



The effect of acclimation temperature on thermal activity thresholds in polar terrestrial invertebrates



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ABSTRACT

In the Maritime Antarctic and High Arctic, soil microhabitat temperatures throughout the year typically range between -10 and $+5$ °C. However, on occasion, they can exceed 20 °C, and these instances are likely to increase and intensify as a result of climate warming. Remaining active under both cool and warm conditions is therefore important for polar terrestrial invertebrates if they are to forage, reproduce and maximise their fitness. In the current study, lower and upper thermal activity thresholds were investigated in the polar Collembola, *Megaphorura arctica* and *Cryptopygus antarcticus*, and the mite, *Alaskozetes antarcticus*. Specifically, the effect of acclimation on these traits was explored. Sub-zero activity was exhibited in all three species, at temperatures as low as -4.6 °C in *A. antarcticus*. At high temperatures, all three species had capacity for activity above 30 °C and were most active at 25 °C. This indicates a comparable spread of temperatures across which activity can occur to that seen in temperate and tropical species, but with the activity window shifted towards lower temperatures. In all three species following one month acclimation at -2 °C, chill coma (=the temperature at which movement and activity cease) and the critical thermal minimum (=low temperature at which coordination is no longer shown) occurred at lower temperatures than for individuals maintained at $+4$ °C (except for the CTmin of *M. arctica*). Individuals acclimated at $+9$ °C conversely showed little change in their chill coma or CTmin. A similar trend was demonstrated for the heat coma and critical thermal maximum (CTmax) of all species. Following one month at -2 °C, the heat coma and CTmax were reduced as compared with $+4$ °C reared individuals, whereas the heat coma and CTmax of individuals acclimated at $+9$ °C showed little adjustment. The data obtained suggest these invertebrates are able to take maximum advantage of the short growing season and have some capacity, in spite of limited plasticity at high temperatures, to cope with climate change.

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1. Introduction

As poikilothermic ectotherms, invertebrates have limited means of regulating their own body temperature and are instead dependent on the thermal conditions of their environment (Speight et al., 2008). It is widely acknowledged therefore that the spatial and temporal distribution and abundance of invertebrates are partly determined by the range of temperatures they can tolerate and by the range of temperatures at which they perform optimally (Gaston, 2009; Terblanche et al., 2011). Investigations into the thermal tolerance limits of invertebrates are accordingly necessary to fully understand the ecology of a species or population and to infer the impact of climate change (e.g. Deutsch et al., 2008; Everatt et al., 2013; Somero, 2005). A common limitation of many current thermal biology studies, however, is

their emphasis on organismal survival. While survival clearly underpins the fitness of a species, there are also a number of other attributes which are greatly affected by temperature (Bale, 2002). These attributes, termed sub-lethal characteristics, include courtship, reproduction, foraging/feeding and predator avoidance (Kelty and Lee, 1999; Korenko et al., 2010). When these attributes can occur is governed by the upper and lower activity thresholds of the organism, and this thermal activity 'window' demonstrates phenotypic plasticity depending on the geographic location and the thermal/physiological history of the organism being studied (Addo-Bediako et al., 2000; Bale and Hayward, 2010). Because thermal activity thresholds are affected by less extreme temperatures, more regularly encountered than those which cause mortality, the extent to which sub-lethal characteristics are affected could be of more importance than the ability to survive temperature extremes *per se*.

The limits of movement under low temperatures have been a source of fascination since the late 19th Century. Rossbach

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(1872) observed the frequency of contractions of the contractile vesicle of three protist species and noticed that, at some low temperature, contractions ceased. He termed the absence of movement 'chill coma'. By 1939, the terminology relating to chill coma encompassed four potential states; chill coma¹ – absence of activity and movement, chill coma² – final peak of activity and movement, chill coma³ – loss of coordination, and chill coma⁴ – absence of spontaneous movement, and these terms have remained in use to this day (Hazell and Bale, 2011). Within this paper, the first definition will be used, i.e. the absence of activity and movement. Cowles and Bogert (1944) applied a new term to describe chill coma³ or the loss of coordination. This term was the 'Critical Thermal minimum' (CTmin) and will be used here to define the complete loss of coordination (inability to walk or move forward). The upper thermal thresholds of activity are analogous to those of low temperature and include heat coma and the Critical Thermal maximum (CTmax) (Hazell et al., 2008).

The Antarctic and Arctic are characterised by long, cold winters and brief, cool summers (Avila-Jimenez et al., 2010; Block et al., 2009). During the winter, air temperatures regularly fall below -10°C , and to lower than -40°C , in regions of the High Arctic and maritime and continental Antarctic (Block et al., 2009; Coulson et al., 1993; Strathdee and Bale, 1998; Walton, 1984). Buffered microhabitat temperatures in the soil or underneath the snow are likewise sub-zero during winter, though generally these temperatures do not fall much lower than -10°C (Coulson et al., 1993; Davey et al., 1992; Rinehart et al., 2006; Strathdee and Bale, 1998). Water is also transformed into ice in winter and is inaccessible to living organisms (Block et al., 2009). Activity is virtually impossible under these conditions. Accordingly, polar terrestrial invertebrates are dormant during this period and wait until the short, four to six month, summer period to resume activity (Convey, 1996). Summer air temperatures are still very cool, however, rarely rising above 0°C in the continental Antarctic, 5°C in the maritime Antarctic, and slightly higher in the Arctic (Davey et al., 1992; Block et al., 2009; Coulson et al., 1993; Strathdee and Bale, 1998). To benefit from these relatively favourable conditions, these invertebrates are capable of activity at low and even sub-zero temperatures. Hågvar (2010) has identified several invertebrate groups, including Collembola, Mecoptera, Diptera, Plecoptera and Araneae, which are active at or below 0°C on the snow of Fennoscandia. Block et al. (1990) and Sinclair et al. (2006) have also shown sub-zero activity in the Antarctic mites *Alaskozetes antarcticus* and *Nanorchestes antarcticus*, and the Collembola *Isotoma klovstadi*, *Cryptopygus cisantarcticus* and *Friezea grisea*, respectively.

Activity at high temperatures may also be important in the polar regions. Currently, buffered microhabitat temperatures range up to c. 20°C in the maritime Antarctic (Convey et al., 2009; Davey et al., 1992; Everatt et al., 2013), and to slightly higher temperatures in the Arctic (Coulson et al., 1993). Climate warming is also rapidly affecting the polar regions. Over the last 50 years, polar amplification of global climate trends has led to an average 2°C rise in air temperatures in parts of the Arctic and Antarctic, with even greater increases experienced in regions such as the northern and western Antarctic Peninsula, or when looked at on a seasonal basis (Arctic Council, 2005; Convey et al., 2009; Turner et al., 2009). This trend is set to continue, with general circulation models predicting particularly rapid warming at polar latitudes (Convey et al., 2009; Kattenberg et al., 1996). In addition, specific microhabitats, such as the surfaces of rocks and bryophyte clumps, can experience maximum temperatures approaching or exceeding 30°C (Convey, 1996; Everatt et al., 2013; Smith, 1988). Climate warming may increase the prevalence and duration of these exposures (Bokhorst et al., 2011; Nielsen and Wall, 2013). The ability of polar terrestrial invertebrates to remain active at high temperatures has only as yet been explored in three continental Antarctic Collembola, and all

show a remarkable capacity to remain active above 30°C (Sinclair et al., 2006).

The vast majority of polar terrestrial invertebrates express seasonal and shorter term thermal tolerance strategies to enable survival of shifts in temperature (Cannon and Block, 1988; Worland and Convey, 2001; Denlinger and Lee, 2010). However, the ability of polar terrestrial invertebrates to acclimate or acclimatise their thermal activity thresholds is less well known. Only two polar species, the aphid, *Myzus polaris*, and the collembolan, *Isotoma klovstadi*, have been demonstrated to have this ability, with a depression in the CTmin of individuals reared at, or taken from, lower temperatures (Hazell et al., 2010; Sinclair et al., 2006). In the current study, the lower and upper thermal activity thresholds are characterised in three common polar invertebrates widely regarded as 'model' species in their respective ecosystems: *Cryptopygus antarcticus* (Block et al., 2009; Tilbrook, 1967) and *Alaskozetes antarcticus* (Block and Convey, 1995; Burn, 1986) from the maritime Antarctic, and *Megaphorura arctica* (Fjellberg, 1994) from the High Arctic. In particular, how the thermal activity thresholds of these species respond to acclimation is explored.

2. Materials and methods

2.1. Invertebrate collection and storage conditions

Summer acclimatised individuals of *M. arctica* were collected from moss-covered slopes at Krykkefjellet and Stuphallet, near Ny-Ålesund, Spitsbergen, Svalbard ($78^{\circ}55'\text{N}$, $11^{\circ}56'\text{E}$) in August 2011. Summer acclimatised individuals of *C. antarcticus* and *A. antarcticus* were collected from moss and algae, and the underside of rocks, on Lagoon Island ($67^{\circ}35'\text{S}$, $68^{\circ}16'\text{W}$) and Léonie Island ($67^{\circ}36'\text{S}$, $68^{\circ}21'\text{W}$), near to Rothera Research Station, Adelaide Island (western Antarctic Peninsula, maritime Antarctic), between January and March 2012.

Samples of *C. antarcticus* and *A. antarcticus* were held at $+4^{\circ}\text{C}$ (24:0 L:D) in plastic bags or boxes containing substratum from the sites at which they were found whilst at Rothera Research Station and were used shortly after collection in experiments 2.3, 2.4 and 2.6. These individuals were designated as the "summer acclimatised" group. Following each respective field season, samples of *M. arctica*, and *C. antarcticus* and *A. antarcticus*, were transported to the University of Birmingham under refrigerated conditions and then held in plastic boxes containing substratum from the site of collection at $+4^{\circ}\text{C}$ (0:24 L:D). The duration of travel was ~ 2 d from the Arctic and ~ 2 months from the Antarctic. Each species was split into two additional acclimatory groups (-2 and $+9^{\circ}\text{C}$, 0: 24 L:D), representing early spring/late autumn microhabitat temperature and upper summer microhabitat temperature, respectively. Samples were held for at least two weeks at $+9^{\circ}\text{C}$, and for at least one month at -2°C prior to experimentation. The age of individuals used for experimentation was not uniform, as it was not possible to breed same age populations of the polar invertebrates in a laboratory setting. Difficulties in obtaining active individuals of *M. arctica* from acclimation at -2°C meant that individuals used in observations of locomotion (Section 2.5) were instead taken from a one month acclimation at 0°C .

2.2. Experimental conditions

Activity thresholds were assessed within an aluminium block arena. The temperature within the arena was regulated using an alcohol bath (Haake Phoenix II C50P, Thermo Electron Corporation), and activity monitored using a digital video camera with a macro lens (see Hazell et al., 2008). Thirty individuals were transferred into the arena in groups of 10 (initially set to $+4^{\circ}\text{C}$), and

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