Heat tolerance and physiological plasticity in the
Antarctic collembolan, Cryptopygus antarcticus, and
mite, Alaskozetes antarcticus

M. J. Everatt*a, P. Conveyb,c, M. R. Worlandb, J. S. Balea and S. A. L. Haywarda

aSchool of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK
bBritish Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road,
Cambridge, CB3 0ET, UK
cNational Antarctic Research Center, IPS Building, University Malaya, 50603 Kuala Lumpur,
Malaysia

*Corresponding author. Tel.: + 44 789 620 1770. Email address: mxe746@bham.ac.uk (M. J.
Everatt).

Abstract

Polar amplification of global warming has led to an average 2°C rise in air temperatures in parts of the
polar regions in the last 50 years. Poikilothermic ectotherms that are found in these regions, such as
Collembola and mites, may therefore be put under pressure by changing environmental conditions.
However, it has also been suggested that the thermal sensitivity of invertebrates declines with higher
latitudes and, therefore, that polar ectotherms may not be at risk. In the current study, the heat
tolerance and physiological plasticity to heat stress of two well-studied Antarctic invertebrates, the
collembolan, Cryptopygus antarcticus, and the mite, Alaskozetes antarcticus, were investigated. Both
species showed considerable heat tolerance, with each having an Upper Lethal Temperature (ULT)
avbove 35°C (1 hour exposure). These species were also able to survive for over 43 d at 10°C and for
periods of 5-20 min at 40°C. Across all experimental procedures, A. antarcticus possessed a
somewhat greater level of heat tolerance than C. antarcticus. Water loss during short duration
exposures did not differ between the two species at 30, 35 and 40°C, suggesting that the greater
tolerance of A. antarcticus over this timescale was not due to higher desiccation resistance.
Physiological plasticity was investigated by testing for Rapid Heat Hardening (RHH) and long-term
acclimation. RHH was observed to a small degree in both species at a warming rate of 0.5°C min⁻¹,
and also 0.2°C min⁻¹ in A. antarcticus alone. Longer-term acclimation (1 week at 10°C) did not
enhance the heat tolerance of either species. Even with this limited physiological plasticity, the results
of this study indicate that C. antarcticus and A. antarcticus have capacity in their heat tolerance to
cope with current and future environmental extremes of high temperature.

Keywords: Global warming, Rapid Heat Hardening, Acclimation, Thermal sensitivity, Invertebrate

1. Introduction

Over the last century, the mean surface temperature of the Earth has increased by 0.6°C (IPCC 2001).
However, the rate of warming has been amplified at higher latitudes, with an average 2°C rise in parts
of the polar regions in the last 50 years (Arctic Council 2005; Convey et al. 2009; Turner et al. 2009).
The northern and western parts of the Antarctic Peninsula have been particularly affected; over the
period 1951-2006, data from Vernadsky (Faraday) station in the Argentine Islands recorded an 0.53°C rise in temperature per decade. A further consequence of this warming at a global scale has been a decrease in snow and ice cover of over 10% since the 1960s (Walther et al. 2002). These trends are set to continue, with general circulation models predicting further warming across the planet, and especially rapid warming in the polar regions.

Invertebrates are poikilothermic ectotherms, meaning that their body temperature is highly influenced by, and varies markedly with, the external environment (Speight et al. 2008). In essence, they are unable to regulate their body temperature as do birds and mammals, and are therefore susceptible to injuries, and developmental and reproductive impairment, resulting from temperature changes (Bale and Hayward 2010). Invertebrates can respond to these changes through alterations in their behaviour, phenology, physiology and genetic make-up, with these responses acting within or between generations (Lachenicht et al. 2010). Behaviourally, they can track favourable temperatures by moving towards either higher latitudes or altitudes (Walther et al. 2002; Sinclair et al. 2003; Gobbi et al. 2006). Several alpine spiders, for instance, have been shown to remain in their preferred temperature range by tracking the recession of the Forni Glacier in Italy (Gobbi et al. 2006).

Invertebrates can also adapt behaviourally on a smaller scale, via microhabitat selection. Habitats, such as the Antarctic fellfields, are host to a diversity of microclimates and invertebrates select those which are the least stressful (Hodkinson et al. 1999; Holmstrup and Zachariassen 1996; Hoshikawa et al. 1988; Spaull 1973). Hayward et al. (2000, 2003, 2004) have gone on to show thermal and hygric preferences that are suggestive of this type of behavioural selection in a laboratory setting. A further response identified is a shift of spring and autumn phenology with the changing of the growing season (Ibanez et al. 2010; Walther et al. 2002).

Within generations, physiological adaptation is demonstrated through experimental acclimation or natural acclimatisation - permitting an organism to adapt to changing conditions via a change in form, movement or rate of physiological activity (Lachenicht et al. 2010). In the context of climate change, acclimatisation may involve the improvement of heat tolerance and upper thermal sub-lethal characteristics, such as physical activity, as temperatures rise. This form of adaptation has been shown in a number of organisms, including plants (Meyer and Santarius 1998), nematodes (Jagdale and Grewal 2003) and insects (Lachenicht et al. 2008). Over generations, invertebrates can adapt their physiology through the process of natural selection (Somero 2010).

The thermal sensitivity of terrestrial invertebrates to temperature change has been reported to decline from the tropics to the poles (Addo-Bediako et al. 2000; Deutsch et al. 2008). Some tropical species live very close to their upper thermal limits and, in some cases, at temperatures that exceed their physiological optima (Somero 2010). Polar species, in contrast, may live chronically below their temperature optima, and are suggested to have sufficient scope to tolerate higher temperatures. Warming might even help to alleviate the stress associated with low temperatures in the polar regions. Climate warming simulation studies using screens, solar domes and other controlled environmental systems (Bokhorst et al. 2008; Bale and Hayward 2010) suggest a rise in temperature will indeed lead to greater invertebrate numbers in Antarctic communities (Convey et al. 2002; Convey & Wynn-Williams 2002; Day et al. 2009). However, some manipulation studies also suggest the opposite outcome, with responses depending both on the detailed changes at micro-environmental level associated with the manipulation, and also on the group of invertebrates being considered (Convey et al. 2002, 2003; Bokhorst et al. 2011). Studies into upper thermal thresholds are also used in conjunction with climate manipulation studies and support the view that polar terrestrial invertebrates have low sensitivity to temperature change. Slabber et al. (2007), for example, showed that five Collembola species from a sub-Antarctic island, including Cryptopygus antarcticus, possessed Upper
Lethal Temperatures (ULT<sub>50</sub>) above 30°C, far higher than the mean summer temperature in the Antarctic.

In the current study, the capacity of the collembolan, Cryptopygus antarcticus, and the mite, Alaskozetes antarcticus, to tolerate exposure to high temperatures was investigated, and their physiological plasticity to heat stress explored. In particular, this study addressed the ability of each species to respond to rapid increases in temperature, as might occur as a result of solar insolation of their microhabitats during diurnal cycles, and their tolerance to more prolonged exposures to high temperatures based on climate warming predictions. These species were selected as they represent two of the most successful arthropod groups in the maritime Antarctic and are considered ‘model’ organisms in polar research (Block and Convey 1995; Block et al. 2009), reaching numbers of up to 1.5 x 10<sup>6</sup> individuals m<sup>-2</sup> (Burn 1986; Convey and Smith 1997; Tilbrook 1967). Consequently, any effect warming may have on them will likely be reflected throughout the community.

2. Materials and methods

2.1. Invertebrate collection and storage conditions

Naturally occurring summer-acclimatised individuals of C. antarcticus and A. antarcticus were collected from algae, moss and rocks on Léonie Island (67°S, 68°W), near to the British Antarctic Survey’s Rothera Research Station, Adelaide Island between January and March 2012. Samples were stored at 4°C (24:0 L:D) in plastic buckets containing substratum from the site of collection. For water loss experiments (sub-section 2.2.1.), samples were transported to the University of Birmingham under cool conditions (4 to 6°C), taking approximately two months, before being stored at 4°C (0:24 L:D). All other experiments described were carried out at Rothera Research Station.

2.2. Microhabitat temperatures

The temperature range on Léonie Island on the soil surface underneath a rock was measured between 24 January and 12 March 2012. To illustrate the extremes of temperature potentially experienced by an animal on an exposed surface, temperature was also recorded every 5 min on a rock between 5 and 21 February 2012 at Rothera Research Station, using a Tinytag Transit 2 Datalogger (Gemini Data Loggers, Chichester, UK). Data were uploaded using Tinytag Explorer Software (Gemini Data Loggers, Chichester, UK).

2.3. Upper Lethal Temperatures (ULTs)

The upper temperature at which invertebrates no longer survived was determined by warming individuals of C. antarcticus and A. antarcticus at 0.2°C min<sup>-1</sup> from 4°C to progressively higher temperatures (30 to 37°C for C. antarcticus and 30 to 40°C for A. antarcticus). Individuals were subsequently held at the target temperature for 1 h, before being cooled back to 4°C at the same rate. Three replicates of 10 individuals of each species were placed in Eppendorf tubes, which were packed inside glass test tubes plugged with sponge and placed in an alcohol bath (Haake Phoenix II C50P, Thermo Electron Corporation), prior to each experimental treatment. Control groups were handled, and exposed, in the same way at 4°C. The temperature experienced by the invertebrate was measured by placing a thermocouple within an identical Eppendorf tube into one of the glass test tubes. At the end of experimental treatments, individuals were rapidly transferred (over ice) from the Eppendorf tubes into plastic universal tubes containing moist Plaster of Paris, and returned to the rearing conditions (4°C, 0:24 L:D). Survival, defined by individuals moving either spontaneously or in response to gentle contact stimulus, was assessed 24 and 72 h after treatment. Replicate collection,
controls, thermocouple use, recovery and survival assessment were the same for all following experimental procedures unless stated otherwise.

2.3.1. Water loss following high temperature exposure

For both species, five replicates of 10 individuals were exposed to three temperatures (30, 35 and 40°C) as described in sub-section 2.2. Individuals were weighed prior to and upon removal from each treatment, then following drying to constant mass at 60°C for 24 h. From these values, initial water content and percentage water loss or gain were calculated (cf. Hayward et al. 2007).

2.4. Rapid Heat Hardening (RHH)

2.4.1. Determination of the discriminating temperature

In rapid cold and heat hardening experiments the discriminating temperature is defined as the temperature at which there is 10-20% survival after an exposure time of e.g. 1 h (Lee et al. 1987). This temperature was determined here by exposing individuals (three replicates of 10 individuals) of C. antarcticus and A. antarcticus directly (i.e. without ramping from 4°C) to progressively higher temperatures (30 to 36°C for C. antarcticus and 36 to 40°C for A. antarcticus) for 1 h, before returning to the rearing temperature (4°C) at 0.2°C min⁻¹.

2.4.2. Induction of RHH

To investigate the RHH response, individuals of C. antarcticus and A. antarcticus (3 replicates of 10 individuals for each species) were warmed to the discriminating temperature at three different rates (0.5°C min⁻¹, 0.2°C min⁻¹ and 0.1°C min⁻¹). As before, individuals were held for 1 h at the discriminating temperature and then cooled back to the rearing temperature (4°C) at 0.2°C min⁻¹.

2.5. Long-term heat tolerance

Five replicates of 10 individuals of C. antarcticus and A. antarcticus were transferred to either 4 or 10°C for up to 49 d. Individuals were held in universal tubes with a base of moist Plaster of Paris and a small amount of substratum within an incubator. Survival was assessed every 7 d for the first four weeks and then every 3 d thereafter. The temperature inside the incubator was measured using a Tinytag Transit 2 Datalogger.

2.6. Acute heat exposure

Three replicates of 10 individuals of C. antarcticus and A. antarcticus were exposed directly to three temperatures: 40, 45 and 50°C. At each temperature, individuals were held for 5, 10 or 20 min. Following high temperature treatment, they were transferred directly to recovery conditions (4°C, 24:0 L:D).

2.7. Effect of acclimation on heat tolerance

Stock cultures of C. antarcticus and A. antarcticus were held for one week at 10°C prior to experimental treatments. Three replicates of 10 individuals of each species were subsequently warmed at 0.2°C min⁻¹ to three temperatures (33, 34 and 35°C for C. antarcticus and 39, 39.5 and 40°C for A. antarcticus), and held there for 1 h, before being cooled to the rearing temperature (4°C) at 0.2°C min⁻¹.

2.8. Statistical analysis
The Kolmogorov-Smirnov test was used to check for normal distribution of survival and percentage water loss data. Normally distributed data were analysed using analysis of variance (ANOVA) and Tukey’s multiple range test; data that were not normally distributed were analysed using the Kruskal-Wallis test.

3. Results

3.1. Microhabitat temperatures

Soil surface temperatures beneath a rock on Léonie Island ranged from 13.5 to -6.1°C, and averaged 1.9°C, between 24 January and 12 March 2012 (Fig. 1), whereas the temperature on the rock surface ranged between 31.2 and -8.7°C (Fig. 2). The diurnal temperature range on the rock surface was high, regularly exceeding 20°C (with temperature changing at rates > 2.5°C/h), and on seven occasions the temperature ranged from below 0°C to above 20°C within 12 h.

3.2. Upper Lethal Temperatures (ULTs)

Survival declined dramatically at temperatures close to the ULT for both species (Fig. 3). After 1h at 34°C, almost 90% of *C. antarcticus* survived, while only 3% survived 1 h at 36°C, and none survived at 37°C. *Alaskozetes antarcticus* had greater heat tolerance than *C. antarcticus*, with 100% survival of 1 h at 37°C, 81% survival at 39°C, but 0% survival at 40°C. The difference between species was not significant at 35, 36 and 37°C, according to the Kruskal-Wallis test (*P* > 0.05 Kruskal-Wallis test).

3.2.1. Water loss following high temperature exposure

Water loss was minimal following a 1 h exposure to 30, 35 and 40°C in both species (Table 1). The amount lost did not differ significantly from the control (1 h at 4°C) in all treatments, except for a 1 h exposure at 40°C in *C. antarcticus* (*P* < 0.05 Tukey’s multiple range test). There was no significant difference between the amount of water lost in *C. antarcticus* and *A. antarcticus* across each of the three treatments (*P* > 0.05 Tukey’s multiple range test).

3.3. Rapid Heat Hardening (RHH)

3.3.1. Determination of the discriminating temperature

The discriminating temperature was determined to be 35°C for *C. antarcticus* (10% survival), and 39.5°C for *A. antarcticus*, a temperature which although resulting in 0% survival, was chosen because it was closer to the 10-20% survival required than the 37% value obtained at 39°C (Fig. 4).

3.3.2. RHH induction

In both species, all three warming treatments (0.5, 0.2 and 0.1°C min⁻¹) gave greater survival compared to direct exposure to the discriminating temperature (Fig. 5). The increase in survivorship was significant for 0.5°C min⁻¹ in *C. antarcticus* (*P* < 0.05 Tukey’s multiple range test), and for 0.5 and 0.2°C min⁻¹ in *A. antarcticus* (*P* < 0.05 Tukey’s multiple range test). For *A. antarcticus*, survival declined as the rate of warming was lowered, from 73% at 0.5°C min⁻¹ to 30% at 0.1°C min⁻¹. The rate of 0.5°C min⁻¹ also gave the greatest survival in *C. antarcticus*.

3.4. Long-term heat tolerance

*C. antarcticus* was more susceptible at both 4 and 10°C than *A. antarcticus* (Fig. 6). Survival of *C. antarcticus* decreased significantly at 4°C to 70% after 46 d (*P* < 0.05 Tukey’s multiple range test),
and to 0% at 10°C ($P < 0.05$ Kruskal-Wallis test) (Fig. 6). *Alaskozetes antarcticus* survival also decreased significantly at 10°C ($P < 0.05$ one-way ANOVA), but only to 63% after 49 d, and was not significantly different at 4°C (80% survival, $P > 0.05$ Kruskal-Wallis test).

### 3.5. Acute heat exposure

At 40°C, *A. antarcticus* outperformed *C. antarcticus* in all treatments (5, 10 and 20 min, Fig. 7), but this was not significant ($P > 0.05$ Mann-Whitney U test; one-way ANOVA). At 45 and 50°C, both *C. antarcticus* and *A. antarcticus* survived poorly (Fig. 7).

### 3.6. Effect of acclimation on heat tolerance

Acclimation at 10°C did not significantly enhance the heat tolerance of *C. antarcticus* or *A. antarcticus* at any of the temperatures tested ($P > 0.05$ Mann-Whitney U test; one-way ANOVA, Fig. 8).

### 4. Discussion

The Antarctic environment is unable to support large biological communities and, in extreme cases, may only support a food web of less than five animal species (Block *et al.* 2009; Hodgson *et al.* 2010). The few terrestrial invertebrates that inhabit these communities play an important role in processes such as soil conditioning and nutrient cycling (Bokhorst *et al.* 2007). In contrast to the temperate and tropical regions, which have greater species diversity and subsequently greater functional redundancy, polar communities will struggle to compensate for the loss of species and their associated services. Changing environmental conditions as a result of climate warming may put pressure on polar species. However, the thermal sensitivity of polar invertebrates to temperature increase has been suggested to be low, and warming may even result in more optimal conditions and a reduction in environmental constraints on invertebrate physiology (Addo-Bediako *et al.* 2000; Convey *et al.* 2009; Deutsch *et al.* 2008). The acute and chronic tolerances, as well as the physiological plasticity, of the collembolan, *C. antarcticus*, and the mite, *A. antarcticus*, are discussed here in the context of their ability to respond to climate warming.

#### 4.1. Basal heat tolerance

The collembolan, *C. antarcticus*, and the mite, *A. antarcticus*, demonstrated considerable heat tolerance, with each having a ULT of over 35°C (Fig. 3). In two sub-Antarctic studies on Marion Island (Deere *et al.* 2006; Slabber *et al.* 2007) and one study at Cape Hallet, North Victoria Land (Sinclair *et al.* 2006), several mites and Collembola, including *C. antarcticus* on Marion Island, were also shown to possess ULTs above 30°C. While this level of tolerance is somewhat lower than found in temperate or tropical species, such as the Asian brown planthopper, *Nilaparvata lugens*, which has a ULT$_{50}$ of 41.8 to 42.5°C (Piyaphongkul *et al.* 2012), this nevertheless demonstrates a considerable capacity to cope with current conditions (Convey 1996). Indeed ULTs above 35°C are high when considering the temperatures these Antarctic species typically experience during the summer. Tinytag measurements on Léonie Island through February and March did not show surface temperatures exceeding 15°C (Fig. 1). Likewise, temperatures recorded between 2002 and 2008 on nearby Anchorage Island did not rise higher than 20°C. However, it should be noted that diurnal fluctuations in some microhabitats and years can exceed 30°C for short periods of minutes to hours (Fig. 3; Smith 1988; Convey 1996). Both *C. antarcticus* and *A. antarcticus* were also able to survive for over 43 d at 10°C (Fig. 6) and showed survival at 40°C over periods of 5-20 min (Fig. 7). These two species are
therefore well adapted to survive the summer on Léonie Island and have some capacity to tolerate
higher temperatures than those that are currently experienced (Day et al. 2009; Convey et al. 2009).

Survival alone is not an accurate measure of fitness. Success is also influenced by the sub-lethal
characteristics of a species, such as the effects of heat stress on reproduction and development. In
many species, survival is possible at extremes of temperature, but they are then unable to fully
develop and reproduce once usual temperatures are restored (Shreve et al. 2004). Invertebrates are
also hampered during temperature extremes (Piyaphongkul et al. 2012; Powell and Bale 2006; Shreve
et al. 2004; Wang and Kang 2003). Uncoordinated movement 72 h after high temperature treatment in
the current study (> 30°C, data not shown) indicates that permanent damage might have been incurred
as a result of high temperature exposure, which could subsequently result in impaired development
and reproduction. Thus, whilst C. antarcticus and A. antarcticus can survive above 35°C, negative
effects on them and their communities might be seen at much lower temperatures.

4.2. Interspecific comparisons

Alaskozetes antarcticus showed significantly greater heat tolerance than C. antarcticus. This capacity
was demonstrated across all experimental procedures; A. antarcticus had a higher ULT (Fig. 3),
exhibited higher survival of acute heat exposure (Fig. 7) and survived for longer at 10°C (Fig. 6).
Previous studies also show that mite species tend to have higher heat tolerance than Collembola
(Deere et al. 2006; Sinclair et al. 2006). It was initially hypothesised that higher desiccation resistance
accounted for the greater heat tolerance in A. antarcticus. This is because C. antarcticus is a hygric
species, with little or no control of water loss (Convey et al. 2003; Worland and Block 1986, 2003),
whereas A. antarcticus is a mesic species and has good control over its water content (Benoit et al.
2007; Worland and Block 1986). However, there was little difference in water loss with temperature
and no significant difference in the water lost between the two species over the experimental durations
under all temperature treatments (Table 1). It seems, therefore, that A. antarcticus possesses a more
adaptive heat tolerance physiology than C. antarcticus. Possible physiological adaptations capable of
operating over these experimental timescales include the activation of heat shock proteins (Schill et
al. 2004; Rinehart et al. 2006; Michaud et al. 2008) and membrane remodelling (Hazel 1995).

The results of this study suggest that, in a rapidly warming Antarctic, A. antarcticus would have some
advantage over C. antarcticus. Climate manipulation studies also suggest that mites will be favoured
over Collembola under warming. In both the Arctic (Coulson et al. 1996) and the Antarctic (Bokhorst
et al. 2008; Convey et al. 2002), Collembola numbers decreased significantly under artificially
warmed conditions over three years, while mite numbers remained largely unchanged. However,
Webb et al. (1998) proposed that oribatid mite populations are slow to show a response to short-term
environmental changes and that manipulations longer than those used in the aforementioned studies
are required to identify any effect. A further consideration is how the heat tolerance of these species
relates to their behaviour. Collembola are more mobile than oribatid mites, and so may be better able
to relocate to habitats in their preferred temperature range. Consequently, the more rapid movement of
C. antarcticus could compensate for reduced heat tolerance in this species. It is therefore only in a
uniform thermal environment where A. antarcticus would be favoured (see also Hayward et al. 2003).

4.3. Physiological plasticity

The Antarctic hosts a diversity of microclimates. In some of these, the daily temperature can fluctuate
by as much as 50°C (Convey 1996a). In the current study, measurements on a rock surface showed
temperature variation approaching or exceeding 30°C on a diurnal timescale (Fig. 2). Similar patterns
have been reported in other microhabitats; temperatures within the moss cushion, *Schistidium antarctici*, were shown to cycle between -9.2°C and 42.8°C over 24 h (Smith 1988). It could, therefore, be to an invertebrate’s advantage to adapt quickly to changes in temperature. One means of tracking temperature changes is via a process termed Rapid Heat Hardening (RHH), which is the rapid induction of heat tolerance over minutes to hours (Benoit *et al.* 2009). Both *C. antarcticus* and *A. antarcticus* showed evidence of RHH, with enhanced survival at their discriminating temperatures following warming at the three rates of 0.1, 0.2 and 0.5°C min⁻¹ (Fig. 5). The rate of 0.5°C min⁻¹ gave the greatest increase in survival for both species, and was likely due to the reduced time spent at harmful temperatures. Overall, the RHH response was small, however, giving an average rise in survivorship of only 38% across all treatments. It is possible that RHH has more of an influence on the sub-lethal characteristics of *C. antarcticus* and *A. antarcticus*. Although there is as yet little support for this occurring in other species, there is ample evidence of a sub-lethal influence during Rapid Cold Hardening (RCH) (Denlinger and Lee 2010). For example, courting, reproduction, and the Critical Thermal minimum (CTmin – loss of coordination at low temperatures) were all improved in *D. melanogaster* following RCH (Shreve *et al.* 2004; Kelty and Lee 1999).

Physiological plasticity can also be seen over longer timescales in the form of experimental acclimation (Lachenicht *et al.* 2010). The nematodes, *Steinernema carpocapsae* and *Steinernema feltiae*, for instance, showed enhanced heat tolerance, and higher virulence under heat stress, when reared at higher, and thus acclimatory, temperatures (Jagdale and Grewal 2002). Similarly, heightened heat tolerance following time at higher rearing temperatures was exhibited in both marine and terrestrial mites found on Marion Island (Deere *et al.* 2006). In the current study, a one week acclimation at 10°C had no significant impact on survivorship in either *C. antarcticus* or *A. antarcticus* (Fig. 8). A null response in the sub-Antarctic collembolan *Tullbergia bisetosa*, and a decline in heat tolerance in *C. antarcticus*, was also shown following acclimation at 15°C (Slabber *et al.* 2007).

Physiological plasticity across generations may also be important; species with sufficient genetic variation that produce progeny with higher physiological thermal optima may end up as the ‘winners’ in scenarios of climate warming (Somero 2010). In a number of species, life at low temperatures has resulted in the loss of physiology suited to warming conditions (Somero 2010). The polar marine ectotherms of the Southern Ocean provide a particularly good illustration. These species are stenothermal and have experienced a narrow range of low temperatures for millions of years (at present -1.9 to +1.8°C or much less) (Somero 2010). As a result, many have lost their ability to initiate a heat shock response (Clark *et al.* 2009). The same might be true of polar terrestrial invertebrates with regard to their physiological plasticity, and if so these will therefore become less successful as climate change intensifies. However, it has also been suggested that the greater thermal variability typical of polar terrestrial environments will preserve heat tolerance adaptation (Peck *et al.* 2006).

Indeed, the climatic variability hypothesis (Stevens 1989) suggests that the greater thermal variability at higher latitudes means that invertebrates must have a greater physiological range and subsequently retain physiological plasticity at higher temperatures. Also of note are the long generation times of these animals, which frequently extend to five years or more, and therefore limit their ability to adapt across generations (Convey 1994, 1996b).

5. Conclusion

It has been suggested that the thermal sensitivity of invertebrates to temperature change decreases from the tropics to the poles (Deutsch *et al.* 2008). This statement is supported by the current study, which shows that both *C. antarcticus* and *A. antarcticus* have scope with which to tolerate current and
future conditions. Warming may even alleviate the stresses experienced by these invertebrates and provide an opportunity for population growth. If these species are assumed to be characteristic of other Collembola and Acari in the maritime Antarctic, a positive impact on the community and on ecosystem functions such as nutrient cycling, may also be seen.

Acknowledgements

MJE was funded by the Natural Environment Research Council (RRBN15266) and was supported by the British Antarctic Survey and the University of Birmingham. We thank Sharon Duggan (BAS) for help in the location of sample sites. This paper contributes to the BAS ‘Polar Science for Planet Earth’ and SCAR ‘Evolution and Biodiversity in Antarctica’ research programmes.

References


Figure and Table legends

**Fig. 1.** Surface temperature beneath a rock on Léonie Island, near Rothera Research Station, Adelaide Island, between 24\textsuperscript{th} January and 12\textsuperscript{th} March 2012.

**Fig. 2.** Temperature on a rock surface outside the Bonner Laboratory at Rothera Research Station, Adelaide Island, between 5\textsuperscript{th} and 21\textsuperscript{st} February 2012.

**Fig. 3.** Mean percentage survival of *C. antarcticus* and *A. antarcticus*, following exposure to progressively higher temperatures (30 to 37\textdegree C – *C. antarcticus*, 30 to 40\textdegree C – *A. antarcticus*) for 1h, before cooling at 0.2\textdegree C min\textsuperscript{-1} to 4\textdegree C. Means ± S.E.M. are presented for three replicates of 10 individuals. Survival was assessed 72 h after treatment. Means with the same letter (*A. antarcticus*) and same number of * symbols (*C. antarcticus*) are not significantly different within each species group at *P*< 0.05 (Kruskal-Wallis test and Tukey’s multiple range test, respectively). *A. antarcticus* was not tested at 33 or 34\textdegree C.

**Fig. 4.** Mean percentage survival of *C. antarcticus* and *A. antarcticus*, following direct exposure to progressively higher temperatures (30 to 36\textdegree C for *C. antarcticus* and 36 to 40\textdegree C for *A. antarcticus*) for 1 h, before cooling at 0.2\textdegree C min\textsuperscript{-1} to 4\textdegree C. Means ± S.E.M. are presented for three replicates of 10 individuals. Survival was assessed 72 h after treatment. Means with the same letter (*A. antarcticus*) and same number of * symbols (*C. antarcticus*) are not significantly different within each species group at *P*< 0.05 (Kruskal-Wallis test).

**Fig. 5.** Mean percentage survival of *C. antarcticus* and *A. antarcticus*, following exposure to the discriminating temperature (35\textdegree C – *C. antarcticus*, 39.5\textdegree C – *A. antarcticus*) for 1 h, after being warmed to the discriminating temperature at one of three rates (0.5, 0.2 or 0.1\textdegree C min\textsuperscript{-1}). Means ± S.E.M. are presented for three replicates of 10 individuals. Survival was assessed 72 h after treatment. Means with the same letter (*A. antarcticus*) and same number of * symbols (*C. antarcticus*) are not significantly different within each species group at *P*< 0.05 (Tukey’s multiple range test).

**Fig. 6.** Mean percentage survival of *C. antarcticus* and *A. antarcticus* at +4 and +10\textdegree C over a period of 46 (C. antarcticus) and 49 d (*A. antarcticus*). Means ± S.E.M. are presented for five replicates of 10 individuals. Means with the same letter (*A. antarcticus*) and same number of * symbols (*C. antarcticus*) are not significantly different within each species group at *P*< 0.05 (Kruskal-Wallis test).

**Fig. 7.** Mean percentage survival of *C. antarcticus* and *A. antarcticus* following exposure to 40\textdegree C for 5, 10 or 20 min. Means ± S.E.M. are presented for three replicates of 10 individuals. Survival was assessed 72 h after treatment. Means with the same letter (*A. antarcticus*) and same number of * symbols (*C. antarcticus*) are not significantly different within each species group at *P*< 0.05 (Kruskal-Wallis test).

**Fig. 8.** Mean percentage survival, following exposure to 33, 34 and 35\textdegree C – *C. antarcticus*, and 39, 39.5 and 40\textdegree C – *A. antarcticus*) for 1 h, before cooling at 0.2\textdegree C min\textsuperscript{-1} to 4\textdegree C. Both species were held at 10\textdegree C for one week prior to experimentation. Means ± S.E.M. are presented for three replicates of 10 individuals. Survival was assessed 72 h after treatment. Means with the same letter (*A. antarcticus*) and same number of * symbols (*C. antarcticus*) are not significantly different within each species group at *P*< 0.05 (Tukey’s multiple range test).
Table 1. Mean percentage water loss of *C. antarcticus* and *A. antarcticus*, following exposure to 30, 35 and 40°C for 1 h, prior to cooling at 0.2°C min⁻¹ to 4°C. Water content of control sample held at 4°C for 1 h also given. Means ± S.E.M. are presented for five replicates of 10 individuals.
Figure 2
Survival (%) vs Temperature (°C)

- A. antarcticus
- C. antarcticus

* denotes significant difference.
Figure 4
Figure 5

A. antarcticus

C. antarcticus

Rate of warming

Survival (%)
Figure 6
Figure 7
Figure 8
Table

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Water Content change (%)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C. antarcticus</td>
<td>A. antarcticus</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>3.19 ± 2.86</td>
<td>-0.02 ± 1.82</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>-1.58 ± 1.76</td>
<td>0.12 ± 0.38</td>
<td></td>
</tr>
<tr>
<td>35</td>
<td>0.88 ± 3.65</td>
<td>-3.82 ± 1.61</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>-6.68 ± 0.81</td>
<td>-2.08 ± 0.45</td>
<td></td>
</tr>
</tbody>
</table>

Table 1