

WINTER SURVIVAL AND OVERWINTERING BEHAVIOR IN SOUTH DAKOTA ONISCIDEA (CRUSTACEA, ISOPODA)

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ABSTRACT

Six species of terrestrial isopod from the sub-order Oniscidea are currently recorded from South Dakota, all being recent (19th C.–present) introductions from Europe. Although introduced isopods have become naturalized in a range of indigenous habitat types in other regions of North America, distributions in the Great Plains are highly synanthropic. Experimental data presented here shows that moderate cold-tolerance in these species and resultant winter mortality can explain observed synanthropy. Lower lethal temperatures resulting in 50% mortality (LLT_{50} s) vary from -4.3 to -6.3°C depending on season; only minor interspecific variation is evident. Seasonal acclimatization depresses the LLT_{50} by approximately 2.0°C in the winter, and laboratory acclimation at 20°C and 0°C induces a smaller though significant shift in cold tolerance. Nevertheless, LLT_{50} determinations are invariably far above winter ambient lows in South Dakota. Subnivean microsites afford some thermal insulation from ambient extremes but sub-lethal temperatures persist only at significant snow depths (>20 cm) or in subterranean refuges. Given that these species are not active burrowers, this restricts viable overwintering refuges to two essentially anthropogenic habitat types: thermally buffered microsites adjacent to heated buildings, and deep accumulations of coarse or friable material permitting vertical migration. The restriction of viable overwintering populations to such habitats is borne out by field observations. Shingle banks beside large or fast-flowing waterways permit deep vertical migration of isopods during cold periods, and are the only semi-natural habitat types known to support isopod populations in South Dakota. Cities are replete with anthropogenic examples such as compost piles and refuse dumps which facilitate overwinter survival and can explain the abundance and wide dispersal of populations typical in areas of extensive human settlement.

INTRODUCTION

At least twenty species of terrestrial isopods of the sub-order Oniscidea, popularly known as woodlice or sowbugs, have been recorded in the northern United States and Canada (Blake, 1931; Hatch, 1939; Hatchett, 1947; Johansen, 1926; Longnecker, 1924; Van Name, 1936; Walker, 1927). Although

the North American fauna includes several native oniscideans, the fauna is impoverished by comparison with Europe and the most widespread and familiar species are European introductions. Genetic distances between populations of *Armadillidium vulgare* indicate that the major avenues of colonization were the St. Lawrence and Mississippi valleys (Garthwaite, Lawson and Sassaman, 1993). In many regions of North America, introduced isopods have become widely naturalized in the native habitat types. In Southern Ontario, at least seven species can be found in the Carolinian woodlands, and naturalized populations are common in limestone scree and riparian woodlands (personal observation). *Trachelipus rathkei* has even become a widespread component of the macrodecomposer fauna in boreal forest litter in central Ontario (Walker, 1927; personal observation). Hatchett (1947) reports ten terrestrial Oniscidea in Michigan, most of which have invaded a wide range of natural habitat types, and Jass and Klausmeier (1996) have recently documented eleven terrestrial species in Wisconsin.

In the Great Plains, isopod distribution and abundance differ markedly from patterns in Ontario and the Great Lakes basin. In South Dakota, only five genera and six species have been recorded: *Trachelipus rathkei*, *Porcellionides pruinosus*, *Porcellio scaber*, *Porcellio spinicornis*, *Cylisticus convexus* and *Armadillidium vulgare*. Of these, *P. scaber* and *A. vulgare* are currently recorded only from Sioux Falls (Dr Leland Johnson, personal communication) and *Porcellio spinicornis* is known only from Sioux Falls and Aberdeen. All of these genera belong to the section Crinocheta, a predominantly mesic taxon with species characterized by, among other features, a capacity for the active absorption of water vapor from sub-saturated humidities (Wright and Machin, 1993a,b). Prior to the present study, there were no recordings of Oniscidea in the Dakotas, and only scant records exist for the adjacent mid-western states (Longnecker, 1924; Richardson, 1905). This is most likely to reflect a paucity of regional interest rather than very recent introductions since three of the species (*T. rathkei*, *Porcellionides pruinosus* and *C. convexus*) are generally widespread. All six species are, however, strikingly synanthropic, frequently abundant in towns but virtually absent from the natural habitat types. The present author has never found animals in the mixed-grass prairie or in riparian woodlands, except where these adjoin areas of human settlement. Isopods appear similarly excluded from agricultural soils and ranchland. The only recordings of isopods from semi-natural habitat types are findings of *Trachelipus rathkei* in riverine shingle banks near Mobridge (shores of the Missouri) and in Spearfish Canyon in the Black Hills. The significance of this habitat is considered further in the Discussion.

Synanthropic distributions may occur as a simple consequence of recent human introduction—characterized by a progressive decline of synanthropy over time—or as a result of human activities favoring the survival of particular species. Where synanthropy reflects an obligatory dependence, no dissemination from regions of human settlement will occur. The abrupt disappearance of isopods at the edges of South Dakota towns indicates such an obligatory association. Recent introduction to those towns may explain the restricted ranges of *Porcellio spinicornis*, *P. scaber* and *A. vulgare*. *Porcellio spinicornis* and *A.*

vulgare may also have a lower dispersal index by virtue of their pronounced calciphily, both species being closely associated with limestones or with anthropogenic sources of lime such as cement and mortar. But the catholic habitat preferences of the remaining species, and their extensive dispersal within areas of human settlement, strongly suggest obligatory synanthropy.

Given the ability of introduced isopods to disperse many miles from human settlements in other regions of North America, distributions in South Dakota indicate that one or more environmental factors fall outside the species' ranges of tolerance. Low rainfall is one possibility but this does not explain the inability of these isopods to colonize flood plains and riparian woodlands. Furthermore, these and related species have successfully colonized markedly xeric habitats in the Southwestern USA and Mexico (Miller, 1936; Warburg, 1965). A more plausible limiting factor is low-temperature tolerance as a determinant of winter survival. In the only studies performed to date on isopod thermal tolerance, Edney (1964a) and Tanaka and Udagawa (1993) both showed only modest cold tolerance (-1.4 to -4.6°C) for *Porcellio scaber*. Several isopods have European ranges that follow northern isotherms closely indicating probable significance of low-temperature tolerance in limiting northward range expansion.

The present study was conducted to determine the lower lethal temperatures (LLT₅₀s) of isopod species in Aberdeen, South Dakota. Comparisons of these data with field temperature measurements in various microsites, and identification of overwintering refugia, provide a basis for testing the hypothesis that cold-tolerance is an ultimate factor explaining the synanthropy of introduced isopods in the region.

MATERIALS AND METHODS

Specimens of the three common oniscideans in Aberdeen—*Trachelipus rathkei*, *Porcellionides pruinosus*, and *Cylisticus convexus*—were used for study, together with commercially available *Porcellio scaber* (Carolina Biological) which were used for acclimation studies. *Porcellio spinicornis*, which is known to occur at one locality within Brown County, was not available in sufficient numbers for study. For determinations of lower lethal temperatures (LLT₅₀), animals were either collected promptly from field populations, or maintained at controlled acclimation temperatures for various periods prior to study. The effect of acclimation was studied using temperatures of 20°C and 0°C. Natural acclimatization in field populations was studied by comparing the LLT₅₀ at different times of the year and comparing these with weekly ambient temperature records from the area meteorological office. Separate sub-samples of animals were used for all cooling trials.

LLT₅₀ determinations used a fixed cooling-warming cycle starting at 5°C, cooling with a linear curve to the test temperature over a period of 5 hours, holding the test temperature for 10 hours, then warming at a uniform rate to 5°C again over a further 5-hour period. The bath was subsequently maintained at 5°C. Selection of this cooling cycle gives the data complementarity with those of Edney (1964a), and the time-course provides an approximate simula-

tion of the nocturnal cooling regimes encountered *in vivo*. Test animals were transferred to individual 50 ml Plexiglas vials containing moistened filter paper discs and sealed with foam plugs to reduce evaporative water loss but allow for diffusional gas exchange. Vials were immersed to a depth of 8 cm in a Cole Permer 'Polystat' programmable heating-refrigerating water bath containing a 1:1 mixture of ethylene glycol and water. Survival was assessed as soon as possible following the completion of the cooling cycle and was based on the resumption of normal locomotory ability on return to laboratory temperature.

Field measurements of microclimate temperatures used a Barnant 115 Thermocouple Thermometer connected to an insulated copper-constantan thermocouple. The insulated cable was taped to a 2 mm diameter steel rod with the terminal 2 cm of the thermocouple projecting beyond the tip. This probe was used to measure subterranean and subnivean temperatures at various depths and at a range of distances from north-facing walls of heated buildings. Temperature recordings were confined to areas where isopods are active during the summer months. Winter recordings of ambient temperatures and soil temperatures were also obtained from the US National Weather Service, the National Climate Data Center, and the High Plains Climate Center (University of Nebraska at Lincoln, NE). Microsites were studied throughout the fall, winter and early spring months to assess which sites were used as overwintering refugia, and to observe the viability of those populations in the spring.

RESULTS

A representative plot of survivorship as a function of cooling temperature is shown in Figure 1. Isopod populations showed minor intraspecific variation in cold tolerance, with mortality increasing abruptly over a small temperature range (0.2–0.4°C). This facilitates accurate determination of LLT₅₀s without probit transformations, and these could readily be assessed from survivorship plots to within 0.05°C.

Field-collected populations of the three study species revealed only modest cold tolerance, with LLT₅₀ values ranging from -4.8 to -6.3°C in early spring (cold-acclimatized), and -4.3 to -4.5°C in summer populations. Collective data for *Cylisticus convexus* and *Trachelipus rathkei* are shown in Figure 2 (a,b). Animals were not collected during the winter months, primarily because of the difficulty of finding them, but specimens active in the early spring revealed significant depression of the LLT₅₀ (by approximately 2.0°C) compared with animals field-collected in the summer months (*Cylisticus convexus*: $t = 4.7$, $p < 0.001$; *Trachelipus rathkei*: $t = 5.4$, $p < 0.0001$).

Laboratory acclimation studies revealed a small but significant effect, with 1-week acclimation at 20°C and 0°C resulting in LLT₅₀s differing by 1.0–1.2°C in both *Porcellio scaber* and *Cylisticus convexus*. Results are summarized in Table 1. Long-term acclimation (>1 month) to 20°C elevated the LLT₅₀ only slightly more than a 1-week acclimation period.

Daily high and low ambient temperatures for the winter months in years 1995-1996 in Aberdeen, South Dakota, are shown in Figure 3. Ambient daily maxima and minima routinely fell below observed LLT₅₀s for isopods during the

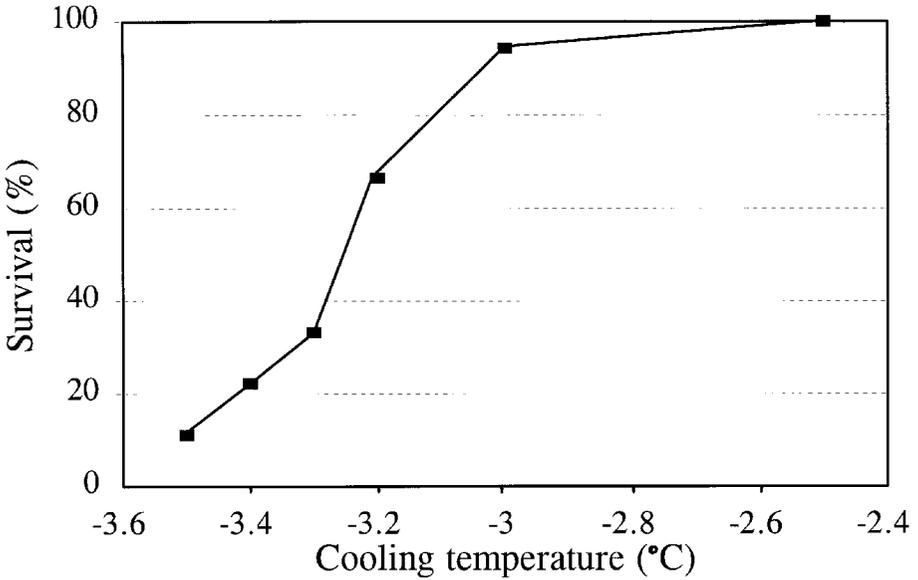


Figure 1. An example of a survivorship curve (*Porcellionides pruinosus*) showing the % survival of animals following controlled cooling to different temperatures and the sharply defined LLT₅₀, in this case approximately -3.25°C.

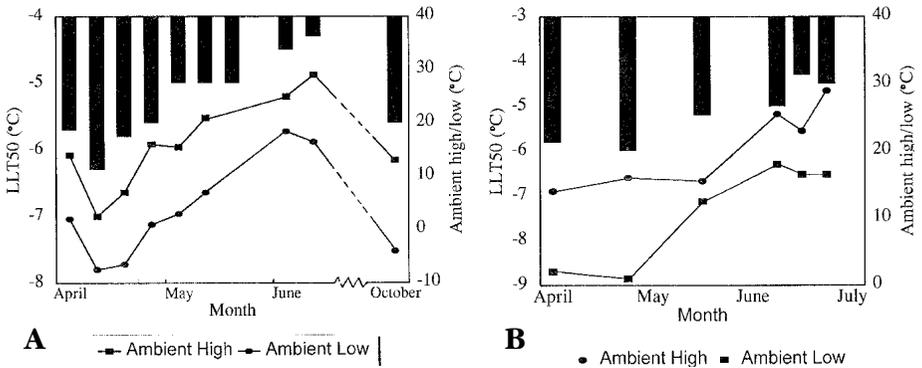


Figure 2. Seasonal variation in LLT₅₀ showing acclimatization of cold tolerance in field-collected populations of *Cylisticus convexus* (a) and *Trachelipus rathkei* (b). Cold tolerance shows a long-term acclimatory depression of approximately 2°C between the mid-summer and winter months. Variation in LLT₅₀ is closely correlated with seasonal changes in the high and low ambient temperature.

Table 1. Determinations of LLT_{50} in isopods following laboratory acclimation to 20°C and 0°C. All determinations were made from 4-8 trials using a minimum of 10 animals per cooling cycle.

| Species | Acclimation regime | | |
|---------------------------------|--------------------|---------------|--------------|
| | 20°C (>1 month) | 20°C (1 week) | 0°C (1 week) |
| <i>Porcellio scaber</i> | -4.0 | -4.2 | -5.1, -5.3 |
| <i>Porcellionides pruinosus</i> | -3.25 | - | - |
| <i>Cyclisticus convexus</i> | -4.0 | -4.2 | -5.4 |

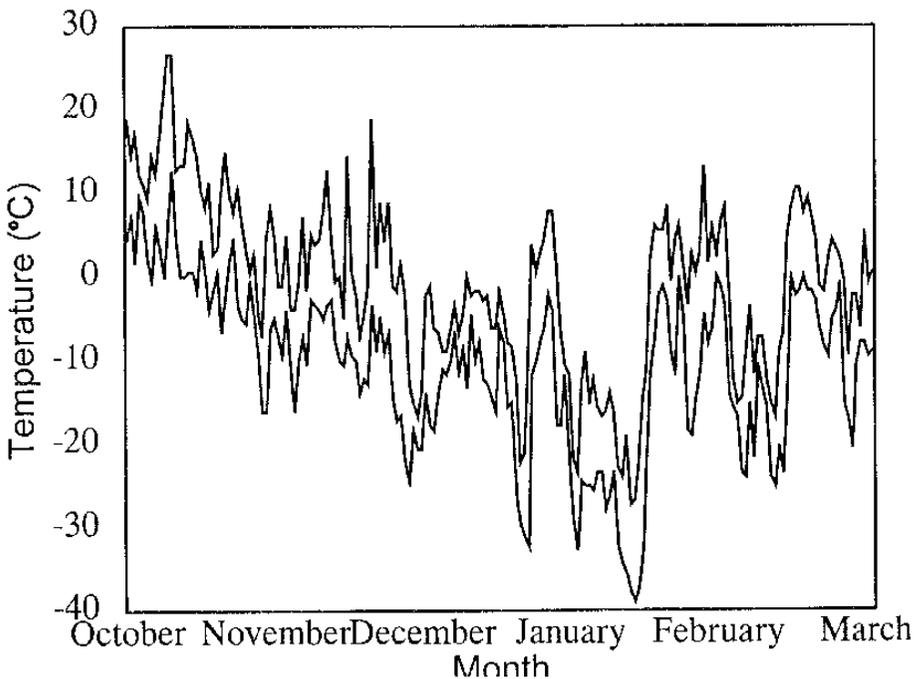


Figure 3. Daily high and low temperatures for the study area (Aberdeen, South Dakota) for 1996. (Data, courtesy of the High Plains Climate Data Center).

months of November through March. Soil temperatures, even at modest depths, reveal much smaller fluctuations. Soil temperature records from fixed-site thermistors (20 cm depth) at Redfield, South Dakota, are plotted in Figure 4. Data show winter soil temperatures (November through March) and mean monthly ambient lows. Soil temperatures at 20 cm never fell below -2.6°C over this period.

The significance of snow as an insulator to the litter fauna, and the effects of heated buildings on local microclimate, are shown in Figure 5 (a-c). These plots show temperature recordings for different subnivean depths and various distances from heated buildings in Aberdeen during three mornings in the win-

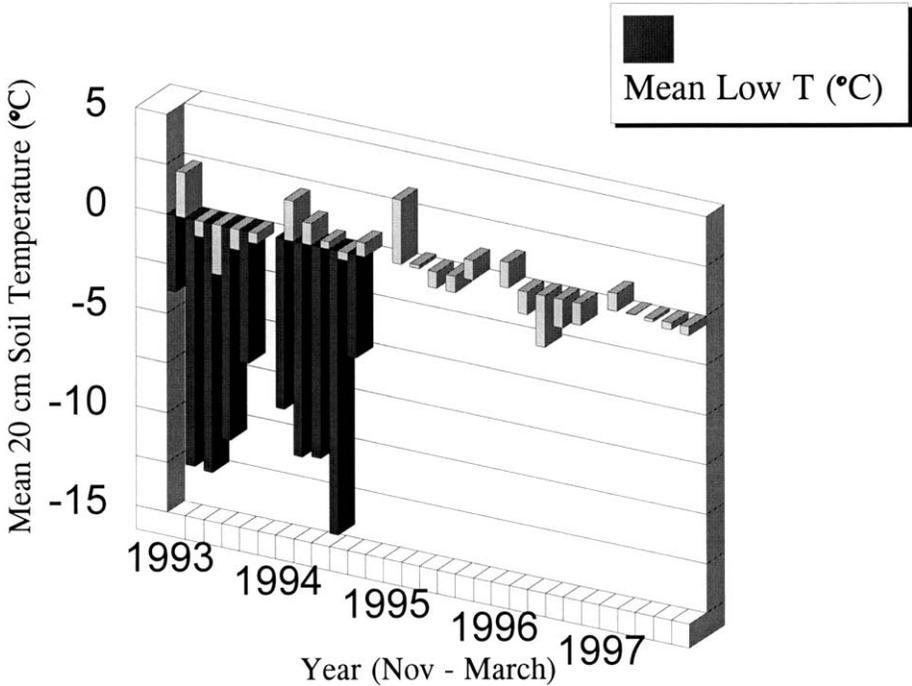


Figure 4. Soil temperatures for Redfield, South Dakota, for the winter months (November-March) from 1993-1997. All measurements were from fixed-site thermistors at a depth of 20 cm. Monthly mean ambient lows are also plotted for the winters of 1993-5 (dark bars).

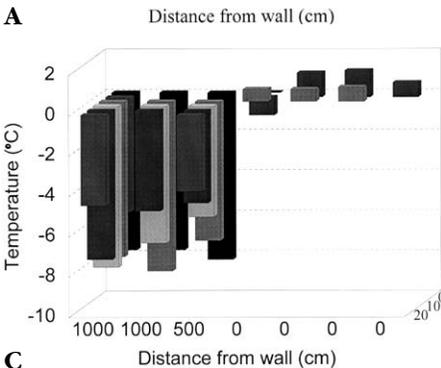
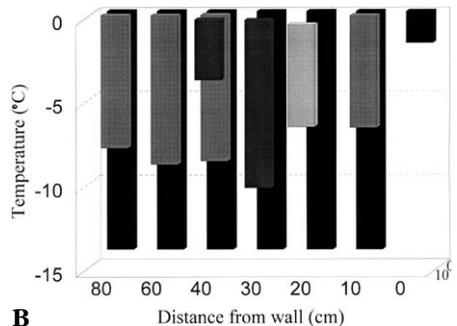
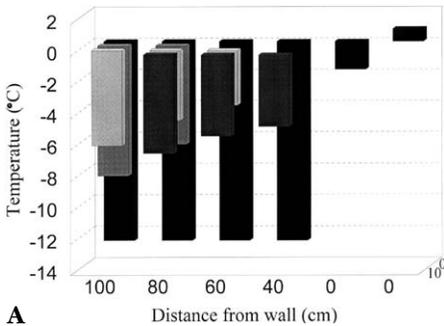


Figure 5. Subnivean temperatures recorded with a thermocouple probe at various distances from North-facing walls of heated buildings (x axis) and at various depths (z axis) in March 1997. Temperatures were measured in depth increments of 5 cm from 0 cm to 25 cm which was the deepest snow cover during any of the measurement periods. Snow depth data illustrate the insulating effect of snow cover and the abrupt temperature elevation (to approximately 0°C) at the base of exterior walls.

ter of 1996-7. All measurements were made in shaded locations in the proximity of north-facing walls. While snow exerts a pronounced insulating effect, it is clear from these data that, during the winter months, sub-lethal temperatures persist only at significant subnivean depths (>10 cm) or within a few centimeters of the walls of heated buildings.

Field observations early and late in the year revealed a number of overwintering refugia. While summer populations use a wide range of microsites as diurnal retreats, winter populations show a very restricted distribution. Overwintering sites which supported viable spring populations could be classified under two basic categories: deep accumulations of friable or coarse materials permitting deep vertical migration; and shallow retreats around the perimeters of heated buildings. Examples of the former are municipal dumps, abandoned tips or rubble piles, and deep accumulations of garden compost or leaf litter. Possible overwintering refugia around the perimeters of buildings are much more widespread and include marginal cracks, stone or gravel margins, and essentially any retreat permitting vertical migration of a few centimeters at a wall edge.

One overwintering site, comprising a lagged stone border and adjacent crevices at the North edge of a large house (ca. 1904), supported large populations of *Porcellionides pruinosus* and *Cylisticus convexus* in the winters of 1995-6 and 1996-7. Renewed surface activity in the Spring of 1997 was observed on March 30 at an ambient temperature of 5°C following an overnight low of -3°C. Renewed surface activity of *C. convexus* at an abandoned, concrete-lined dump was observed on March 31 as soon as the overlying snow accumulations had melted. Abundant air spaces among the soaked elm litter and underlying refuse provided refuges for animals away from melt water. In the same site, subnivean activity was observed beneath remnant patches of snow cover.

Certain microsites, in both late fall and spring surveys, showed mass mortality of overwintering populations. In some cases, these were beneath rocks or wood, at considerable distances from buildings, and lacked coarse underlying substrates which could have permitted vertical migration. In other sites, mass mortality was noted in deeper refugia, apparently the result of drowning during snow-melt.

DISCUSSION

It is evident from observations of fall and spring populations that oniscidean populations in South Dakota possess only very modest cold-tolerance. These findings concur with those of Edney (1964a), and of Tanaka and Udagawa (1993) who reported LLT_{50} values for *Porcellio scaber* of -1.37°C in August and -4.58°C in December. The rather lower values reported in the present study for *Cylisticus convexus*, *Porcellionides pruinosus* and *Trachelipus rathkei*, may be the result of selection. Although these species are only recent introductions, their critical dependence on thermally buffered winter refuges—and the significant winter mortality evident in field populations—would impose a strong directional selection pressure for increased cold-tolerance. Oniscideans

survive sub-freezing temperatures by supercooling, and are not freeze-resistant (Tanaka and Udagawa, 1993). Cold acclimation in *P. scaber* is associated with the accumulation of low molecular weight carbohydrates during the winter months which may function as cryoprotectants preventing regional freeze-injury. Composition and millimolar accumulation of cryoprotectants would constitute a likely basis for selection in South Dakota populations. More profound supercooling, widespread in insects and arachnids (see Franks, 1985, for a useful review), may be precluded by other factors. Tanaka and Udagawa (1993) showed that *Porcellio scaber* populations in Hokkaido maintain a whole-body supercooling point (the limit of freeze-avoidance) of approximately -7.0°C throughout the year which they attributed to ice-nucleation by gut contents. Although the onset of freezing was not assessed in the present study, it is interesting that our animals also retained gut contents during cooling trials and LLT₅₀ values never fell below -7.0°C . However, when experimental animals were fasted prior to cooling to clear the gut, there was no evident depression of the LLT₅₀.

Acclimation at 20°C in the laboratory elevated the LLT₅₀ significantly above that of summer-acclimatized populations ($p < 0.01$; 2-sample t-test comparing data for all species) in spite of the fact that mean ambient summer temperatures exceed 20°C . This supports the well established point that acclimatization is a complex process, depending on the range and incidence of temperature variation as well as the mean temperature over the acclimatization period. In the only other studies to date exploring acclimation of cold-tolerance in terrestrial isopods, Edney (1964a) obtained respective LLT₅₀ estimates for *P. laevis* and *A. vulgare* of -2.4°C and -2.7°C following 14 days acclimation at 10°C , -0.7°C and -1.7°C following 14 days acclimation at 20°C , and $+5.5$ and $+3.0^{\circ}\text{C}$ following 14 days acclimation at 30°C . Edney's isopods were collected from the University of California at Riverside. The fact that long-term acclimation at 20°C did not elevate the LLT₅₀ above -3.3°C in the three species examined in the present study again suggests the likely impact of selection (the *P. scaber* used in the present study came originally from populations in Burlington, NC).

It is clear that ambient winter lows in South Dakota fall far below the LLT₅₀ for any of the study species—exceptionally by as much as 40°C . Although snow cover affords significant thermal insulation, prolonged temperatures below -10°C readily depress the ground temperature below LLT₅₀s, even with 80 cm of snow cover. Fixed-site thermistors in Bismark, ND, indicate that with more modest snow cover (12 cm) the frost line occurs at soil depths over 140 cm, and animals would need to burrow below 20 cm to evade lethal temperatures. With a few exceptions, such as the desert species *Hemilepistus reaumuri*, oniscideans are not active burrowers and can only migrate vertically in coarse or friable substrates. Winter temperatures in the Dakotas will therefore preclude them from the indigenous prairie soils and compacted agricultural soils.

These predictions are borne out by field observations. Overwintering isopod populations in South Dakota are apparently confined to two major habitat types: deep accumulations of coarse or friable material permitting deep vertical migration, and thermally buffered microsites around the edges of heated

buildings. Even at depths of only a few centimeters, crevices at the perimeter of a heated building remain at or above freezing temperatures. Deep accumulations of coarse material allow isopods to escape from the confines of heated buildings but are of essentially anthropogenic origin. They include leaf and compost piles, dumps and rubble piles, and landfills. One naturally occurring example is the coarse shingle banks built up by large or fast-flowing waterways and which support adventitious populations of *Trachelipus rathkei* in two known locations. Coarse materials not only permit vertical migration, but also provide for drainage of snow-melt. Terrestrial oniscideans generally only survive submergence for a few hours at most (Taylor and Carefoot, 1993) and drowning during snow-melt is probably a significant contributing factor to overwinter mortality; recently drowned populations are a common sight in the early spring.

Following the spring emergence of overwintering populations, terrestrial isopods may disperse quite widely. Summer populations beneath wood and rocks have been found over 50 meters from the closest known overwintering sites, and it is likely that isopods disperse much more extensively than this. Return to overwintering refugia in the fall could involve gradual movements toward a 'preferred temperature' and resultant aggregation in deep or locally heated microsites. Aggregation is largely olfactory (Kuenen and Nooteboom, 1963) and is augmented by one or more short-range pheromones (Takeda, 1980, 1984). The exaggerated effect of olfactory cues in large populations may alleviate 'stranding' of remnant populations in unsuitable locations. Once amassed, vertical migration to avoid lethal cooling presumably involves movement up the temperature gradient, whether by a thermokinetic or thermotactic orienting mechanism (Cloudsley-Thompson, 1952, 1977).

The Crinocheta appear to have originated in the Mediterranean (Vandel, 1960), and species ranges have been greatly extended by man. Natural ranges of species used in the present study do, however, extend into Northern Europe. Why they should not have evolved the remarkable supercooling capacities of many temperate insects and arachnids is unclear. One possibility is that viable overwintering habitats in low temperature extremes are dictated as much by water balance requirements as by thermal tolerance. The integumental permeabilities of oniscideans are substantially higher than those of most insects and arachnids (Wright and Machin, 1993a; Hadley, 1994). A typical value is $0.8 \mu\text{g h}^{-1} \text{cm}^2 \text{kPa}^{-1}$ which would result in water losses of approximately $1\% \text{h}^{-1}$ for a 15 mm (80 mg) animal in 50% RH at 0°C . Such a flux would result in lethal desiccation within 30 hours. During the summer months, diurnal refugia will tend to be cooler than the ambient air and thus maintain elevated humidities. In overwintering habitats the opposite is true. Furthermore, the ability of isopods to replenish water losses by active absorption of water vapor in elevated humidities (Wright and Machin, 1993a,b) will be greatly reduced or eliminated at low temperatures. This is a consequence both of metabolic depression (Edney, 1964b; Wieser, 1984) and the reduction in vapor density ('absolute humidity') at low temperatures. If one assumes a Q_{10} of 1.72 (data from Edney, 1964b), metabolism would be depressed 4.3-fold on cooling from 20°C to -5.0°C . When this is combined with the approximately 6-fold decline in vapor

density over this temperature range, the overall capacity for water recovery by active water vapor absorption would be reduced by a factor of twenty six. It is thus clear that maintenance of near-saturated humidities by evaporation from local water or ice will be an essential feature of overwintering microsites. The vapor pressure of ice is very similar to that of supercooled water at the same temperature (Wagner *et al.*, 1994) and animals resting beneath snow cover will not be exposed to significant vapor pressure gradients. In this respect, as well as serving as a thermal insulator, snow cover is likely to facilitate winter survival. It does however impose the dangers of drowning during spring melt. Water-balance requirements would preclude isopods from overwintering in thermally harsh above-ground habitats, such as bark or rock crevices, which are exploited by many insects and arachnids.

These findings provide an explanation for the extreme synanthropy of oniscideans in South Dakota.

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