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COLD-HARDINESS IN THE ANTARCTIC TICK, IXODES URIAE[1]

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Ixodes uriae White (Ixodidae, Acarina) is the predominant tick on the Antarctic peninsula. This species has a circumpolar distribution in both hemispheres and is associated with or known to parasitize 48 species of seabirds. Large colonies of 1,000 or more individuals of all life stages were found beneath rocks on the periphery of Adélie penguin rookeries near Palmer Station, Anvers Island. All life stages (egg, larva, nymph, and adult) were intolerant of freezing. Engorged nymphs and larvae had supercooling points between −18 and −20 C. Eggs had the lowest supercooling points (−28.7 C), while adults had the highest values (from −7 to −13 C). Acclimation to temperatures between −12 and +25 C for 2 wk had no effect on the supercooling point of engorged immobile nymphs. Desiccation of engorged nymphs to 80% of their initial weight resulted in no change in supercooling points or glycerol levels. In January, engorged nymphs enter a state of apolysis and lose mobility. Correlated with this change is an increase in cold tolerance as evidenced by a decrease in supercooling points from −11.5 to −19.5 C. This species exhibits the greatest range of thermal tolerance, from −30 to 40 C, reported for any Antarctic terrestrial arthropod. Except for a short period associated with feeding, *I. uriae* remains in a permanent state of cold-hardiness throughout the year.

INTRODUCTION

Terrestrial arthropods of the Antarctic may experience subzero temperatures during any month of the year. A variety of physiological and biochemical mechanisms of low-temperature tolerance have been identified in recent years. The wingless fly *Belgica antarctica* is freeze tolerant and produces an array of cryoprotective compounds including glycerol, erythritol, glucose, and trehalose (Baust and Edwards 1979; Baust 1980). Most Antarctic forms, however, are freeze susceptible and avoid freezing by depressing the whole body supercooling points and by selecting hibernacula that both moderate and dampen ambient temperature fluctuations (Baust 1980; Block 1980; Somme 1981). The mite *Alaskozetes antarcticus* and the collembolan *Cryptopygus antarcticus* avoid tissue freezing by lowering supercooling points to −30 C (Block et al. 1978; Somme 1978). Both low-temperature acclimation and desiccation induce glycerol production in *A. antarcticus* (Young and Block 1980). Seasonal changes in cold-hardiness, similar to those commonly observed in temperate species, have been identified (Lee and Baust 1981).

On the Antarctic peninsula, *Ixodes uriae* White is the predominant tick. This ixodid has a circumpolar distribution in both hemispheres and is associated with or known to parasitize 48 species of seabirds (Wilson 1964, 1970). Aggregations, sometimes numbering several thousand individuals, are found in well-drained tussocks or rock piles near seabird rookeries (Karpovich 1970; Murray and Vestjens 1967). This three-host tick typically requires 4–5 yr to complete its life cycle (Eveleigh and Threlfall 1974), although, on Macquarie Island where royal penguins remain on the rookeries for 6 mo, *I. uriae* may reach maturity within 2 yr (Murray and Vestjens 1967). Ticks attach during the nesting period and complete engorgement within 1 wk (Eveleigh and Threlfall 1974). Although eggs, engorged larvae, and engorged

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nymphs are the primary overwintering stages, some individuals engorge and molt in the same summer before overwintering (Eveleigh and Threlfall 1974).

Owing to its wide distribution, the diversity of its seabird hosts, and the fact that *I. uriae* occasionally bites man, this species has been investigated as a possible vector of viruses (Thomas et al. 1973; Yunker et al. 1973). More than 80 strains of arboviruses have been recovered from *I. uriae* in eastern Canada, western United States, and eastern Russia (Main et al. 1973). In a subantarctic study on Macquarie Island, Doherty et al. (1975) isolated viral strains that were antigenically related to ones found in subarctic regions—a result that suggests a bipolar route of dispersal.

Aspects of the respiratory metabolism of females, males, and nymphs of *I. uriae* have been reported by Lee and Baust (1982*a*). Laboratory acclimation to 0 and 10 C had no effect on respiration rates, which suggests a lack of compensatory acclimation in this species. Further, the metabolic rates of females of *I. uriae* are similar to those of temperate species, indicating the absence of metabolic cold adaptation. Little is known about the physiological aspects of cold-hardening in Antarctic ectoparasites. This report provides information on low temperature tolerance for several life stages of *I. uriae* on the Antarctic peninsula.

MATERIAL AND METHODS

Supercooling points (SCP) were measured using a Leeds and Northrup multichannel recorder and 30-gauge copper-constantan thermocouples attached to the tick. The cooling rate was ca. 1 C/min. The lowest temperature reached prior to the release of the latent heat of fusion was identified as the SCP. The SCP of blood samples from known hosts of *I. uriae* was determined by attaching a thermocouple to a capillary tube containing 3–5 µl of blood. The water content of ticks was taken as the loss in weight after drying at 45 C until a constant weight was attained, relative to the initial live weight. Chill coma temperatures were determined using a thermoelectric cold plate (Thermoelectrics Unlimited, Inc.). The temperature of the cooling stage was gradually lowered (0.5 C/min) until the tick was unable to walk in a coordinated manner. This was taken as the chill coma temperature.

In the desiccation experiment (fig. 1) groups of approximately 30 engorged immobile ticks were weighed initially and held at 10 C in a desiccator over calcium sulfate desiccant that produced an assumed relative humidity of 0%. Prior to testing, each group was reweighed to determine weight loss. In this experiment, the glycerol concentrations were based on the initial weight prior to desiccation.

Pooled tick samples weighing 300–450 mg were homogenized in 3 ml of distilled water in a Teflon-glass pedestal homogenizer. An equal volume of chloroform: methanol (2:1) was added to the homogenate and centrifuged to accelerate separation. The precipitate was washed twice with 1 ml of water, and the combined supernatants were heated for 15 min at 50 C. Further deproteinization was accomplished using 1.5 ml of 0.3 N barium hydroxide and 0.3 N zinc sulfate. After 10 min, the precipitate was pelleted and washed twice. The combined supernatants were evaporated to dryness at 50 C, resuspended in 0.65 ml of distilled water, and filtered (0.22 µm pore). Glycerol levels were measured by high performance liquid chromatography using a Waters Radial-Pak silica car-

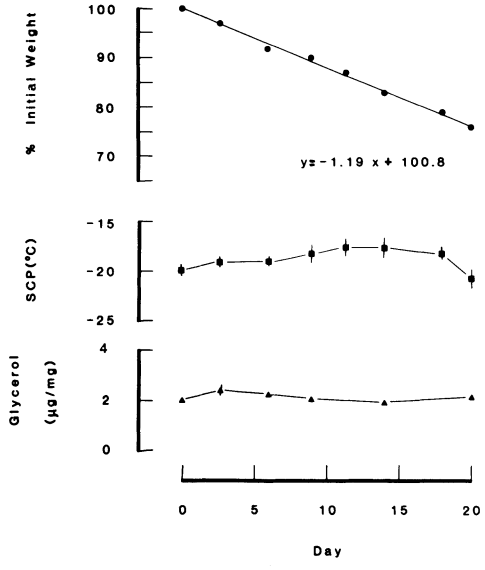

FIG. 1.—Effect of desiccation at 10 C and 0% RH on the supercooling point and glycerol content of engorged immobile nymphs ($\bar{X} \pm$ SEM).

tridge modified with tetraethylenepentamine as described by Hendrix et al. (1981). Glycerol concentrations are expressed as μg glycerol per mg live weight.

RESULTS

FIELD OBSERVATIONS

Ixodes uriae were collected from small islands adjacent to Palmer Station, Anvers Island, on the Antarctic peninsula (64°46′ S, 64°03′ W). All life stages of the tick (egg, larva, nymph and adult) were found in aggregations numbering from a few individuals to more than a thousand. Aggregations were located beneath rocks in well-drained sites within 5 m of the periphery of Adélie penguin (*Pygoscelis adeliae*) rookeries. Underlying some aggregation sites were exuviae and the bodies of dead individuals, which had accumulated to a depth of 3 cm, suggesting that these sites have been used for many years. A few individuals were found 30 cm beneath the ground surface within cracks in the soil and rocks.

In early January, 50% of the engorged females were collected *in copulo,* often with two or more males clinging to a copulating pair. At this time, about 5% of the light gray, engorged nymphs were mobile. Typically, the upper layer of an aggregation was composed of a single layer of engorged nymphs positioned with their ventral surface up in direct contact with overlying rocks. Individuals nearer the center of the colony were a darker gray. These nymphs were unable to walk and had stiff and immovable legs, which were spread and held away from the body. This loss of mobility is characteristic of entry into a state of nymphal adult apolysis, during which the epidermal cells separate from the old exoskeleton in preparation for ecdysis (Jenkin and Hinton 1966; Hinton 1971). In this paper, these two groups will be referred to as mobile and immobile nymphs. Throughout January, the lighter gray, mobile nymphs joined the colony on the outer edges and gradually lost mobility. By the end of January, no mobile nymphs were observed. On January 20, 20% of engorged adult females were ovipositing, usually in small groups, 5 cm or more below the surface. By January 28, 25% of the females that had laid eggs were dead.

COLD TOLERANCE

Freeze tolerance was assessed by removing nymphs, larvae, and adults from the refrigerated bath at the termination of the exotherm associated with the freezing of body water and allowed to thaw at 20 C. No individual survived tissue freezing, although short-term cooling to temperatures immediately above the SCP caused no apparent injury.

The supercooling point values for various life stages of *I. uriae* ranged from −7 C to a low of approximately −30 C (table 1). Newly laid eggs collected in late January

TABLE 1

LIVE WEIGHT, WATER CONTENT, SUPERCOOLING POINT AND GLYCEROL CONTENT FOR FIELD COLLECTIONS OF *Ixodes uriae* DURING 1981 AT PALMER STATION, ANTARCTICA

Stage	Live Weight (mg) ($\bar{X} \pm$ SEM, N)		Water Content (%)	Date	Supercooling Point ($\bar{X} \pm$ SEM, N)		Glycerol (μ/mg)
Engorged adult female	111.4 ± 5.6	8	59.5	5 Jan	−7.1 ± .3	6	1.7 ± .1
				22 Jan	−12.7 ± 1.6	9	2.0 ± .3
Adult male	7.4 ± .3	8	66.5	5 Jan	−8.4 ± 1.8	6	...
				22 Jan	−13.5 ± 1.0	7	...
Engorged immobile nymph	10.1 ± .4	5	65.2	17 Jan	−19.5 ± 1.0	5	...
				22 Jan	−18.7 ± .5	15	2.3 ± .4
Engorged mobile nymph	10.4 ± .8	6	66.9	5 Jan	−11.5 ± 1.9	11	2.0
				22 Jan	−15.4 ± 1.3	14	...
Engorged larva	1.3	40*	66.8	9 Jan	−20.9 ± .7	10	...
				22 Jan	−18.9 ± 1.4	7	2.0
Unengorged larva	...		...	22 Jan	−16.7 ± 2.0	9	...
Egg	...		...	22 Jan	−28.7 ± .3	16	3.5

* Mean of 40 individuals weighed as a group.

TABLE 2

SEASONAL SUPERCOOLING POINT DETERMINATIONS FOR FIELD-COLLECTED ENGORGED NYMPHS OF *Ixodes uriae* DURING 1981 AT PALMER STATION, ANTARCTICA

	Jan 5	Jan 17	Jan 22	Feb 21	Mar 6	Apr 5	Apr 25	May 17	Jul 18	Dec 7
Mobile nymphs:										
X	−11.5	−15.2	...	...	...	...	...	...	...	...
SEM	1.9	1.4	...	...	...	...	...	...	...	...
n	11	11	...	...	...	...	...	...	...	...
Immobile nymphs:										
X	...	−19.5	−18.7	−20.2	−18.7	−18.9	−17.0	−16.0	−15.1	−20.2
SEM	...	1.0	.5	.6	.7	1.6	2.0	.7	2.6	.9
n	...	5	15	10	10	7	9	6	8	8

had the lowest mean values of −28.7 C. Engorged larvae and engorged immobile nymphs, both typical overwintering stages, had the next lowest SCPs ranging between −18 and −20 C. The highest supercooling points were found in adults. Body water content was relatively constant at 65%–66% for all life stages except for females with 59.5% (table 1). Glycerol levels for all stages ranged between 1.7 and 2.3 μg/mg, except for eggs which had a concentration of 3.5 μg/mg.

Supercooling point values for engorged nymphs were determined throughout the year (table 2). In early January when many nymphs were still able to walk, SCPs were relatively high (from −11 to −15 C). Few engorged mobile nymphs were found in field collections after January 17. A decrease in SCPs for the engorged nymphs was associated with the transition from the mobile to the immobile state; otherwise SCPs remained at a constant level throughout the year.

The chill coma temperature provides an index of the potential for activity at low temperatures. The range of chill coma temperatures extended to −4.5 to −5.5 C for each of the life stages tested (table 3). All individuals survived chill coma tests with no apparent injury.

REGULATION OF COLD TOLERANCE

In order to determine the effect of temperature on the SCP and glycerol levels, engorged immobile nymphs were acclimated in the laboratory at various temperatures between −12 C to +25 C for 15 days. Supercooling points remained essentially constant throughout this period (table 4). Glycerol levels remained constant (ca. 2 μg/mg) regardless of acclimation temperature or duration of exposure. By day 7, some nymphs of both sexes held at 25 C had molted to the adult stage. Likewise, a few individuals molted after 15 days at 15 C.

A number of species appear to have a common set of adaptations for low-temperature tolerance and survival under anhydrobiotic conditions (Crowe, Crowe, and Mouradian 1983; Young and Block 1980). In order to test the effect of desiccation on cold tolerance in *I. uriae,* engorged immobile nymphs were held at 10 C and 0% RH for up to 20 days. Since these nymphs had progressed to the immobile stage, survival was assessed by checking for oxygen consumption using constant pressure microrespirometers as described by Lee and Baust (1982*b*). All nymphs survived the 20-day test period. During this time, weight loss was constant at a rate of 1.19 mg per 100 mg live weight per day (fig. 1). Assuming that weight loss was primarily water,

TABLE 3

CHILL COMA TEMPERATURES FOR FIELD COLLECTIONS OF VARIOUS STAGES OF *Ixodes uriae* DETERMINED ON FEBRUARY 6–7, 1981

Stage	Chill Coma Temperature (°C)
Adult female, engorged	−4.0 to −5.0
Adult female, unengorged	−1.5 to −5.5
Adult male	−3.0 to −4.5
Nymph, unengorged	−1.5 to −5.5

NOTE.—Each range is based on five to 10 individuals.

TABLE 4

EFFECT OF ACCLIMATION TO VARYING TEMPERATURES ON THE SUPERCOOLING POINT OF ENGORGED IMMOBILE NYMPHS

	TEMPERATURE (°C)				
DAY	−12	0	10	15	25
0	−19.0 ± .5*	...	...	...	...
1	−18.7 ± .5	−19.6 ± .5	−17.5 ± 1.2	−17.8 ± .7	−18.2 ± .7
2	−17.1 ± .5	−18.3 ± .7	−19.1 ± .6	−17.2 ± .3	−17.8 ± .7
4	−18.2 ± .8	−18.0 ± .6	−18.8 ± .5	−17.2 ± .7	−14.4 ± 2.3
7	−17.9 ± .9	−18.6 ± .9	−18.6 ± .7	−17.2 ± 1.2	−18.8 ± 1.2
15	−19.5 ± .9	−20.1 ± .8	−20.8 ± .9	−23.2 ± .5	...

NOTE.—Each mean (±SEM) is based on eight to 10 individuals.
* Initial supercooling point.

this corresponded to a loss of 35% of the total body water. Despite the substantial reductions in body weight and water content of the nymphs, SCPs and glycerol levels, expressed relative to weight prior to desiccation, remained unchanged as compared to initial values.

A number of workers have demonstrated that, for freeze-susceptible species, feeding causes a reduction in low-temperature tolerance (Block et al. 1978; Somme 1981). Presumably, the potential for extended supercooling is reduced by the presence of nucleating agents in the food or in foreign material ingested with food that acts to induce freezing at a relatively high sub-zero temperature. In order to evaluate the possible effect of feeding on the supercooling potential of *I. uriae,* the nucleating activity of host blood was examined (table 5). Two known hosts of *I. uriae* were selected, the giant fulmar (*Macronectes giganteus*) and the Adélie penguin (*Pygoscelis adeliae*). The addition of heparin to the distilled water controls or the host blood samples had no effect on the supercooling capacity (table 5). Second, the SCP of blood samples was 2–3 C higher than that of water and agreed closely with the whole body SCP of −11.5 C recorded for recently engorged nymphs collected on January 5 (table 1).

DISCUSSION

LIFE CYCLE

Two types of diapause are described for ticks (Belozerov 1982). Behavioral diapause refers to a suspension of host-seeking activity in unfed larvae, nymphs, and adults. Morphogenetic diapause is a delay (1) during embryogenesis of the developing egg, (2) in the metamorphosis of larvae and

TABLE 5

SUPERCOOLING POINTS OF 3–5 μL OF BLOOD FROM AVIAN HOSTS OF *Ixodes uriae*

	SCP (°C)	
SAMPLE	Without Heparin	With Heparin
Distilled H_2O	−12.6 ± 1.0 (8)	−13.3 ± .8 (6)
Giant fulmar (*Macronectes giganteus*)	−10.6 ± 1.8 (6)	−10.5 ± .5 (5)
Adelie penguin (*Pygoscelis adeliae*)	...	−9.3 ± 1.0 (10)*

NOTE.—Each value is the mean (±SEM) with the sample size noted in parentheses.
* Penguin had low levels of circulating heparin in the blood.

nymphs after engorgement, or (3) delay of oviposition in females. *Ixodes uriae* is known to overwinter in all life stages as well as in both behavioral and morphogenetic diapause (Eveleigh and Thelfall 1974; Flint and Kostyrko 1967; Murray and Vestjens 1967).

In the vicinity of Anvers Island, incubation and brooding by Adélie penguins primarily occurs during December and January (Parmelee, Fraser, and Neilson 1977; P. Pietz, personal communication). As such, *I. uriae* has access to its host for only a relatively short period each year, an interval that allows only one blood meal per individual per year. In the maritime Antarctic, it is likely that *I. uriae* must overwinter at least three times—as an egg or unengorged larva, an engorged larva, and, finally, as an engorged nymph/pharate adult—in order to complete its life cycle. Similar life-history patterns are known for populations in Newfoundland (Eveleigh and Threlfall 1974) and on Macquarie Island (Murray and Vestjens 1967).

COLD TOLERANCE

Among the Acarina, which include mites and ticks, there are no reports of species that are freeze tolerant (Somme 1981). These data are consistent with this pattern, as no life stage survived tissue freezing. The only commonly reported cryoprotective substance identified in whole body extracts from *I. uriae* was glycerol (table 1). Using the same extraction and analytical techniques, we found glycerol levels of greater than 20 μg/mg for the cryptostigmatid mite, *Alaskozetes antarcticus* (Lee and Baust 1981), while concentrations for *I. uriae* were 10-fold lower. Furthermore, glycerol levels remained unchanged after laboratory acclimation to low temperature and desiccation (fig. 1). These data may allow one to raise the question as to what role, if any, glycerol plays in mechanisms of cold tolerance of this species.

REGULATION OF COLD-HARDINESS

In order for freeze-intolerant species to cold-harden by depressing the whole body SCP, endogeneous ice-nucleating agents must be removed or their nucleating activity masked. Although not examined in this study, it is possible that antifreeze proteins may be involved in this process (Duman and Horwath 1983). For two other Antarctic microarthropods, *Alaskozetes antarcticus* and *Cryptopygus antarcticus,* maximal cold tolerance is achieved only after a period of starvation (Block et al. 1978). Our data suggest that cold-hardiness in *I. uriae* may also be influenced by feeding.

In early January, the recently engorged mobile nymphs had relatively high SCPs of −11.5 C (table 1). This value corresponds closely to the SCP values recorded for the blood of its avian hosts (table 5). One possible explanation for this correlation is that nucleating agents in the ingested blood meal are responsible for the relatively high SCPs (i.e., reduced cold tolerance) in the mobile engorged nymphs.

The 2–3 wk period after feeding is an especially active one for metabolic and digestive processes in ixodid ticks. While the ixodid ticks are still attached to the host, the blood meal is concentrated as excess water and ions are removed by the salivary glands (Akov 1982). Since the marked decrease in SCPs did not occur until days or weeks after leaving the host, it appears that the concentration of the blood meal that occurs on the host is not directly responsible for increasing cold tolerance (table 2). Hemolysis of the ingested red blood cells followed by hemoglobin crystallization also occurs during this period. Entry into the state of apolysis or postfeeding digestive processes may be involved in the breakdown or masking of the ice-nucleating agents that, in turn, allow for enhanced supercooling capacity in the overwintering nymphs.

RELATIONSHIPS BETWEEN MICROHABITAT AND TEMPERATURE

The chill coma temperatures of *I. uriae* are similar to ones recorded for other active terrestrial arthropods from alpine and polar regions. Block and Somme (1982) reported chill coma temperatures between −4.6 and −8.9 C for four species of mites from Signy Island in the maritime Antarctic. Two species of Collembola from the Austrian Alps had chill coma temperatures of −7.7 and −4.9 C (Somme 1979). Baust (1980) reported that microhabitat temperatures at Palmer Station, similar to the collection sites for *I. uriae* in this study, are strikingly

uniform, remaining between 0 and −2 C for more than 300 days of the year. These data suggest that, with respect to microhabitat temperature, *I. uriae* could be active for most of the year.

Although most studies have focused on the tolerance of low temperatures in polar arthropods, tolerance of high-temperature exposure may be of critical importance as well. Young (1979) concludes that acclimation for 2 wk at 15 C is stressful for the Antarctic mite *Alaskozetes antarcticus.* Short-term exposure to 15 or 20 C produces high mortality in freeze tolerant larvae of *Belgica antarctica,* a wingless chironomid (Baust 1980). Both of these species are found in abundance near our collection sites for *I. uriae.*

As compared to other terrestrial polar arthropods, *I. uriae* appears to be exceptionally tolerant of exposure to high temperatures. No mortality was observed in engorged immobile nymphs exposed to 15 C and 25 C (table 4). In fact, acclimation to these high temperatures stimulated nymphs to molt to the adult stage. Karpovich (1970) examined the distribution of feeding *I. uriae* with respect to the surface temperatures beneath the feathers of the common murre (*Uriae aalge*). The greatest proportion of larvae and nymphs were found at body surface temperatures of 40.6 C or higher. Although it is not surprising that an ectoparasite is able to tolerate temperatures encountered on its host, these data show that *I. uriae* has the greatest overall range of thermal tolerance, from −30 C to 40 C, reported for any Antarctic terrestrial arthropod.

The aggregations of free-living *I. uriae* were characteristically found in well-drained areas beneath large rocks or in cracks in the substrate. Good drainage may be critical to avoid flooding during snow and ice melt-off in the spring and after summer rains. The thermal buffering (Baust 1980) afforded by these microhabitats may also be of special significance. Since respiration rates are temperature dependent in *I. uriae* (Lee and Baust 1982*a*), selection of a relatively cool microhabitat may aid in the conservation of nutrients during the summer months. A positive cryotaxic response has been demonstrated for an arctic carabid beetle (Baust and Miller 1970).

Although temperate species exhibit seasonal changes in cold tolerance, *I. uriae* retains hardiness throughout the year except for a short interval associated with the consumption and processing of the annual blood meal. Furthermore, the cold-hardening process is unaffected by temperature acclimation or desiccation, environmental factors that function as triggers regulating cold tolerance in other terrestrial arthropods. Since environmental cues may be difficult to detect in the off-host microhabitat occupied by this tick, the maintenance of a permanent state of cold-hardiness may obviate the need to rely on such cues.

LITERATURE CITED

AKOV, S. 1982. Blood digestion in ticks. Pages 197–211 *in* F. D. OBENCHAIN and R. GALUN, eds. Physiology of ticks. Pergamon Press, Oxford.

BAUST, J. G. 1980. Low temperature tolerance in an antarctic insect: a relict adaptation? Cryo-Letters **1**:360–371.

BAUST, J. G., and J. S. EDWARDS. 1979. Mechanisms of freezing tolerance in an Antarctic midge (*Belgica antarctica*). Physiol. Ent. **4**:1–5.

BAUST, J. G., and L. K. MILLER. 1970. Variations in glycerol content and its influence on cold hardiness in the Alaskan carabid beetle, *Pterostichus brevicornis.* J. Insect Physiol. **16**:979–990.

BELOZEROV, V. N. 1982. Diapause and biological rhythms in ticks. Pages 469–500 *in* F. D. OBENCHAIN and R. GALUN, eds. Physiology of ticks, Pergamon Press, Oxford.

BLOCK, W. 1980. Survival strategies in polar terrestrial arthropods. Biol. J. Linn. Soc. **14**:29–38.

BLOCK, W., and L. SOMME. 1982. Cold hardiness of terrestrial mites at Signy Island, maritime Antarctic. Oikos **38**:157–167.

BLOCK, W., S. R. YOUNG, E. M. CONRADI-LARSEN, and L. SOMME. 1978. Cold tolerance of two antarctic terrestrial arthropods. Experientia **34**:1166–1167.

CROWE, J. H., L. M. CROWE, and R. MOURADIAN. 1983. Stabilization of biological membranes at low water activities. Cryobiology **20**:346–356.

DOHERTY, R. L., J. G. CARLEY, M. D. MURRAY, A. J. MAIN, B. H. KAY, and R. DOMROW. 1975. Isolation of arboviruses (Kemerovo group, Sakhalin group) from *Ixodes uriae* collected at Macquarie Island, southern ocean. Amer. J. Trop. Med. Hyg. **24**:521–526.

DUMAN, J., and K. HORWATH. 1983. The role of hemolymph proteins in the cold tolerance of insects. Ann. Rev. Physiol. **45**:261–270.

EVELEIGH, E. S., and W. THRELFALL. 1974. The biology of *Ixodes (Ceratixodes) uriae* White, 1852 in Newfoundland. Acarologia **16**(4):621–635.

FLINT, V. B., and I. N. KOSTYRKO. 1967. On biology of the tick *Ixodes putus* Pick.-Camb. [In Russian, English summary]. Zool. Zh. 46: 1253–1256.

HENDRIX, D. L., R. E. LEE, H. JAMES, and J. G. BAUST. 1981. Separation of carbohydrates and polyols by a radially compressed HPLC silica column modified with TEPA. J. Chromatoraphy **210**:45–53.

HINTON, H. E. 1971. Some neglected phases in metamorphosis. Proc. R. Entomol. Soc. Lond. **35**:55–64.

JENKIN, P. M., and H. E. HINTON. 1966. Apolysis in arthropod moulting cycles. Nature **211**:871.

KARPOVICH, V. N. 1970. Properties of *Ceratixodes putus* Pick.-Camb. parasitism on birds. [In Russian] Parazitologiya, Leningrad. **4**:345–351.

LEE, R. E., and J. G. BAUST. 1981. Seasonal patterns of cold-hardiness in antarctic terrestrial arthropods. Comp. Biochem. Physiol. **70A**:579–582.

———. 1982*a*. Respiratory metabolism of the antarctic tick, *Ixodes uriae*. Comp. Biochem. Physiol. **72A**:167–171.

———. 1982*b*. Absence of metabolic cold adaptation and compensatory acclimation in the antarctic fly, *Belgica antarctica*. J. Insect Physiol. **28**:725–729.

MAIN, A. J., W. G. DOWNS, R. E. SHOPE, and R. C. WALLIS. 1973. Great Island and Bauline: two new Kemerovo group orbiviruses from *Ixodes uriae* in eastern Canada. J. Med. Entomol. **10**:229–235.

MURRAY, M. D., and W. J. M. VESTJENS. 1967. Studies on the ectoparasites of seals and penguins. III. The distribution of the tick *Ixodes uriae* White and the flea *Parapsyllus magellanicus heardi* de Meillon on Macquarie Island. Aust. J. Zool. **15**:715–725.

PARMELEE, D. F., W. R. FRASER, and D. R. NEILSON. 1977. Birds of the Palmer Station area. Antarctic J. U. S. **12**:14–21.

SOMME, L. 1978. Cold-hardiness of *Cryptopygus antarcticus* (Collembola) from Bouvetoya. Oikos **31**: 94–97.

———. 1979. Overwintering ecology of alpine Collembola and oribatid mites from the Austrian Alps. Ecol. Entomol. **4**:175–180.

———. 1981. Cold tolerance in alpine, arctic and antarctic Collembola and mites. Cryobiology **18**:212–220.

THOMAS, L. A., C. M. CLIFFORD, C. E. YUNKER, J. E. KEIRANS, E. R. PATZER, G. E. MONK, and E. R. EASTON. 1973. Tickborne viruses in western North America. I. Viruses isolated from *Ixodus uriae* in coastal Oregon in 1970. J. Med. Entomol. **10**:165–168.

WILSON, N. 1964. Insects of Campbell Island: Metastigmata: Ixodidae. Pac. Insects Monogr. **7**:132–137.

———. 1970. Acarina: Metastigmata: Ixodidae of South Georgia, Heard and Kerguelen. Pac. Insects Monogr. **23**:78–88.

YOUNG, S. R. 1979. Respiratory metabolism of *Alaskozetes antarcticus*. J. Insect Physiol. **25**:361–369.

YOUNG, S. R., and W. BLOCK. 1980. Experimental studies on the cold tolerance of *Alaskozetes antarcticus*. J. Insect Physiol. **26**:189–200.

YUNKER, C. E., C. M. CLIFFORD, J. E. KEIRANS, L. A. THOMAS, and J. CORY. 1973. Tickborne viruses in western North America. II. Yaquina Head, a new arbovirus of the Kemerovo group isolated from *Ixodes uriae*. J. Med. Entomol. **10**:264–269.