Sheltering behavior of terrestrial isopods in grasslands

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Abstract. The hypotheses that the sheltering behavior of four species of terrestrial isopods varies in relation to differences in their morphological, physiological, and behavioral adaptations to the terrestrial environment were tested using artificial refugia together with independent estimates of density to derive an index of sheltering activity. (1) *Porcellio scaber* sheltered significantly more than *Platyarthrus hoffmannseggi, Armadillidium vulgare,* or *Philoscia muscorum,* which sheltered the least. (2) There was a decline in the sheltering index (SI) for all four species after the breeding season, continuing through to the autumn and remaining low throughout the winter. (3) Changes in the sheltering behavior of each species in relation to changes in environmental conditions were used to interpret known differences in the position and breadth of their resource utilization curves along a gradient of rabbit grazing intensity. (4) *Porcellio scaber* sheltered more where the soil was more calcareous, *P. muscorum* more under the shade of trees, and both *P. muscorum* and *A. vulgare* more in grazed than in ungrazed swards. (5) Sheltering behavior was found to be positively correlated to both rainfall and soil temperature the day before sampling for *A. vulgare* but negatively to rainfall for *P. muscorum.* There was a positive relationship between the SI for *P. scaber* and daily air temperature range. (6) Variations in the sheltering behavior of these four species of terrestrial isopod are discussed in the context of their foraging and digestive strategies and in relation to their morphological, physiological, and behavioral adaptations to the terrestrial environment.

Additional key words: foraging, habitat structure, woodlice

Sheltering behavior can be defined as actively seeking to avoid adverse environmental conditions, considered broadly here to include predation. For example, tiger prawns, *Penaeus esculentus* HASWELL, shelter in the substrate to avoid fish predators (Kenyon et al. 1995) and juvenile crayfish, *Pacifastocus leniusculus* DANA use shelter to avoid predation by back swimmers, *Notonecta lutea* MÜLLER (Hirvonen 1992). Other aquatic animals, including many freshwater fish, seek shelter from strong currents (Valdimarsson & Metcalfe 1998; Valdimarsson et al. 2000) while on land both sheep (Pollard & Littlejohn 1999; Armstrong & Robertson 2000) and red deer (Conradt et al. 2000) shelter from the wind. Poikilotherms on land actively avoid both high and low temperatures by sheltering; for example, grasshoppers may move vertically to avoid overheating on hot sunny days (Lensink 1963), while in the Antarctic mites seek

shelter from extremely low temperatures in the warmer microclimate of moss hummocks (Block & Convey 1995).

Many invertebrates such as terrestrial isopods can acclimate to a slow and progressive reduction in temperature (Edney 1968; Sutton 1980) but are susceptible to a rapid drop in temperature, which can cause significant mortality (Brody et al. 1983). This may be one reason why they shelter in the more buffered microclimate of dense tussocks in grasslands (Davis 1984). Another reason may be to avoid desiccation by sheltering in the higher relative humidity conditions below a thick litter layer, just as in deserts many animals burrow into the soil during daytime to avoid excess water loss in the drier air above ground.

In all these examples, sheltering behavior has very clear fitness benefits to individuals exhibiting the trait, due to reductions in the risk of mortality. However, sheltering individuals may also incur fitness costs as a result of this behavior. For example, the need to shelter from strong winds may prevent deer from foraging on the highest-quality patches of food

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(Conradt et al. 2000); similarly, time spent sheltering can reduce the oviposition rates of parasitoids (Fernando & Walter 1999).

For many animals there is thus a fitness trade-off between the survivorship benefits of avoiding adverse conditions and the constraints this imposes on optimal foraging strategies, with consequent fecundity costs (Gilliam 1982). Where the balance point on this trade-off occurs is partly determined by the digestive strategies of the animals. If they have a large pre-gastric crop that can be filled rapidly in a relatively exposed position, and the food is digested later in a relatively safe position, then more time can be spent sheltering and digesting. Where the digestive anatomy is simpler, with rapid, straight throughput of food, the optimal ingestion pattern will be more continuous, and larger assimilation and growth rate costs will be paid for time spent sheltering if the shelters do not coincide spatially with patches of optimal quality food.

For soil animals, both high-quality food patches and shelter are very heterogeneously distributed (Wallwork 1976), and can also be inversely correlated for litter-dwelling macroarthropods (Hassall 1996). Isopods are a prominent component of the macroarthropod decomposer fauna in many ecosystems, including some extremely xeric ones (Warburg 1965a,b; Shachak & Yair 1984). Evolution of highly developed sheltering behavior, including strong thigmo- and photo-tactic and hydrokinetic responses (Sutton 1980), has been a major factor contributing to members of the Oniscidea having become the most successful group of terrestrial crustaceans (Warburg 1987). Sheltering behavior strongly influences their population dynamics (Paris 1963) and their life histories (Dangerfield & Hassall 1994), and varies seasonally with weather conditions (Hornung & Warburg 1996), among different habitats (Hornung & Warburg 1995b, 1996), among species (Hornung & Warburg 1995a), and between sexes within a species (Dangerfield & Hassall 1994).

The responses of terrestrial isopods to differences in both temperature (Edney 1968; Warburg 1987) and relative humidity (Takeda 1984) have been studied extensively in the laboratory. In this article, we develop a new approach to quantifying sheltering behavior in the field. This is difficult to observe for any soil animal without destroying the shelter sites that it is using. We have therefore developed the use of artificial refugia or "cryptozoan boards," pioneered for studies of soil animals by Cole (1946), by combining their use with simultaneous but independent sampling of the same habitats to estimate densities using a modified high-gradient extractor (Kempson et al. 1963) as described by Hassall et al. (1988).

Using this combination of methods, variation in the number of animals found using refugia can be partitioned into variation due to differences in sheltering behavior and variation due to changes in the background density of the population. This enabled us to test the following hypotheses concerning the sheltering behavior of isopods:

(1) Sheltering behavior will differ among members of different morphological categories identified by Schmalfuss (1984), i.e., we predict clingers, e.g., *Porcellio scaber* LATREILLE, will rest against the flat undersurface of the shelter more than either "rollers," e.g., *Armadillidium vulgare* LATREILLE, which can burrow to reach more favorable microclimatic conditions, or "runners," e.g., *Philoscia muscorum* SCOPOLI.

(2) Species whose members aggregate strongly, such as *P. scaber* and *Platyarthrus hoffmannseggi* BRANDT, will use the shelter sites more than those that aggregate less strongly, such as *P. muscorum*.

(3) Members of species that are more susceptible to water loss, such as *P. muscorum,* will show larger differences in sheltering behavior among habitats differing in the availability of natural shelter sites.

(4) Members of species that are less well adapted to dry conditions (e.g., *P. muscorum*) will change their sheltering behavior in relation to rainfall more than species better adapted to desiccation stress (e.g., species that originated in drier regions such as the Mediterranean, and subsequently spread to wetter regions, such as *A. vulgare*).

Methods

Study site

This study was carried out at Lakenheath Warren, a chalk grassland with Scots pine, *Pinus sylvestris* L., and Corsican pine, *P. nigra* ARNOLD, woodland in Suffolk in the Breckland district of East Anglia, UK. Breckland has the most semi-continental climate in the UK (Duffey 1976), with low annual rainfall and hot dry summers, but frost may occur at any time of the year. Thus, shelter from climatic extremes is particularly important for terrestrial isopods in this area.

The study site is situated in an area of flat, type C grassland (Watt 1940) with pine trees nearby. The dominant species present are the grasses *Festuca ovina* L. and *Koeleria cristata* L., which due to the light grazing pressure have formed dense tussocks with distinct areas of intertussock between them in which dicotyledonous species such as lady's bedstraw, *Galium verum* L., germander speedwell, *Veronica chamaedrys* L., and purple milk-vetch,

Astragalus danicus RETZ., are more abundant (Benton et al. 1998). Two soil types occur: a brown earth of a phase of the Worlington Series (Corbett 1973), with a pH of 4.5–6, and a calcareous brown earth of the Methwold Series (Corbett 1973), with a pH of 6.5–8. The pine trees along two sides of the sample area created shade underneath, and grazing by sheep occurred on half of the site in 1999.

The sampling grid consisted of eight compartments, each 24.5×10.5 m in size and divided into 3.5×3.5 m squares. One compartment was positioned in each combination of three variables: shading by trees (*P. nigra*), grazing, and soil type.

Cryptozoan board samples

Artificial refugia, cryptozoan boards, made of $300 \times 200 \times 12$ mm of plywood, were positioned 1.25×1.75 m from the NW corner of each of the 20 squares in each of the compartments. A building brick was placed on top of each board to stop it from being moved by sheep. Woodlice were collected from beneath the boards, on the underneath of the board, and on the surface of the soil underneath the board, twice a month in 1998 and once a month in 1999 throughout the year. The litter layer and soil beneath the boards was not disturbed during collection; therefore, those animals out of sight in the deeper layers of the soil/litter profile were not collected.

Population density

The abundance of isopods was monitored by taking ten 22-cm-diameter core samples on a stratified random basis from each compartment, approximately every 2 months from spring 1998 through to autumn 1999. Isopods were extracted from them using the modified high-gradient extractor described by Hassall et al. (1988). The densities on the dates on which cryptozoan boards were sampled were then determined by interpolation.

Index of sheltering behavior

A sheltering index (SI) was calculated as

$$\text{SI} = \frac{c}{d}$$

where c is the mean number of individuals collected under the 600 cm^2 cryptozoan board and d is the background density (600 cm^{-2}) of woodlice determined from the high-gradient extractor samples. The greater the SI, the more actively isopods seek shelter beneath the boards. As individuals lower in the soil beneath the boards were not collected,

because of the destruction this would have caused, SI values should not be taken as absolute measures, but rather as a relative index of sheltering behavior.

Meteorological data

Rainfall, soil temperature at 10 cm, and maximum, minimum, and mean air temperature, on the day the cryptozoan boards were sampled and on the previous day, were obtained from Santon Downham, the nearest weather station to Lakenheath Warren, via the United Kingdom Meteorological Office through the British Atmospheric Data Centre (http://www.badc.rl.ac.uk/).

Ground layer variables

The following habitat variables were recorded for each 0.038 m^2 core, the day before sampling on August 26 and October 30, 1998, and April 20, June 24, and October 7, 1999: an index of sward height/density of the ground layer vegetation (obtained using a "sward stick" as designed by Green & Bowden 1987), percentage cover of all plant species, percentage cover of tussocks, percentage cover of hollows (soil surface > 3 cm lower than the average surface level of the soil), and litter layer depth. Complex, multi-attribute data, such as vegetation community data, are best summarized by ordination techniques (ter Braak 1987). A principal component analysis using the rotated varimax method was run on the habitat variables to eliminate covariation, and the resulting components were used in a multiple regression with the values of SI. Standard multiple regressions were used, unless there were many zeros and low numbers, in which case a Poisson regression was used.

To give an indication of the heterogeneity of habitat variables in each compartment, an index of dispersion, using the variance to mean ratio (Krebs 1989), was calculated for the habitat variables for the ten cores in each of the eight compartments for all the mapping dates. These were used in a multiple regression, with the mean values of SIs for each species in the compartments as the dependent variable.

Results

Differences among species

Different species of woodlice showed significantly different levels of sheltering behavior beneath the artificial refugia (Fig. 1). Three-way analysis of variance (ANOVA) showed that there were significant interactions between species and season ($F_{8,46} =$
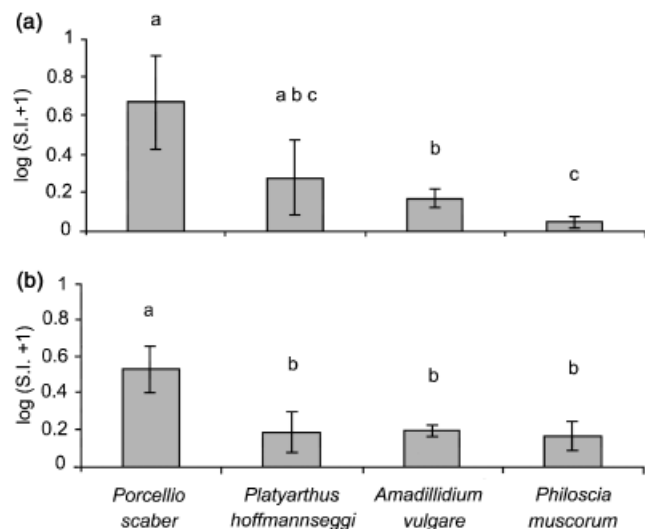
Fig. 1. Sheltering indices (SIs) of four different species of woodlouse in (**A**) spring (March and April) and (**B**) pre-breeding (May and June) (different letters above bars indicate that the values differ at $p < 0.05$).

4.305, $p < 0.001$), indicating that the differences between species vary with the time of year.

In spring (March and April), individuals of *Porcellio scaber* shelter the most, more than those of *Platyarthrus hoffmannseggi* and significantly more than those of *Armadillidium vulgare,* whose members shelter significantly more than *Philoscia muscorum* (Fig. 1A). However, in the pre-breeding season of May and June, while individuals of *P. scaber* still shelter significantly more than those of all three of the other species, differences among *A. vulgare, P. muscorum,* and *P. hoffmannseggi* were no longer significant.

Seasonal variation

Seasonal patterns in sheltering behavior differed among species. Individuals of *A. vulgare* (Fig. 2A) sheltered most in the spring and pre-breeding season, and sheltering significantly decreased in the post-breeding season (July and August) and autumn (September and October), and again in winter (November to February). In *P. muscorum,* a similar pattern was seen, with a significant peak in the pre-breeding season and lower levels for the rest of the year (Fig. 2B). Sheltering in *P. scaber* and *P. hoffmannseggi* peaked earlier in spring and then declined, logarithmically for *P. scaber* and linearly for *P. hoffmanneggi* through the year to the winter (Fig. 2C,D).

Habitat structure

The significant habitat–species interaction term in the three-way ANOVA ($F_{11,43} = 5.529$, $p < 0.0001$)
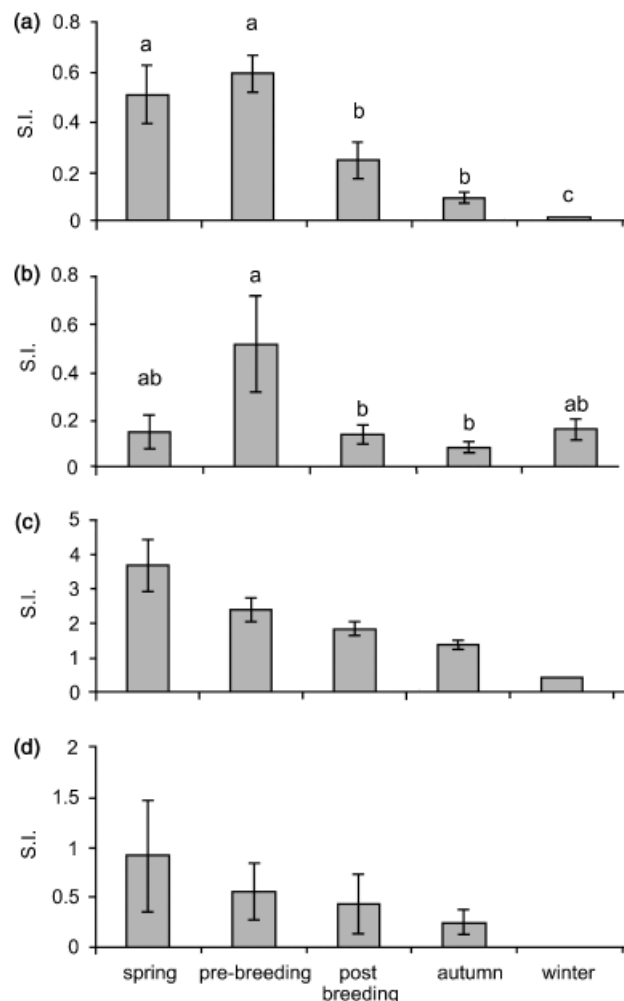

Fig. 2. Sheltering index (SI) in different periods of the year; spring (March and April), pre-breeding (May and June), post-breeding (July and August), autumn (September and October), and winter (November to February). **A.** *Armadillidium vulgare*. **B.** *Philoscia muscorum.* **C.** *Porcellio scaber;* log SI $= -0.134t + 0.773$, $R^2 = 0.940$, $p = 0.006$, where t is time in months after March 1. **D.** *Platyarthrus hoffmannseggi;* log SI $= -0.086t + 0.825$, $R^2 = 0.973$, $p = 0.002$ (different letters above bars indicate that the values differ at $p < 0.05$).

reflects differences among species in how their sheltering behavior differs in response to the three habitat variables of shading, grazing, and soil conditions.

Shading. Shading by a pine canopy layer had a significant effect on sheltering behavior in *P. hoffmannseggi* and *P. muscorum* (Fig. 3A). Members of the former shelter more in unshaded compartments, whereas the latter shelter more in shaded compartments. Shading had no significant effect on sheltering behavior in *P. scaber* or *A. vulgare.*

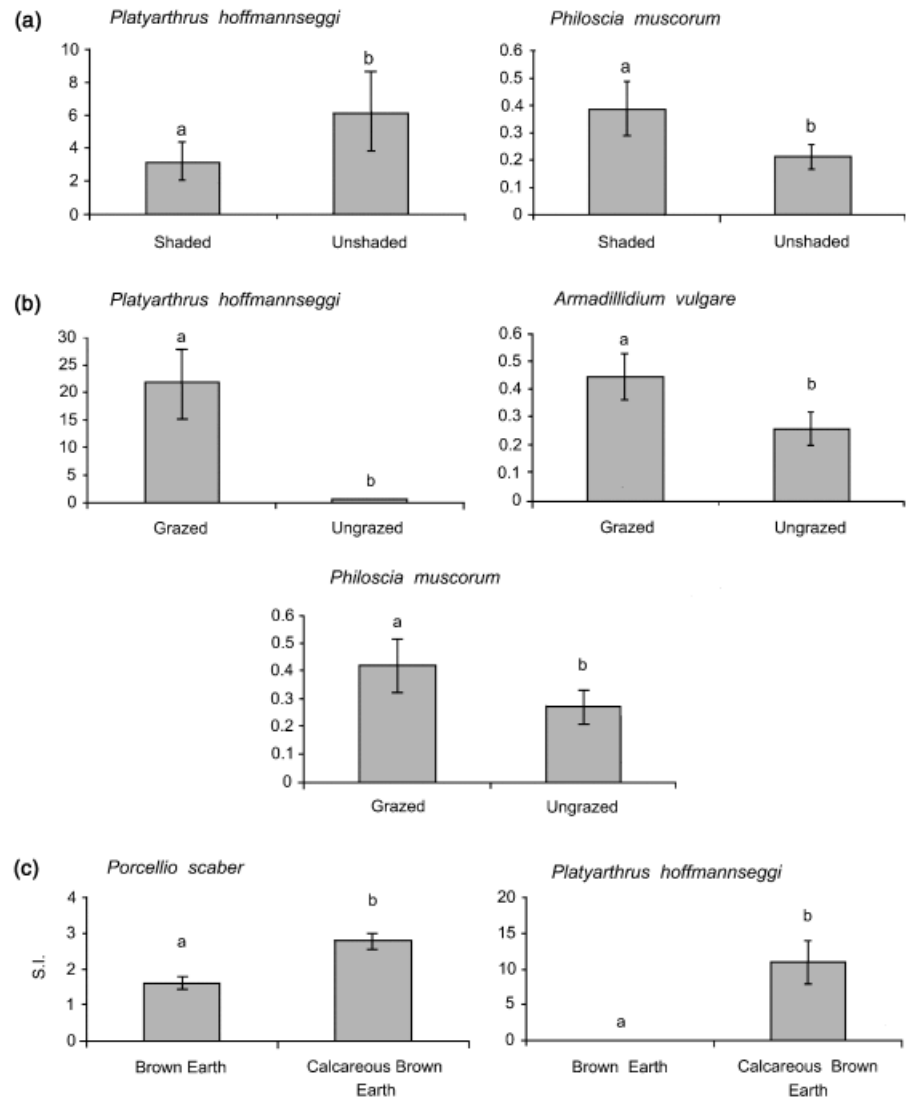**Grazing.** Differences in habitat structure influenced by sheep grazing had a significant effect on sheltering

Fig. 3. Sheltering index (SI) of *Porcellio scaber, Platyarthrus hoffmannseggi, Armadillidium vulgare,* and *Philoscia muscorum,* with differences in habitat structure influenced by (**A**) canopy layer causing shading, (**B**) grazing, and (**C**) type of soil. All axes are of SI (letters above bars indicate that the values differ at p < 0.05).

behavior in *P. hoffmannseggi, A. vulgare,* and *P. muscorum* (Fig. 3B). All three of these species shelter more in the grazed compartments than in the ungrazed ones. However, grazing has no significant effect on sheltering behavior in *P. scaber.*

Type of soil. Differences in habitat structure influenced by the type of soil have a significant effect on sheltering behavior in *P. scaber* and *P. hoffmannseggi* (Fig. 3C). Both these species shelter more in compartments with the calcareous brown earth soil than in compartments with the brown earth soil. Type of soil had no significant effect on sheltering behavior in *A. vulgare* and *P. muscorum.*

Interactions between habitat and season

Philoscia muscorum was the only species for which the effects of habitat changed significantly with time of year ($F_{23,68} = 2.611$, p < 0.001), due to the SI increasing much more in the grazed swards in autumn and winter than it did in the longer, more tussocky, ungrazed swards.

Ground layer variables

No significant relationships were found between the SI and the mean levels of any of the variables used to quantify ground layer vegetation and structure, but the spatial heterogeneity of some habitat variables did correlate with the sheltering behavior of the isopods (Table 1). *Armadillidium vulgare* shelters less as the patchiness of hollows increases. Individuals of *P. muscorum* shelter less as the patchiness of grass increases and the patchiness of tussocks decreases.

Table 1. Multiple regression of the sheltering indices of *Armadillidium vulgare* and *Philoscia muscorum* on the index of dispersion (variance:mean ratio) of habitat variables in core samples on five dates in 1998 and 1999.

Species	R^2	Habitat variable (variance:mean)	b	df	p
A. vulgare	0.127	% cover of hollows	−0.151	31	0.045
P. muscorum	0.247	% cover of grass	−0.169	22	0.045
		% cover of tussocks	0.101	22	0.054

Meteorological conditions

Sheltering behavior in *A. vulgare* increased significantly when either soil temperature or rainfall increased on the day prior to observation (Table 2, Fig. 1A). In contrast, sheltering behavior in *P. muscorum* decreased with higher levels of rainfall on the previous day (Table 2, Fig. 4B), but was not related to either soil temperature or diurnal air temperature range. The SI for *P. scaber* was not related to either rainfall or soil temperature, but was significantly positively related to the diurnal range of air temperature (Fig. 4C). Sheltering in *P. hoffmannseggi* was not significantly related to any of the meteorological variables.

Discussion

For many animals, the trade-off between time allocated to sheltering and time spent feeding has important fitness consequences. While much attention has been focused on factors determining when and where animals feed, and a substantial body of optimal foraging theory has developed (Emlen 1966; MacArthur & Pianka 1966; Pyke 1984; Stephens & Krebs 1986), much less is known about how animals decide when, where, and for how long to shelter to minimize fitness costs of adverse environmental conditions.

These decisions will be partly determined by how well the animals are adapted morphologically to the adverse conditions. Many mammals at higher latitudes have thicker fur and therefore need to shelter less from cold than comparable species from lower latitudes; similarly, many Antarctic invertebrates are physiologically adapted to stay active at sub-zero temperatures. How long an animal can spend sheltering also depends on its digestive strategy. For herbivores with relatively straight alimentary canals (such as widgeon, *Anas penelope* L., and brent geese, *Branta bernicla* L.) with rapid throughput times of sometimes less than an hour (Lane 1994), ingestion has to be a semi-continuous process, any interruption in which can have serious negative implications for balancing their daily energy budget (Belanger & Bedard 1990; Stock 1992). In contrast, ruminants with their compartmentalized stomachs need time free from ingesting in order to chew and digest their cud, which can be done while sheltering—as the African buffalo, *Syncerus caffer* SPARRMAN does while spending a large part of the day sheltering in shady thickets, allowing microorganisms time to digest its food more extensively (Dorst & Dandelot 1972).

Isopods have a very straight alimentary canal, but are able to vary gut throughput time widely. They can either feed semi-continuously, filtering soluble components through the proventriculus into the midgut caecae (Hassall 1977), or retain food for up to several days in the hindgut, where it is digested more extensively, partly by microorganisms, while the products of digestion are conducted to the midgut via the typhlosole channels (Hassall & Jennings 1975; Hames & Hopkin 1989; Zimmer & Topp 1998). Furthermore, isopods are coprophagous (Hassall & Rushton 1982, 1985; Szlavecz & Pobozsny 1995), reingesting feces that have accumulated in their shelter sites, undergoing further microbial digestion and thus acting as an "external rumen" (Mason & Odum 1969).

This versatility in digestive strategies enables all terrestrial isopods to be very flexible in the amount of time they spend sheltering. This may have helped to make them the most successful group of Crustacea to

Table 2. Analyses of covariance between log sheltering index and meteorological variables with habitat and season entered as random factors.

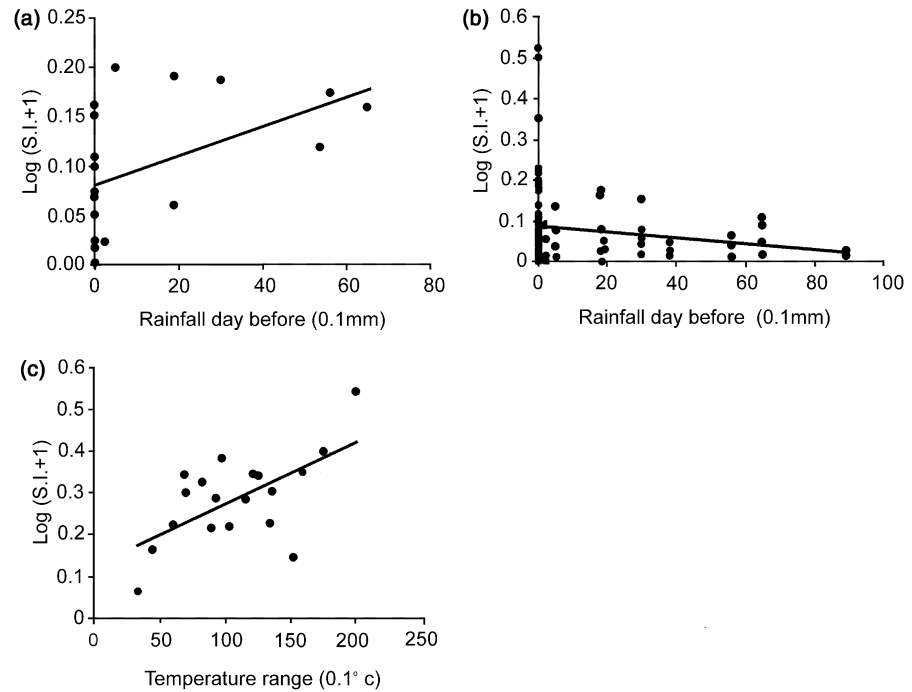| Species	Meteorological variable	b (e–0.4)	F	df	p
Armadillidium vulgare	Rainfall on previous day	+6.81	5.598	1, 71	0.021
	Soil temperature on previous day	+5.46	4.246	1, 71	0.043
Philoscia muscorum	Rainfall on previous day	−8.0	5.313	1, 66	0.024
Porcellio scaber	Air temperature range on sampling day	+9.7	6.441	1, 34	0.016

Fig. 4. Relationship between local meteorological conditions and sheltering index (SI). **A.** Rainfall on the day before sampling and SI of *Armadillidium vulgare* ($b = 0.002$, $p = 0.036$). **B.** Rainfall on the day before sampling and SI of *Philoscia muscorum* ($b = -0.001$, $p = 0.034$). **C.** Air temperature range on the sample day and SI of *Porcellio scaber* ($b = 0.002$, $p = 0.005$).

have invaded the terrestrial environment, where they are subjected not only to higher risks of desiccation but also to a much more widely fluctuating thermal environment. Different families of the Oniscidea show different levels of morphological, physiological, and behavioral adaptations to these adverse environmental conditions that, combined with their digestive flexibility, result in a very wide range of variation in sheltering behavior. They thus form very suitable models for analyzing how sheltering behavior changes in response to differences in environmental conditions.

On grass heaths in the Breckland district in eastern England, different species of isopod occupy different positions along a gradient of grazing intensity (Hassall 1996). When lightly grazed, the swards are long, tussocky, and dominated by grasses. This provides good shelter, and hence mortality rates are lower, but the coarse grasses out-compete broad-leaved dicotyledonous plants, whose litter forms a much higher quality food for terrestrial isopods (Rushton & Hassall 1983). This results in lower growth rates and fecundity than in tightly grazed swards, where dicotyledonous plants are more abundant but where there is less shelter from microclimatic extremes, and thus higher mortality (Hassall & Dangerfield 1997). The four species of isopod that occur on Breckland grass heaths have different positions along a gradient of grazing intensity and different breadths of resource utilization curves (Hassall 1996). *Philoscia muscorum* occupies the narrowest range of sward

heights, restricted to the least grazed sites, which have the tallest, thickest swards; *Porcellio scaber* occupies the broadest range of conditions extending to shorter swards than the other species, but is also present in the long swards; *Armadillidium vulgare* occupies an intermediate range of sward conditions, peaking at moderate levels of grazing, while the position of *Platyarthrus hoffmannseggi* is determined primarily by the nesting preferences of its host, the ant *Lasius flavus* FABRICUS, in the nests of which it lives commensally.

Different species of isopods found in grasslands have very similar food preferences; hence, we hypothesize that the observed differences between species in their positions along an axis of grazing intensity reflect differences in their sheltering strategies. That there will be differences in their sheltering behavior can be predicted from other aspects of their biology, as three of the different species represent three of the major morphological categories identified by Schmalfuss (1984): "clingers" (*P. scaber*), "rollers" (*A. vulgare*), and "runners" (*P. muscorum*). *Porcellio scaber* consistently used the artificial refugia more than the other species, which can be predicted from its dorsoventrally flattened morphology, enabling it to clamp against flat surfaces as a defense against predators. In contrast, *A. vulgare*, with a more cylindrical body, rolls into a ball to escape predators and is also best able to burrow to more favorable microclimatic conditions (Davis et al. 1977), while *P. muscorum* has long legs and can

escape by running. Members of these species are thus unlikely to use the flat surface under the cryptozoan boards as much as *P. scaber*. Individuals of *P. scaber* also differ from those of the other two species in their behavior, as they aggregate much more (Davis 1978). Aggregations form when one individual comes to rest and then other individuals stop alongside it, thus building up clumps or aggregations as described by Allee (1926) in sites that may be marked by aggregating pheromes (Takeda 1984). If one individual of *P. scaber* comes to rest on the flat surface of the refugia, there is therefore a higher probability that other individuals will join it than is the case for either of the other two species.

While differences in SIs among species can be related to other aspects of their biology, differences within a species under different environmental conditions provide more insight into the trade-off between foraging and sheltering behavior. Populations of *P. hoffmannseggi* showed no significant changes in relation to any of the meteorological variables, possibly because they both feed and shelter within ant nests (*L. flavus*), a buffered microclimate that is subject to less fluctuation in both temperature and relative humidity than the open litter layer. Which cryptozoan boards they shelter beneath is also largely determined by the nesting preferences of the ants, which use these as solanaria on more exposed sites. Members of *L. flavus* also prefer more calcareous soils, which could account for the higher SI on the calcareous brown earth sites.

In *P. muscorum*, woodlice sheltered least in their most preferred habitats, where long, thick, tussocky swards provided an abundance of their preferred natural shelter sites in the unshaded and ungrazed plots. They sheltered more where the tussocks in the sward were more heterogeneous, as they were in the grazed plots. Shading caused by the canopy layer of pine trees resulted in a higher proportion of bare ground. It was notable that individuals of *P. muscorum,* which do not have pseudotrachea to reduce moisture loss from their respiratory surfaces and, among the species studied, are most vulnerable to water loss (Edney 1954, 1968), sheltered significantly more in this habitat. In a similar way, the percentage of stones used as shelter sites by Mediterranean isopods was higher in forests than in grasslands (Hornung & Warburg 1996). *Philoscia muscorum* was the only species with a significant negative relationship between its SI and rainfall, indicating that its members sheltered less when the sward surrounding the cryptozoan boards was wetter. These changes in sheltering behavior, in response to environmental conditions, are consistent with the species being restricted to the narrowest range of the grazing pressure gradient, where the sward is highest and thickest, and provides the most natural shelter sites.

In contrast to *P. muscorum,* there was a significant *positive* relationship between SI and rainfall in *A. vulgare,* indicating that individuals of this species took refuge from wetter swards under the cryptozoan boards following heavy rain, when the shelter of the boards temporarily provided drier conditions than in the surrounding sward. Similar sheltering behavior following heavy rain was observed in *A. vulgare* in California (Paris 1963), where significant mortality is caused by high rainfall. Mortality in *A. vulgare* is also positively correlated to rainfall in grasslands in the Breckland (Hassall & Dangerfield 1997). This susceptibility to high rainfall may be related to the Mediterreanean origin of this species, whose members are better adapted to drier conditions than those of *P. muscorum,* in that they have well-developed pseudotrachea and can roll into a ball to further reduce water loss from their ventral surfaces. They can also burrow deeper into the soil to avoid adverse microclimatic conditions in the litter layer (Davis et al. 1977). As in *P. muscorum,* individuals of *A. vulgare* sheltered more under the cryptozoan boards, where there were less thick tussocks to provide natural shelter sites in the grazed swards (Fig. 3B), but also where the hollows were more homogeneously dispersed (Table 1).

Their greater resistance to desiccation stress may account for why *A. vulgare* has a broader resource utilization curve in relation to a gradient of sward height than *P. muscorum*. However, being distributed further into the shorter swards may expose individuals of *A. vulgare* to more temperature stress. Breckland has the most continental climate in the British Isles, with frosts occurring in all months of the year (Duffey 1976). A diurnal temperature range from −3°C to 31°C was recorded in July 1990 by Willott (1992) from intertussocks in a short sward on Weeting Heath, seven miles from this site, where temperatures in excess of 55°C on bare earth have been recorded on sunny days in August (M. Hassall, unpubl. data). Such temperatures are well above the lethal limit for individuals of *A. vulgare,* which may account for the positive correlation between its SI and soil temperatures.

Members of *P. scaber* are exposed to the widest daily temperature range because the resource utilization curve for *P. scaber* stretches furthest into the most heavily grazed swards of the four species. It also has the most significant relationship between sheltering behavior and daily temperature range. At the most intensive end of the grazing gradient, there is

the least natural shelter available from rapid temperature changes. While isopods can tolerate a wide range of temperatures when given sufficient time to acclimate (Edney 1968; Sutton 1980), they are much more sensitive to sudden temperature fluctuations, changes of 25°C causing significant mortality to populations of *A. vulgare* (Brody et al. 1983; Hassall et al. 2005a). The clearly developed sheltering response in relation to temperature range in *P. scaber* may therefore be an important factor enabling this species to tolerate a wider range of habitat characteristics than the other two species, including those of the shortest swards, in this study on calcareous brown earth, where it sheltered significantly more.

Unlike individuals of *P. muscorum* and *A. vulgare*, sheltering in *P. scaber* was not significantly related to rainfall. Individuals of *P. scaber* have well-developed pseudotrachea to reduce moisture loss from their respiratory surfaces, but also aggregate into very tightly packed clumps, which further reduces moisture loss (Allee 1926). This may help them to tolerate more exposed conditions in the shorter swards, with less reliance on natural shelter sites, and may also account for why this species changed its sheltering behavior less in relation to grazing and shading than the other species.

Analyses of the sheltering component of the trade-off between sheltering and foraging behavior can thus help to explain patterns of distribution and habitat partitioning that cannot be predicted on the basis of differences in the distribution of food or breeding sites. Feeding strategies of animals have very obvious consequences for their fitness; they have been studied extensively, leading to the establishment of a large body of optimal foraging strategy theory. With some notable exceptions, such as the studies of bats moving between wintering hibernacula to maintain precise optimal hibernating body temperatures, there have been few empirical studies of sheltering strategies and certainly a wide-ranging theory of optimal sheltering strategies has yet to be developed. This study shows that there can be very large differences in sheltering behavior both among species and in how different species respond to changes in their environment. This variation in sheltering behavior has immediate consequences for fitness of individuals and profoundly influences the ecology of the species concerned.

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