtained by first inactivating each animal by rapid deep freezing to −20° C for 10 min. It was then placed on a 2 per cent sterile agar (Oxoid Ltd., No. 3) surface. The head capsule was removed using two fine needles and the gut squeezed from the body through the anterior opening using fine forceps. The gut and its contents were removed intact in about two out of every three animals thus treated.

Faecal pellets were obtained by placing ten animals on a 2 per cent sterile agar surface in a closed Petri dish. After 30 min. many faecal pellets had been produced. The animals were removed from the dish leaving the faeces intact on the moist agar surface. New batches of faeces were obtained from field fresh animals.

Guts with visible contents and faecal pellets were examined microscopically at magnifications up to 1,000 diameters. The contents of both were placed in the following 15 categories:

a. Melanized fungal hyphae.
b. Hyaline fungal hyphae.
c. Septate fungal spores.
d. Aseptate fungal spores.
e. Yeast cells.
f. Diatoms.
g. *Prasiola crispa*, a foliose green alga.
h. Green and yellow-green algal filaments.
i. Green and yellow-green algal unicells.
j. Blue-green algae.
k. Moss protonemata.
l. Dead moss and liverwort tissue.
m. Micro-arthropod remains.
n. Other identifiable material.
o. Unidentifiable material.

The abundance of each category in a gut or a faecal pellet was estimated on a 0–5 scale of

increasing abundance, 0 indicating absence and 5 complete or almost complete filling of the gut or pellet. The analysis included 164 gut contents and 75 faecal pellets of *C. antarcticus*.

Culture techniques for detection of viable micro-organisms in guts and faeces

Three media were used: Sabouraud dextrose agar (SD) (Oxoid Ltd.), tryptone soya agar (TSA) (Oxoid Ltd.) and Bold's modified Bristol's medium (BBM) (Chantanachat and Bold, 1962); the latter was solidified with 2 per cent agar. The first medium was selective for yeasts and filamentous fungi, although bacteria also appeared; the second was selective for bacteria but also supported some fungi; the third was an algal medium which also supported the growth of bacteria and fungi. All were incubated at room temperature (*c.* 18° C) for 3 weeks, the first two in darkness and the third in light provided from four 30 W daylight fluorescent tubes.

Viable micro-organisms in the guts were detected by two techniques. Before surface sterilization, in the first technique, a control was performed in which each animal was agitated in a drop of water on a nutrient agar plate in order to dislodge surface contaminants. Animals were then surface-sterilized by shaking in 1 : 1,000 mercuric chloride solution for 5 min. After washing in sterile water, each animal was macerated over a sector of a nutrient agar medium. After sterilization but before maceration, a check was made for surface contaminants in the same way as in the preliminary control. In the second technique, guts were dissected from animals using aseptic methods, each being spread over the surface of a sector of a nutrient agar medium. As a control, each of the remaining body walls was also cultured to provide a comparison between the number of viable surface contaminants and viable gut constituents.

Faecal pellets were also cultured. Each pellet was transferred on a small block of the underlying agar to a sector of a nutrient agar medium and distributed over its surface. A control was also performed. An equal number of agar blocks to pellets removed was spread on the culture media in order to check whether surface contaminants from the animals had been dislodged on to the agar surface.

Results

Microscopic examination of gut and faecal pellet contents

The mean abundance of each constituent of the guts and faecal pellets is given in Fig. 1. The gut and faecal pellet contents of individual animals from any one site were generally similar in their composition. However, there were often differences between animals collected from different sites.

In most of the guts examined the various constituents were mixed and scattered throughout the whole length of the gut. Only in one of the 164 guts was there a noticeable change in the composition of the contents from the anterior to the posterior, presumably due to digestive processes. Sometimes there were small aggregations of a particular material, e.g. fungal hyphae or algal cells. In *c.* 7 per cent of the guts there were larger aggregations of one particular type of food substance.

Where both gut contents and faeces of *C. antarcticus* were examined (sites 1, 2 and 10), both had similar constituents. The passage of material through the gut had produced no visible change in its nature. For site 7, the gut contents and the faeces were each examined from animals collected on two separate occasions. The differences observed were probably due to sampling from two areas with different available foods.

Unidentifiable material (category o) was common in most guts and faeces. It consisted of fine amorphous material with grains less than 1 μm. in diameter. It was probably decayed plant fragments, mineral soil particles and the contents of fungal hyphae and algal cells. Identifiable material was usually more abundant.

Fungal material (categories a-e) was frequently present and only absent in animals from site 8. It was the dominant identifiable gut and faecal pellet constituent from sites 1, 2 and 3,

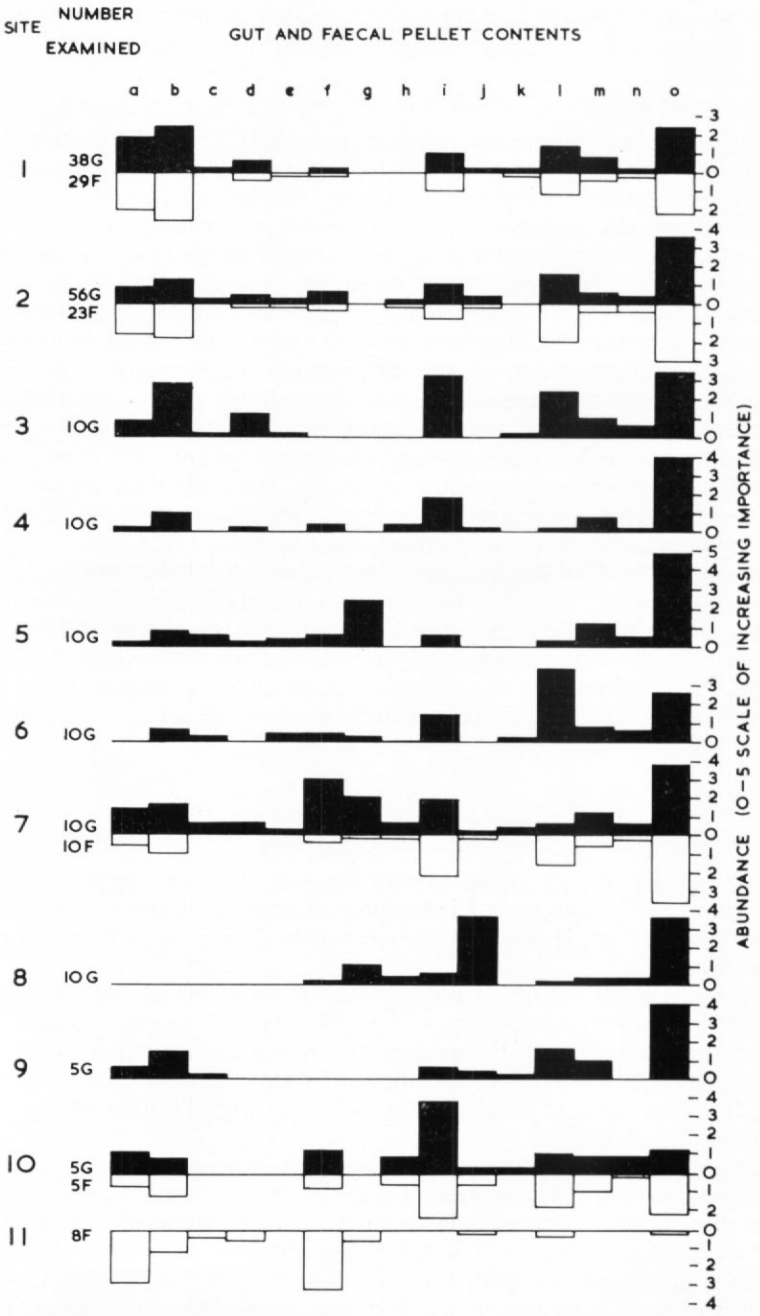

Fig. 1. Mean abundance of each of the constituents in gut contents and faecal pellets of *Cryptopygus antarcticus* from various sites at Signy Island as found by direct microscopic examination of fresh material.
a. Melanized fungal hyphae; b. Hyaline fungal hyphae; c. Septate fungal spores; d. Aseptate fungal spores; e. Yeast cells; f. Diatoms; g. *Prasiola crispa*; h. Green and yellow-green algal filaments; i. Green and yellow-green algal unicells; j. Blue-green algae; k. Moss protonemata; l. Dead moss and liverwort tissue; m. Micro-arthropod remains; n. Other identifiable material; o. Unidentifiable material.
G. Gut contents; F. Faecal pellet contents.

particularly from SIRS 1. Fungal hyphae were of several types, 1–9 μm. wide, septate or aseptate, and either hyaline or melanized. The fragments in the guts had a mean length of *c.* 40 μm. and had been chopped into short lengths by the mouth parts. In a gut full of hyaline hyphae, it was estimated that there was a total length of at least 40 mm. Sometimes the hyphae were lining decaying moss and liverwort cells. Living contents were never recognized within the hyphae even with phase-contrast microscopy. Fungal spores and yeast cells were infrequent or rare.

Algal material (categories f-j) was the dominant identifiable material in animals from six sites. At least 25 algal species were recorded, and green and yellow-green unicells were the most frequent. Empty cell walls, ruptured cells and apparently healthy cells were all observed in both guts and faeces. In all six sites, algae were either the only form of vegetation (sites 4, 5 and 8) or were abundant amongst various mosses (sites 7, 10 and 11). The dominant form of algal growth in the habitat was also dominant in the gut contents and faeces. In guts of animals from site 5, *Prasiola crispa* cells had been ruptured. In animals from site 8 both *P. crispa* and filamentous Cyanophyceae had released their cell contents. The sheaths of the Cyanophyceae did not appear to have been affected by passage through the guts. The extracellular gelatinous matrices of the colonial forms of green and yellow-green algae also remained intact even when the cells within were ruptured. In most animals, diatoms were represented only by occasional empty siliceous frustules or their fragments. However, in animals from site 10, healthy diatom cells and ruptured cells were present.

Moss and liverwort material (categories k-l) invariably comprised dead and decaying cells. No cells were observed with healthy green contents and living bryophytes, although abundant in several sites, were apparently unpalatable to *C. antarcticus*. The decaying cells were usually fragmented and occasionally were associated with fungal hyphae.

Micro-arthropod remains (category m), especially collembolan setae, cuticle fragments and black pigmented body fluids were present in many animals but in low abundance. Many guts contained an occasional seta but few had more substantial remains. Occasionally cuticular material resembled the remains of Acari. This suggests a degree of carnivory and possibly cannibalism in a species hitherto considered to be entirely herbivorous.

Other identifiable material (category n) was of low abundance. When examinations were made at a magnification of 1,000 diameters, bacterial cells were recognized. Cocci and bacilli were seen as single cells, in chains and in small gelatinous colonies. Three guts contained what appeared to be claws of Tardigrada and one contained a fragment of a bird's feather. Mineral particles were also observed.

Culture techniques for detection of viable micro-organisms in guts and faeces

Viable micro-organisms were detected in 58 per cent of the guts by both techniques (Table I). With both methods, the controls confirmed that the growths were produced from the gut contents and not from surface contaminants. Bacteria were most frequently recovered from all three sites with algae second in frequency. Yeasts were rare and detected only at site 1. The total numbers of colonies produced from dissected guts emphasizes the dominance of bacteria and algae in the animals' diet; there were over 1,700 bacterial colonies, 200 algal colonies but only 20 filamentous fungi and a single yeast. There were considerable differences in the numbers of bacterial colonies produced from individual animals, the range being from one to over 100 colonies. Similarly, most guts produced only a few colonies of algae but occasionally large numbers appeared. When this occurred, one algal species usually dominated in each animal, but in different animals from the same site different species were dominant.

A similar total number of faeces (55 per cent) contained viable micro-organisms, which was confirmed by an almost total absence of microbial growth from the controls. Bacteria were

TABLE I. NUMBERS OF *Cryptopygus antarcticus* WHICH PRODUCED MICROBIAL GROWTH FROM THEIR GUT CONTENTS

Method	*Site*	*Medium*	*Total number of animals treated*	*Numbers of animals producing microbial growth*				
				Total	*Bacteria*	*Filamentous fungi*	*Yeasts*	*Algae*
Surface sterilization	1	BBM	40	33	16	15	3	19
		SD	18	7	6	3	0	—
	2	BBM	32	16	16	0	0	2
Dissection of guts	1	SD	8	2	0	2	1	—
		BBM	20	8	7	2	0	1
	2	SD	10	7	7	0	0	—
		BBM	13	13	13	1	0	10
	3	TSA	15	7	7	0	0	—
		SD	15	6	6	1	0	—
		BBM	15	9	9	2	0	5
TOTAL ANIMALS			186	108	87	26	4	37*

Media: BBM, Bold's modified Bristol's medium; SD, Sabouraud dextrose agar; TSA, tryptone soya agar.
— No test; TSA and SD do not support algal growth.
*Total of 130 guts were tested for presence of viable algae on BBM.

again dominant with algae second in abundance, and filamentous fungi and particularly yeasts were comparatively rare (Table II).

DISCUSSION

It is apparent that *C. antarcticus* ingests a wide range of materials and that most of the intake is defaecated with little visible change having occurred, and without loss of viability of at least a proportion of the micro-organisms in the original food. Macnamara (1924), in the first detailed study of feeding in Collembola, provided a general description of collembolan gut contents, which is similar to that found in the present study, the food consisting largely of decaying plant material, fungi and microscopic algae. Christiansen (1964) considered fungal hyphae, dead or decaying plants and algae were the two most frequent dietary groups of Collembola. *C. antarcticus* is thus similar in its diet to other soil Collembola.

Despite the wide variety of gut contents, there is evidence that *C. antarcticus* feeds selectively. The most obvious absence from the guts is green living bryophyte tissue and, although mosses and liverworts were abundant in sites 1, 2, 3, 6, 7, 9 and 10, there was no evidence of them being a constituent of the diet, even though animals were often seen crawling over the vegetation. However, there was a preference for dead and decaying bryophyte tissue. Similarly, Schaller (1949) found that Collembola did not feed on fresh leaves of higher plants but ingested decaying leaf litter, whilst Dunger (1956) noted a preference for leaves which had been partially decomposed by micro-organisms. The Antarctic collembolan *Gomphiocephalus hodgsoni* Carpenter did not feed on living mosses in culture (Fitzsimons, 1971). Although healthy green algae are ingested by *C. antarcticus*, it cannot be described as a general plant feeder (Gressitt, 1967).

The relative abundances of the gut and faecal pellet constituents appeared to be similar to those of palatable material in the habitat. In sites containing abundant fungal hyphae (moss-turf sites 1 and 3), fungi are an important gut constituent, and in sites containing abundant algae

TABLE II. ABUNDANCE OF MICROBIAL GROWTH PRODUCED FROM FAECAL PELLETS OF *Cryptopygus antarcticus*

Site	*Medium*	*Total number of faecal pellets treated*	*Total number of faeces producing microbial growths*					*Total number of microbial colonies produced*			
			Total	*Bacteria*	*Filamentous fungi*	*Yeasts*	*Algae*	*Bacteria*	*Filamentous fungi*	*Yeasts*	*Algae*
1	TSA	24	12	9	4	1	—	39	4	1	—
	SD	34	8	0	6	3	—	0	11	3	—
	BBM	42	35	20	12	3	23	106	21	3	114
2	TSA	34	7	7	0	0	—	51	0	0	—
	SD	24	14	14	0	0	—	85	0	0	—
	BBM	52	19	16	2	0	5	260†	2	0	7
3	TSA	10	10	10	1	0	—	80	1	0	—
	BBM	16	16	16	5	0	7	389†	5	0	21
6	BBM	8	6	6	0	1	3	140†	0	1	3
7	BBM	20	20	20	3	0	10	1700†	4	0	193
TOTALS		264	147	118	33	8	48*	2880†	38	8	338*

Media: BBM, Bold's modified Bristol's medium; SD, Sabouraud dextrose agar; TSA, tryptone soya agar.
—No test; TSA and SD do not support algal growth.
*Total of 138 faecal pellets were tested for presence of viable algae on BBM.
†Number estimated.

(sites 5, 8, 10 and 11) these become the dominant identifiable gut constituent. *C. antarcticus* occupies different habitats because of its ability to feed opportunistically on a variety of readily available material, as found for other Collembola by Agrell (1940), Gilmore and Raffensperger (1970) and Fitzsimons (1971).

The large amounts of fine-grained unidentifiable material found in most specimens of *C. antarcticus* agree with the results of Bödvarsson (1970) and is similar to the "fine debris" described by Poole (1959). Its source is difficult to ascertain, although it possibly includes the released contents of ruptured fungal hyphae and algal cells.

The low frequency of recovery of viable fungi in the culture experiments, despite their high frequency in direct microscopic examination, suggests that the fungal intake was either dead or that maceration and digestive processes had caused the death of a large proportion. Wallwork (1970) suggested that fungal feeders may be highly selective in their digestive processes, utilizing fats and carbohydrates but not interfering with the subsequent germinative powers of the fungus. There was no evidence for this in the present study. Poole (1959) also recognized the difficulty of deciding whether Collembola fed directly on living fungi or on their dead remains. The large amounts of fungal hyphae seen in the faeces of *C. antarcticus* from sites 1 and 2 demonstrate the resistance of the hyphal walls to digestion. It seems that if at least a proportion of the intake did not have hyphal contents its food value would be low.

Some of the ingested material appeared to be without food value, e.g. empty siliceous diatom frustules and mineral grains, which suggests a certain amount of unselectivity in feeding. Observations made on animals in culture, on moist illuminated peat fragments at room temperature, showed that a proportion of animals wandered randomly over the peat surface, whilst others remained stationary. One *C. antarcticus* was observed feeding on another dying individual for over 2 hr. Macnamara (1924) described a similar occurrence with a *Friesea* species. Apparently, once a large enough food source has been located, a collembolan will remain and feed. Gut-content examination also provided evidence for this in *C. antarcticus*. Several guts contained large aggregations of one particular material, suggesting that feeding occurred in one micro-habitat. The apparently random feeding of individuals with very mixed gut contents may reflect the intake of a wandering animal which has not yet located a suitable large food source. Once this has occurred, probably by chance although chemotaxis may play a part, the animal remains and feeds. A similar behaviour was suggested by Petersen (1971).

The importance of bacteria in the diet is hard to assess. Although observed by direct microscopic examination, they were never abundant. The numbers of colonies obtained in culture (Table II) represent a very small bacterial biomass. However, their digestion may be rapid and efficient and, if so, culture techniques would underestimate their importance. The large amount of decaying plant tissue in guts of animals from bryophyte sites may be ingested for the micro-flora coating its surfaces, as suggested by Christiansen (1964) and Butcher and others (1971). Symbiotic gut bacteria may also play a part in the break-down of resistant foodstuffs, e.g. chitin (Hale, 1967) and cellulose, but the importance of these in *C. antarcticus* cannot be assessed by the present study.

The importance of Collembola to soil processes has been discussed by several authors including Macfadyen (1965) and Hale (1967). Particular emphasis has been placed on the role of micro-arthropods in stimulating decomposition processes (Ghilarov, 1963). At Signy Island, *C. antarcticus* plays an important part in alga-dominated habitats as a consumer of living algal material. Maceration of larger growths and rupture of cells prepares the alga for microbial decomposition in the faeces. In bryophyte sites, this role is often unimportant and *C. antarcticus* becomes a consumer of the decomposing micro-organisms. Again, maceration of dead and decaying plant tissue probably aids its further microbial decomposition. Whether collembolan communities are effective in reducing fungal and bacterial biomass by browsing requires further study. They may stimulate microbial growth by grazing on senescent colonies

(Butcher and others, 1971). Whittaker (1974) did not find any correlation of mycelial and bacterial counts with Collembola numbers at several tundra sites.

An important role of Collembola feeding may be the dissemination of viable micro-organisms, into previously uncolonized micro-habitats, in faecal pellets. Preliminary experiments with *C. antarcticus* determined that the mean rate of faecal pellet production at 5° C was *c.* 0·5 pellets ind.$^{-1}$ hr.$^{-1}$ rising to *c.* 2·5 pellets ind.$^{-1}$ hr.$^{-1}$ at 15° C, the latter temperature often being exceeded in soil and amongst vegetation during the Antarctic summer. With populations of *c.* 5,000 animals m.$^{-2}$ amongst mosses (Tilbrook, 1967), large numbers of faecal pellets must be deposited each summer, possibly more than 10×10^6 m.$^{-2}$. These represent large numbers of foci of new, possibly intensified, microbial growth. Faeces deposited on senescent plant material may serve as the initial innoculum of decomposing micro-organisms. It has already been postulated (Broady, 1977) that Collembola are important to non-motile algae epiphytic on bryophytes. Viable algae in faeces deposited in the upper few millimetres of the plants subsequently grow and allow the alga to maintain its population.

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