

Trade-offs between microhabitat selection and physiological plasticity in the Antarctic springtail, *Cryptopygus antarcticus* (Willem)

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Abstract In the maritime Antarctic, terrestrial arthropods have recourse to two strategies to mitigate low summer temperatures: (1) physiological plasticity and (2) avoidance via microhabitat insulation. This study investigated the interaction between these strategies in the springtail, *Cryptopygus antarcticus*, established in situ within contrasting microcosms (buffered vs. exposed) and within two sets of habitat simulations (wet vs. dry) over diurnal scales through the Antarctic summer. Significant differences were found in the cold hardiness of springtails sampled simultaneously from each microcosm. Exposed animals showed greater plasticity in the “true” austral summer, but as field temperatures declined preceding the onset of winter, buffered animals showed greater resilience. Overall, water was found to inhibit the buffering effect of moss and there was a significantly greater discrimination between buffered and exposed microcosms in the dry treatment. Analysis of microhabitat temperatures indicate that it is thermal variability not lower temperature that is responsible for the greater plasticity of exposed animals.

Keywords Phenotypic plasticity · Collembola · Acclimatization · Rapid cold hardening · Thermal variability

Introduction

The importance of microhabitats in providing a buffering medium between terrestrial arthropods and low temperatures has long been recognised (e.g. Mani 1962; Danks 1978, 1991). Numerous studies have illustrated the differences between air and soil temperatures (e.g. Pryor 1962; Geiger 1965; Danks 1978, 1981; Walton 1982; Bale 1991; Coulson et al. 1995). Likewise, the modifying role of factors like snow cover, degree of exposure, water availability, and aspect in determining microhabitat temperatures has been clearly established (e.g. Danks 1981; Coulson et al. 1995; Davey et al. 1992). As poikilotherms, arthropods are highly sensitive to variability in the microclimatic envelope they occupy. To date, however, the sensitivity of polar terrestrial arthropods to such spatial variability has largely only been examined in terms of local distribution and phenology (e.g. Danks 1981, 1991; Strathdee and Bale 1995) or at macro-scales (e.g. Turnock and Fields 2005). This study set out to examine the implications of such micro-heterogeneity on the physiological plasticity of a representative Antarctic terrestrial arthropod, the springtail, *Cryptopygus antarcticus* (Willem).

The acquisition of cold hardiness in Antarctic terrestrial arthropods has traditionally been considered a seasonal phenomenon (Block and Sømme 1982; Sømme and Block 1982; Cannon and Block 1988; Convey 1996). They avoid freezing in the winter by supercooling: lowering their temperature of crystallisation (T_c) from c. -7 to $<-20^\circ\text{C}$ through the accumulation of colligative antifreezes and the

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evacuation of ice nucleating agents (Cannon and Block 1988). However, in the polar summer, when their growth budget is limited (Burn 1981) and sub-zero temperatures are relatively common, animals must reconcile their somatic demands with the physiological pressures of life at low temperatures. Adaptations for low critical thermal minima (CT_{min}) (e.g. Sømme and Block 1982; Hawes et al. 2007a) enable them to feed at or just below 0°C, while extended life cycles obviate the necessity for synchrony in somatic development and reproductive activity (Burn 1984; Convey 1996).

Nonetheless low summer temperatures may constitute a physiological stress to active, feeding animals with nucleating material in their guts (Worland and Convey 2001). The “textbook” ecological response of soil arthropods to low temperatures is behavioural avoidance by migration into thermally buffered environments (Hopkin 1997 and references therein). Indeed, studies of diurnal activity patterns in *C. antarcticus* confirm a temperature-dependent relationship between activity and microclimate, with animals maximising activity opportunistically with higher temperatures (Schenker and Block 1986; Burn and Lister 1988). However, in addition to (or instead of) behavioural avoidance, Antarctic terrestrial arthropods may also rapidly cold harden (RCH) (sensu Lee et al. 1987)—changing their supercooling ability over a matter of hours (Worland and Convey 2001; Hawes et al. 2007a).

In the maritime Antarctic, moss turf provides a thin—vertical migration is delimited by a soil profile that ranges from c.0 to 10 cm—but nonetheless important buffer against ambient temperatures. Its distribution varies from comprehensive moss-banks to patchy fell-field sites (e.g. Schenker and Block 1986). Variability in water availability—an additional stress on polar soil organisms (Kennedy 1993; Block 1996; Hertzberg and Leinaas 1998; Hodkinson et al. 1999)—is equally heterogeneous in space and time, whether it be “locked up” in ice or released by thawing snow. The aim of this study was to examine the interaction between two strategies for mitigating low temperature stress—behavioural avoidance and rapid cold hardening—in the context of manipulations that simulate the naturally occurring extremes of habitat exposure and hydrology.

Methods

Study site and sample collection

Experiments were carried out at Rothera Research Station at Rothera Point, Adelaide Island, on the west coast of the Antarctic Peninsula (maritime Antarctic) (67°34'S, 66°08'W) from January to March 2005. To maximise the impacts of exposure and insulation, manipulations were set

up at an exposed site outside the station on the roof of an ancillary container laboratory. Sample animals of *Cryptopygus antarcticus* and small sections of moss carpet (*Sanionia uncinata* (Hedw.) Loeske) were collected from a moss bank adjacent to the station and established in two sets of microcosms with two treatments.

Habitat temperature

To illustrate the character and variability of temperature in exposed and buffered microhabitats over the summer of 2004–2005, median daily temperatures for each month for air (2 m), soil surface, and below ground (2, 5, 10, and 20 cm) were calculated from hourly measurements collected from the British Antarctic Survey micro-met station on neighbouring Anchorage Island—a typical terrestrial moss habitat for *C. antarcticus*, c. 2–3 km from Rothera Point (BAS Biological Sciences Division). Diurnal temperature variation during the experiments is represented by air temperatures from Rothera met-station (BAS Physical Sciences Division) with means calculated as the mean of the 4 h preceding sampling (temporal resolution = 5 min).

Experimental treatments

Microcosms were established in pairs of sieves (43 µm) (one underneath, one above) sat within open plastic boxes (22 × 23 × 7 cm) to prevent dispersal of animals, but allow direct exposure to air temperatures. Two manipulations were carried out—dry and wet. In the dry treatment animals were established either in sections of moss turf (c.5 cm thick) or were tapped on to the mesh surface of the sieve from moss, and provided with a few strands of moss and moistened tissue to prevent desiccation. In the wet treatment, this was repeated except that sieve microcosms were water-logged, a frequent occurrence in polar habitats (e.g. Hodkinson et al. 1999), and sat within c. 6 cm of water. Sampling of cold tolerance was carried out throughout the austral summer over 24 h periods ($N = 5 \times 24$ h periods for each manipulation). After preliminary inspection of temperature data, diurnal sampling intervals were chosen [based on the alternation of thermo- and cryophases (sensu Beck 1991)] at 3 pm the first day and 7 am and 3 pm the next day.

Measures of cold tolerance

At each sampling interval, c. 50 animals were removed from each treatment using an aspirator (no moss = exposed treatment) or by tapping of the substrate (moss turf = buffered treatment). To ensure sampling of animals from the most insulated moss micro-horizons, the turf was held right side up and springtails dislodged from the bottom

layer by gentle tapping of the moss. All experiments were carried out in an unheated container lab to ensure animals did not alter their state of acclimation. Replicates of five glass tubes (diameter = 0.5 cm) (1 = c.10–15 animals), were cooled from 5 to -15°C and held there for 1 min. After Worland et al. (2007), -15°C was used as the discrimination temperature (sensu Bale 2002). Low temperature survival (LTS) was expressed as the percentage of animals surviving the discrimination temperature i.e. in a “winter” mode of cold hardiness. Elsewhere (Hawes et al. 2006a; Worland et al. 2007) we have delineated the complex multi-modal character of transitions in cold tolerance in Antarctic terrestrial arthropods; here, in order to perform simultaneous measurements, we adopted a simplified index of cold tolerance (survival below -15°C)—which is more conservative as it underestimates the number of animals that can survive minimum summer temperatures. LTS was calculated simultaneously for each microcosm by placing each set of 5 glass tubes within boiling tubes in an alcohol bath (Thermo Haake Phoenix P2 Circulator; Thermo Haake International, Germany) and cooled at $1^{\circ}\text{C min}^{-1}$. A digital thermometer, with thermocouple placed in a replicate glass tube was used to monitor temperature within the tubes.

Water content

To identify whether water loss was involved in any differences found between exposed and buffered microcosms, water content was determined for a second set of five replicates ($N = 10\text{--}15$ animals) collected concurrently with animals for cold tolerance assays at each sampling interval for the dry treatment experiments. Water content was determined gravimetrically. Animals were weighed on a Mettler-Toledo microbalance (UMXW $d = 0.1\ \mu\text{g}$) (Mettler-Toledo Ltd, UK) to determine fresh weight, oven dried for 24 h at 60°C and then reweighed. Water content was calculated as the percentage difference between fresh and dry weight. Water loss was not measured in the wet treatment as surface wetting of the cuticle would have made gravimetric measurements of internal water status too inaccurate.

Data analysis

As the data were not normally distributed, microhabitat temperature data were analysed using nonparametric statistics. In the absence of a suitable multivariate nonparametric statistic, paired comparisons (Mann–Whitney) were made between air temperatures and soil temperatures. Spearman’s rank correlation was used to identify relationships between temperature and thermal variability (calculated as the range between thermal maxima and minima). General linear modelling (GLM) with Bonferroni posthoc compari-

sons was used to compare differences between percentage survival between treatments (buffered/exposed) and thermophase for each replicate. Differences in water status of animals from the dry manipulations were compared using GLM—with the exception of 9–10 March for which non-parametric comparisons were necessary (and prevented the examination of a “time effect” for that day). Linear discriminant analysis was used to compare the percentage successful categorisation of the dry and wet manipulations. All statistical analysis was carried out on MINITAB 14 software (Minitab Ltd, Coventry, UK).

Results

The buffering of microhabitats

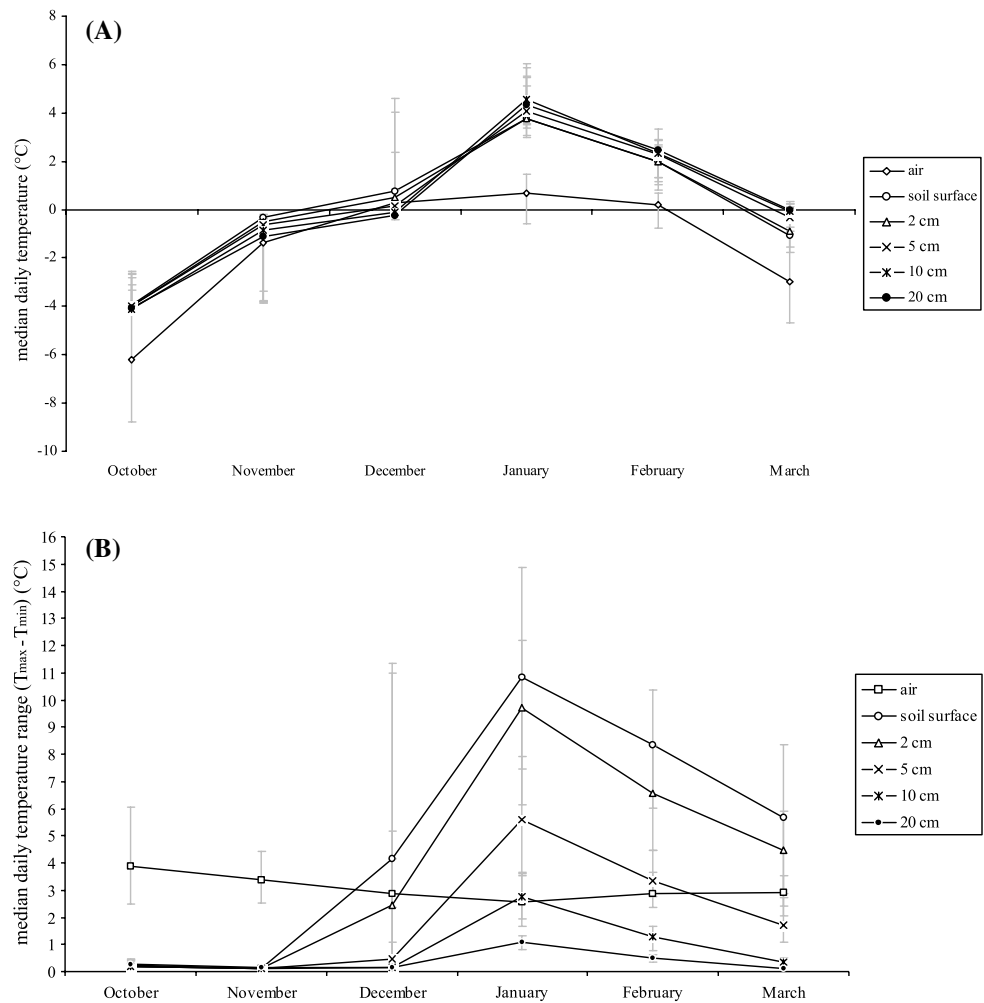
Figure 1a compares the summer thermal regimes for air, soil surface, and below ground (2, 5, 10, 20 cm) at the representative terrestrial site on Anchorage Island. Air temperature was lower than surface and below ground temperatures across the season. Paired comparisons (Mann–Whitney test) found significant differences between soil surface and air temperatures ($N = 182$, $W = 28183$; $P < 0.001$), but no significant difference between soil surface and below ground temperatures. On the other hand, paired comparisons (Mann–Whitney test) found no significant difference in thermal variability between soil surface and either air temperatures or temperature 2 cm below ground, but detected significant differences between soil surface variability and variability at 5 cm ($N = 182$; $W = 29077$; $P < 0.001$), 10 cm ($N = 182$; $W = 26441$; $P < 0.0001$), and 20 cm ($N = 182$; $W = 25387.5$; $P < 0.001$). In other words, at the spatial scale of the experiment—exposed (surface) versus buffered (moss c.5 cm), there was no significant difference between median temperatures, but significant differences between variability. Coincident with higher temperatures (Fig. 1a), variability was greatest in January and February (Fig. 1b). Spearman’s rank correlation found no significant correlation between temperature and variability for air temperature, but significant correlations for all soil temperature measurements, individually ($N = 182$, 182) and pooled with air temperature ($N = 1092$, 1092).

Experiment 1: dry treatment

Survival

Figure 2 shows the diurnal variation in cold tolerance of animals in exposed and buffered (moss) microcosms over the five sample periods. Comparison of means (GLM) found significant differences between buffered (moss) and

Fig. 1 Microhabitat temperatures for Anchorage Island. **a** Median temp, **b** median range. Error bars = interquartile range)



exposed microcosms on 12–13 January ($df_{xy} = 1,23$; $F = 10.21$; $P = 0.004$) with posthoc comparisons (Bonferroni) identifying the cryophase (7am) as the source of the significant difference. Significant differences were also found between habitat simulations on 9–10 March ($df_{xy} = 1,24$; $F = 4.90$; $P = 0.037$) with posthoc comparisons (Bonferroni) identifying significant differences between moss and exposure at 3 pm (first thermophase) and 3 pm (cryophase). Significant differences between microcosms underwent a complete reversal from the start to the end of the experiment, with greater cold tolerance in exposed animals on 12–13 January when temperature variation was greatest (10°C), compared to greater cold tolerance in buffered (moss) animals on 9–10 March (pre-winter) when temperature variation was least (1.4°C). Both microcosms showed greater survival in relation to time (cryophase vs. thermophase) on 24 February ($df_{xy} = 1,24$; $F = 15.70$; $P = <0.001$) with post hoc comparisons finding significant interactions between the first thermophase (3 pm) and the cryophase (7 am) for both microcosms.

Water content

Table 1 shows the differences between water content of springtails in exposed and buffered (moss) treatments for the dry manipulation. Although significant differences were found between treatments on several days, there was no significant effect of time. (The use of non-parametric tests for 9–10 March however means that a time effect could not be tested for that day). Overall, desiccation may have contributed to differences in cold tolerance between treatments (buffered vs. exposed), but physiological plasticity (diurnal variability in cold tolerance)—and therefore differences in plasticity between treatments—cannot be attributed to variation in water content.

Experiment 2: wet treatment

Survival

Figure 3 shows the diurnal variation in cold tolerance of *C. antarcticus* in the wet treatment. Significant differences

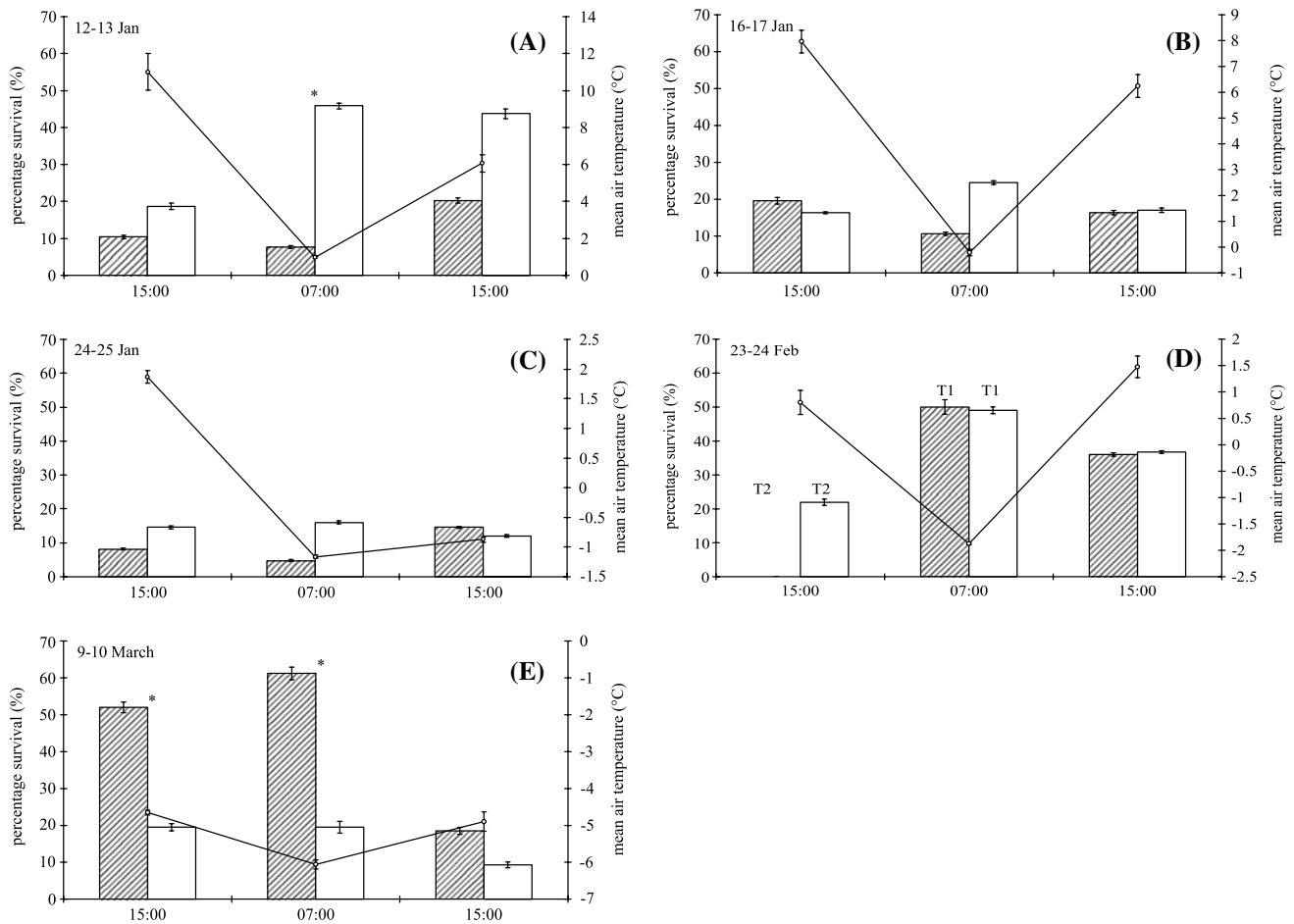


Fig. 2 Comparison of *C. antarcticus* survival below -15°C in moss (shaded bars) and exposed (unshaded bars) microcosms for the dry treatment on **a** 12–13 Jan; **b** 16–17 Jan; **c** 24–25 Jan; **d** 25–26 Feb; and **e** 9–10 March. Black line indicates mean air temperature ($^{\circ}\text{C}$) of the

last 4 h at each sample occasion. Asterisk represents significant differences between moss and exposed microcosms; T1 and T2 represent significant differences between times

(GLM) between moss and exposure were found on 2–3 March ($df_{xy} = 1,24$; $F = 6.97$; $P = 0.015$) with post hoc comparison (Bonferroni) finding significant interactions between habitats during the cryophase and a significant habitat–time interaction between exposed animals during the cryophase and second thermophase. Significant differences were found in diurnal phases of cold tolerance for both 5–6 March ($df_{xy} = 1,24$; $F = 13.81$; $P < 0.001$) and 11–12 March ($df_{xy} = 1,24$; $F = 5.89$; $P = 0.009$). On 5–6 March significant pairwise interactions (Bonferroni) were found between the first thermophase and the cryophase for both microcosms and for just exposed animals, between the cryophase and the second thermophase. Unlike the other sampling days thermo- and cryophases were reversed on 11–12 March and significant pairwise interactions (Bonferroni) were found between the cryophase (7 am) and the second thermophase (3 pm). Pooled mean survival over the sampling period was slightly greater in exposed animals but the pattern of survival was the same in both microcosms and showed no relationship with thermal variability.

Difference between wet and dry treatments

Linear discriminant analysis was carried out to determine the percentage successful categorisation of buffered and exposed habitats for each experimental treatment. Variances were not significantly different (F -test; $N = 5,5$; $T = 1.676$; $P = 0.629$) between treatments. Significant differences were found in percentage successful discrimination of habitats between the two treatments ($N = 5,5$; $T = 2.44$; $P = 0.045$) (T -test).

Discussion

This is the first study to demonstrate the occurrence of an exposure-acclimation interaction at this level of spatio-temporal resolution in a terrestrial arthropod. Despite the importance of microhabitat to arthropod thermal relations, few studies have examined the relationship between physiological acclimation and microhabitat at what are ecologi-

Table 1 A comparison of mean water content (SE \pm 1) of *C. antarcticus* in buffered and exposed microcosms (dry treatment)

Date	Time	Mean water content (%)		Difference between microcosms (GLM)			
		Buffered	Exposed		<i>df</i>	<i>F</i>	<i>P</i>
12/1/04	3 pm	69.64 (\pm 1.26)	62.20 (\pm 3.47)	Microcosm	1	8.55	0.010
	7 am	69.76 (\pm 1.27)	63.53 (\pm 2.57)	Time	1	0.10	0.760
	3 pm	na	na	Time \times microcosm	1	0.07	0.798
16/1/04	3 pm	69.95 (\pm 1.45)	61.18 (\pm 4.49)	Microcosm	1	6.86	0.015
	7 am	71.59 (\pm 1.62)	66.50 (\pm 1.80)	Time	2	1.17	0.326
	3 pm	67.54 (\pm 1.33)	67.26 (\pm 1.14)	Time \times microcosm	2	1.77	0.192
23/2/04	3 pm	70.07 (\pm 0.34)	68.42 (\pm 0.96)	Microcosm	1	0.20	0.655
	7 am	67.55 (\pm 1.74)	70.64 (\pm 2.26)	Time	2	0.01	0.986
	3 pm	70.42 (\pm 0.74)	67.71 (\pm 0.27)	Time \times microcosm	2	3.53	0.048
				Differences between microcosms (Kruskal–Wallis)			
					<i>df</i>	<i>H</i>	<i>P</i>
24/1/04	3 pm	66.08 (\pm 0.96)	70.57 (\pm 1.33)		1	10.71	0.001
	7 am	66.34 (\pm 0.47)	72.04 (\pm 0.66)				
	3 pm	66.99 (\pm 3.12)	69.53 (\pm 1.00)				
9/3/04	3 pm	68.88 (\pm 1.23)	65.97 (\pm 1.60)		1	0	0.983
	7 am	50.41 (\pm 3.02)	50.62 (\pm 9.24)				
	3 pm	61.28 (\pm 1.67)	61.18 (\pm 1.72)				

Significant differences in bold; Mean error = SE \pm 1

na data not available

cally realistic scales of distribution and activity in arthropods—i.e. micro-scales. Irwin and Lee (2003) and Coulson et al. (2000) provide rare examples of studies that have addressed fitness trade-offs at seasonal scales, looking at the responses of the same species of insects to overwintering in qualitatively different microhabitats. The results of this study underline the sensitivity of arthropod acclimation processes to variability in the microclimate envelope at a scale that has previously only been hypothesised (e.g. Shreve et al. 2004).

It is remarkable that a few centimetres of moss—not sufficiently insulated to be warmer than the soil surface—should have such a modifying role on the acclimation potential of a soil arthropod. Certainly, the exposure-buffered interaction is not consistently significantly different—in a realistic context, numerous variables interact with the acclimation process at both endogenous (e.g. feeding state, moult state) and exogenous (e.g. temperature minima, temperature range) scales (Worland 2005; Hawes et al. 2007a, b). However, it is noteworthy that even the wet treatment (with significantly less overall discrimination between exposed and buffered microcosms), still found some evidence of significantly different RCH responses between habitat microcosms.

Although the importance of thermal variability—as opposed to mean temperatures—has been noted frequently in ecophysiological studies (e.g. Davey et al. 1992;

Addo-Bediako et al. 2000; Sinclair et al. 2003; Turnock and Fields 2005), clear examples illustrating the difference between thermal variability and temperature at the level of microhabitat are rarer. The microclimate data here it is suggested—provide a “classic” example of just this kind of scenario: where differences between exposed and buffered organisms are not the result of temperature per se, but thermal variability—i.e. the greater cold tolerance of exposed animals is not the product of acclimatization to lower temperatures, but the product of greater physiological plasticity. Comparisons of phenotypic plasticity in acclimation across meso- and macro-gradients both inter- and intra-specifically have emphasised the role of climatic variability in phenotypic variation (Hawes and Bale 2007). These results provide further support for the link between habitat heterogeneity and phenotypic plasticity (cf. Doughty and Reznick 2004; Hawes and Bale 2007), although here it is found in the context of microclimatic, rather than macroclimatic, variability.

As well as highlighting the sophistication of its acclimation responses, there are a number of implications for the autecology of *C. antarcticus*. In addition to temporal variability in cold tolerance – seasonal and diurnal (Worland and Convey 2001), it is clear that there is spatial variability in their low temperature capabilities, especially in drier habitats. The traditional view of polar terrestrial arthropods as being in either “summer” or “winter” modes of cold

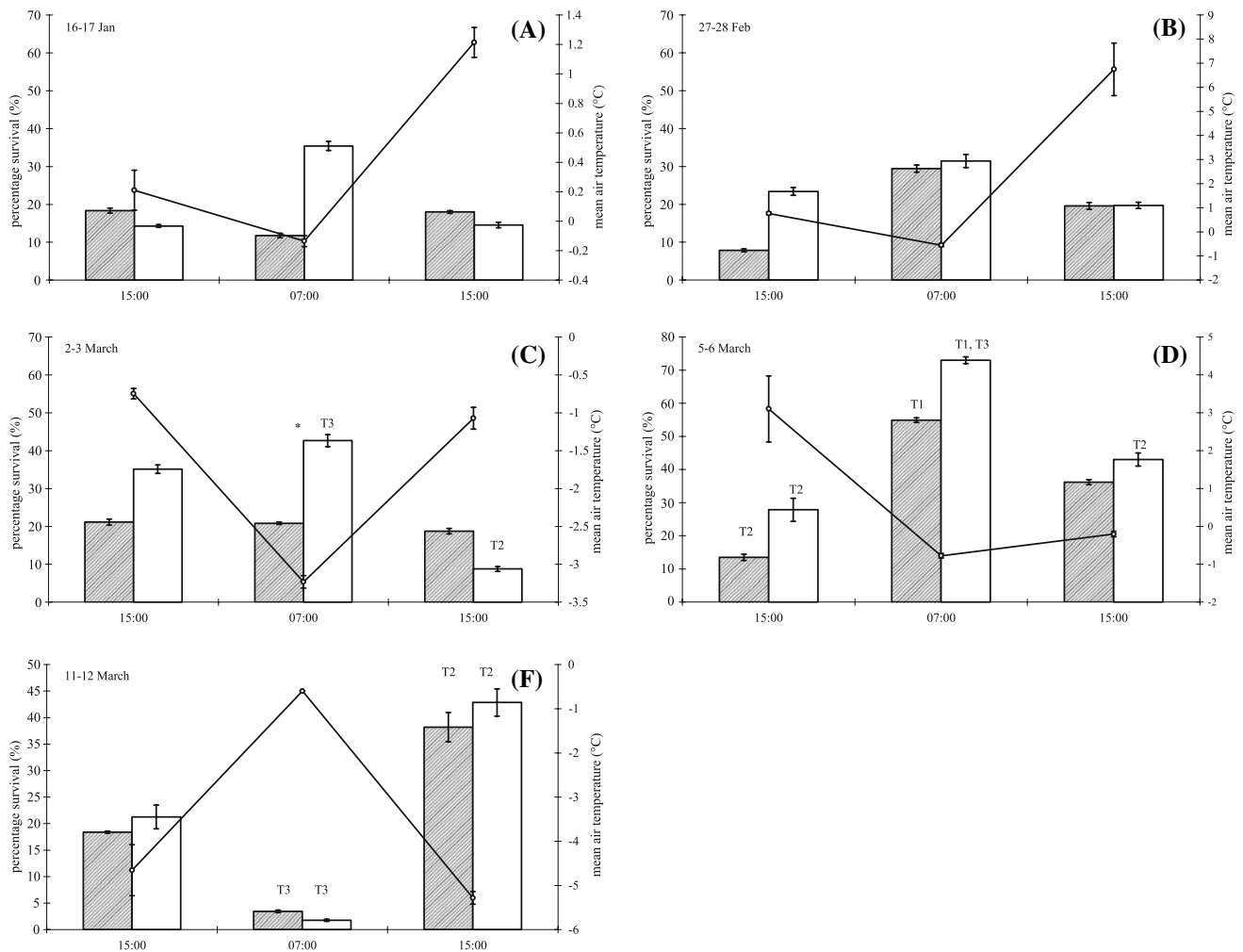


Fig. 3 Comparison of *C. antarcticus* survival below -15°C in moss (shaded bars) and exposed (unshaded bars) microcosms for the wet treatment on **a** 16–17 Jan; **b** 25–26 Feb; **c** 2–3 March; **d** 5–6 March; and **e** 11–12 March. Black line indicates mean air temperature ($^{\circ}\text{C}$) of

the last 4 h at each sample occasion. Asterisk represents significant differences between moss and exposed microcosms; T1, T2, and T3 represent significant differences between times

hardiness (sensu Cannon and Block 1988) has been questioned elsewhere in the context of “transitional” modes of cold tolerance (Hawes et al. 2006a). The responses examined here further underline the physiological complexity of this species’ adaptations to low temperature, across both spatial and temporal gradients. Given the heterogeneity of habitat cover in Antarctic terrestrial habitats at both meso- and micro-scales, exposure to surface thermal variability is frequently encountered by *C. antarcticus* during the austral summer. Plastic responses to diurnal temperature variability enable animals to reduce the risks of such encounters during foraging, local and/or migratory dispersal (cf. Herzberg 1997; Hayward et al. 2004), or even accidental dispersal by winds (cf. Hawes et al. 2007c). (Indeed, in a pilot test of experimental methods in which microcosms were uncovered—all of the “exposed” animals were dispersed by wind within minutes).

In a previous study it was shown that a high Arctic species of Collembola showed little sensitivity in its cold tolerance over short-term time scales (Hawes et al. 2006b). Greater development of the soil profile and therefore greater thermal buffering mean that soil arthropods in the high Arctic may employ behavioural avoidance more effectively (cf. Coulson et al. 1995). In Antarctic terrestrial habitats where microhabitats are virtually isothermal with soil surface temperatures, soil arthropods like *C. antarcticus* may rely to a greater extent on physiological sensitivity to thermal variability, utilising microhabitat thermal properties primarily for overwintering refugia when such dynamism proves inadequate. Indeed, even when overwintering the utilisation of microhabitats may be more directed at avoiding variability than temperature per se. Tilbrook (1967), for example, found seasonal variation in the vertical distribution of *C. antarcticus* with a greater proportion

overwintering in the 3–6 cm moss layer (*Pohlia nutans*) compared to a greater proportion of summer animals in the 0–3 cm layer, noting the temperature difference between layers was no more than 1–2°C.

In conclusion, the “textbook” ecological response of soil arthropods to low temperature stress—vertical migration—is, at least in an Antarctic context, not as straightforward as might be expected. The responses of the springtail, *C. antarcticus*, measured here reveal that the benefits of behavioural avoidance are complicated by a trade-off between the selection of insulation from thermal variability and greater physiological plasticity when exposed to thermal variability. This trade-off facilitates normal summer activities (feeding, somatic development, dispersal) under exposed conditions, while promoting homeostasis in quiescent overwintering animals.

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