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Thermal tolerance limits in six weevil species (Coleoptera, Curculionidae) from sub-Antarctic Marion Island

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Abstract Supercooling points, lower lethal temperatures, and the effect of short-term exposures to low temperatures were examined during both winter and summer in the adults of six weevil species from three different habitats on Marion Island. Upper lethal limits and the effects of short-term exposure to high temperatures were also examined in summer-acclimatized adult individuals of these species. *Bothrometopus elongatus*, *B. parvulus*, *B. randi*, *Ectemnorhinus marioni*, and *E. similis* were freeze tolerant, but had high lower lethal temperatures (−7 to −10°C). Seasonal variation in these parameters was not pronounced. Physical conditions of the habitat appeared to have little effect on cold hardiness parameters because the *Ectemnorhinus* species occur in very wet habitats, whereas the *Bothrometopus* species inhabit drier areas. The adults of these weevil species are similar to other high southern latitude insects in that they are freeze tolerant, but with high lower lethal temperatures. In contrast, *Palirhoeus eatoni*, a supra-littoral species, avoided freezing and had a mean supercooling point of −15.5 ± 0.94°C (SE) in winter and −11.8 ± 0.98°C in summer. Survival of a constant low temperature of −8°C also increased in this species from 6 h in summer to 27 h in winter. It is suggested that this strategy may be a consequence of the osmoregulatory requirements imposed on this species by its supra-littoral habitat. Upper lethal temperatures (31–34°C) corresponded closely with maximum microclimate temperatures in all of the species. This indicates that the pronounced warming, accompanied by the increased insolation that has been recorded at Marion Island, may reduce survival of these species. These effects may be compounded as a consequence of predation by feral house mice on the weevils.

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Introduction

Temperature and water availability are two of the most important abiotic factors determining both the distribution and abundance of animals (Andrewartha and Birch 1954; Cox and Moore 1993). This is especially true of ectotherms. A large body of literature has demonstrated either that rates and efficiencies of physiological processes and the survival of these animals change profoundly outside their optimum temperature and moisture ranges (e.g. Cossins and Bowler 1987; Hadley 1994; Johnston and Bennett 1996), or that these characteristics vary geographically (e.g. Davidson 1990; Garland and Adolph 1991; Kimura et al. 1994). In arthropods, considerable attention has been given to the ways in which various stages and taxa cope with low and sub-zero temperatures, and these survival strategies can be classified into a limited number of functional types (Block 1990; Duman et al. 1991; Lee 1991). This classification is based largely on whether an individual can survive the formation of extracellular ice (Zachariassen 1985; Storey and Storey 1996). Although the length of both the pre-freezing and freezing periods (Sømme 1996) and the absolute temperature to which the insects are exposed are of importance to their later survival and development (Bale 1987), it is the response of the insect to freezing that has formed the basis of an extended insect cold hardiness classification (Bale 1987, 1993, 1996).

Recently, a number of authors (e.g. Ring and Danks 1994; Block 1996; Storey and Storey 1996) have suggested that the cold tolerance strategy adopted by an insect is influenced by its water relations with the surrounding environment. For example, Ring and Danks (1994) argued that those physiological changes that confer desiccation resistance on insects (e.g. elevated levels of solutes) also promote low temperature survival. They suggested that physiological responses to desiccation resistance during diapause may have been the forerunners to cold tolerance. Similarly, Duman et al.

(1991) argued that insects from moist habitats are more likely to be freeze tolerant than those from drier habitats, where freeze avoidance should be more common. If there is a high chance of inoculative freezing, freeze tolerance may be the more successful strategy. Indeed, a number of studies suggest that there is a relationship between freeze tolerance and the presence of water/ice in the insects' immediate environment (Shimada and Riihimaa 1988; Gehrken et al. 1991; Lundheim and Zachariassen 1993), although this relationship is profoundly influenced by the biochemical basis of cold hardiness (e.g. presence or absence of antifreeze proteins). Nonetheless, Klok and Chown (in press) have taken this argument a step further. They suggest that, because the large southern ocean causes terrestrial habitats to be wetter than northern ones at a similar latitude (see Longton 1988), freezing tolerance is likely to be the predominant strategy at high southern hemisphere latitudes, whereas the opposite may be true in the northern hemisphere. However, they also warned that this pattern may be an artefact of the paucity of studies undertaken at high southern latitudes.

In this study we examined the cold tolerance strategies of the adults of six weevil species that occur in three very different habitats on sub-Antarctic Marion Island, to determine whether there is a relationship between cold hardiness strategy and habitat features at a local scale, and to provide additional information on the cold tolerance of sub-Antarctic insects. We also examined the upper temperature tolerances of these species. Due possibly to the ease of examining a phase change, the cold tolerance of insects (as assessed by freezing) has been subject to greater scrutiny than upper lethal limits, although the latter and the absolute range of temperatures that can be tolerated are important physiological characteristics contributing to the survival, abundance and distribution of insects (Vannier 1994; Hodkinson et al. 1996).

Materials and methods

Study site and animals

Marion Island (46°54′ S, 37°45′E) is the larger of two sub-Antarctic islands that form the Prince Edward Islands group, lying approximately 2,100 km southeast of Cape Town, to the north of the Antarctic Polar Front. As a consequence of its small size and isolation, the climate of the island is extremely oceanic. There is little seasonal or daily variation in temperature, and mean (Stevenson Screen) air temperatures are in the region of 2°C in winter and 7°C in summer. Despite the reasonably stable air temperatures, subzero grass minimum temperatures occur in all months of the year, and regularly drop below freezing in winter (May to September). In addition, freeze-thaw cycles at the soil surface may occur at any time of the year at all altitudes on the island, although winter snow cover may preclude this at high elevations (> 700 m) (Blake 1996). Precipitation is in excess of 2,500 mm per annum and is aseasonal, although snow is more common at lower altitudes in the winter (all macroclimate information from Schulze 1971; Smith and Steenkamp 1990). Microclimate temperatures in terrestrial habitats are higher (by as much as 5°C in summer), and show greater extremes (as high as 33°C on sunny, calm days) than do Stevenson Screen ones (Table 1; see also Chown and Crafford 1992; Blake 1996).

On the basis of the presence or absence of closed-angiosperm vegetation, Chown (1989, in press) distinguished two biotopes on sub-Antarctic islands: the epilithic biotope that comprises the supra-littoral, shoreline rock, inland rock face and fellfield habitats, and the vegetated biotope that includes mostly closed angiosperm communities. Habitats in the epilithic biotope tend to be more exposed, cooler, and drier than those in the vegetated biotope (Chown 1993a; Blake 1996; Chown et al. 1997). Much of the vegetated biotope on Marion Island consists of large, waterlogged oligotrophic mires (Gremmen 1981). An exception to this generalization is the supra-littoral zone, which is often wet by seawater, especially during heavy weather (Chown and Van Drimmelen 1992).

Six weevil species belonging to three genera of the monophyletic *Ectemnorhinus* group (Coleoptera, Curculionidae, Brachycerinae) are found on Marion Island (see Chown 1989 for details on the habitats they occur in). These genera are the three most terminal taxa in the pectinate *Ectemnorhinus*-group genus-level phylogeny (Kuschel and Chown 1995). *Palirhoeus eatoni* (C.O. Waterhouse) is an unusual euryhaline, supra-littoral species capable of osmoregulation in both fresh and seawater (Chown and Van Drimmelen 1992). *Bothrometopus randi* Jeannel is a species restricted to rock faces mostly in lowland areas. *Bothrometopus parvulus* (C.O. Waterhouse) occurs in similar habitats and in fellfield, whereas *B. elongatus* (Jeannel) is strictly a fellfield species (Chown 1989). These epilithic species all occur on rock surfaces, in rock crevices and within epilithic bryophytes. In contrast, both *Ectemnorhinus similis* C.O. Waterhouse and *E. marioni* Jeannel occur most frequently in association with angiosperms and bryophytes in amongst vegetation and litter in the vegetated biotope, although the latter species may also be found associated with epilithic bryophytes.

This study was undertaken between May 1993 and April 1994, and beetles were obtained from a limited number of sites on the eastern half of Marion Island. All collections were made by hand. *Palirhoeus eatoni*, *Bothrometopus parvulus* and *B. randi* were collected at Trypot Beach and Archway Bay; *B. elongatus* was collected on Stony Ridge and *Ectemnorhinus marioni* and *E. similis* were collected in Nellie Humps and at Tom, Dick and Harry. Because the larvae of at least two of the species could not be obtained in the numbers required for the experiments (see Chown and Scholtz 1989a; Chown 1993b), only adults were examined. Winter-acclimatized beetles were those collected between May and August, whereas summer-acclimatized beetles were those collected between November and March. During winter, adults of *E. similis* are scarce (Chown and Scholtz 1989b) and their rarity at this time is compounded by heavy summer predation by mice (Chown and Smith 1993). Hence winter-acclimatized adults of this species were not examined. In all cases, beetles were returned to the laboratory within 6 h of collection. Here they were held, together with the plants they were collected on, at either 10 ± 0.5°C (L:D 16:8) (summer) or 2 ± 0.5°C (L:D 8:16) (winter) in incubators for no more than 72 h. Therefore, all experiments were conducted on field-fresh individuals.

Table 1 Yearly mean, daily minima and maxima, and absolute habitat temperatures (°C) at the soil surface along an altitudinal gradient (three sites) on Marion Island (from Blake 1996)

Site	Mean (°C)	Mean daily min. (°C)	Mean daily max. (°C)	Absolute min. (°C)	Absolute max. (°C)
25 m	6.7	1.7	11.6	−4.8	29.2
600 m	3.9	1.0	11.0	−6.4	32.8
750 m	3.8	−0.4	7.6	−6.1	31.7

Supercooling point and lower thermal tolerance

The supercooling point (SCP) of individual weevils was determined by placing individuals tightly in pipette tips and inserting 40-gauge copper-constantan thermocouples between them and the pipette tip wall. These were then transferred individually to air-filled vials, submerged in a Grant LTD 20 water bath (accuracy of 0.1°C) and cooled from 0°C at 0.1°C min^{-1} to −25°C using a Grant PZ1 controller (see Grubor-Lajsic et al. 1992; Worland et al. 1992). The thermocouples were connected to a Kane-May 457XP recording digital thermometer. The temperature logged just prior to the freezing exotherm was taken as the supercooling point (Lee 1991; Block 1995).

For lower lethal temperatures, Worland et al.'s (1992) method was followed. Batches of five to ten weevils were placed in one or two sealed glass vials submerged in the programmable water bath. The specimens were cooled from 0°C at 0.1°C min^{-1} until the first temperature, −3°C (1°C higher than the highest individual SCP recorded for any species in the winter treatments of the previous experiment), was reached. After 1 h at this temperature, one (five individuals) or two (ten individuals) vials were removed from the bath, and the weevils were transferred to petri dishes lined with moist filter paper, and given 24 h to recover at 5°C. The temperature was subsequently lowered by 1°C at the same rate, and the above procedure repeated, to −15°C. After 24 h weevils were checked for survival and only those with full locomotory function were assessed as survivors.

The method of Worland et al. (1992) was modified slightly to examine short-term survival of constant low temperatures. Vials containing five weevils were cooled from 0°C at a rate of 0.1°C min^{-1} to a single treatment temperature of −8°C. This temperature represented the mean of the lowest temperature that 100% of the individuals, in each of the six species (winter treatment), survived in the previous experiment. After every 3-h interval in a 30-h period, one vial was removed, and the weevils were transferred to petri dishes lined with moist filter paper, and given 24 h to recover at 5°C. Only those weevils with full locomotory function were assessed as survivors

Upper thermal tolerance

The experimental procedures used were similar to those used in the previous experiments, but here only summer-acclimatized individuals were examined. To determine upper lethal limits, weevils were warmed at 0.1°C min^{-1} from 10°C to 25°C, where the experiment commenced. A vial containing five individuals was removed after 1 h, the temperature raised by 1°C and the procedure repeated. The upper temperature, 38°C, was chosen based on a more rapid, preliminary assessment of high temperature tolerance. As in the low temperature assessments, weevil adults were returned to petri dishes lined with moistened filter paper, and given 24 h to recover at 5°C.

For short-term survival at constant high temperatures, weevils were assessed at 33°C. This corresponded with the highest temperature where 100% survival was shown by most species in the previous experiment. Weevils were warmed at 0.1°C min^{-1} from 10°C to this temperature, and after every 3-h interval in a 30-h period, five individuals were removed. The recovery period and survival assessment procedure were the same as above.

Results

Supercooling points and lower lethal temperatures for the six weevil species are shown in Table 2. *Bothrometopus elongatus*, *B. parvulus*, *B. randi*, *Ectemnorhinus marioni* and *E. similis* all survived freezing under the experimental conditions, whereas this was not the case in *Palirhoeus eatoni*. Winter SCPs were significantly lower than summer ones in *P. eatoni* and *E. marioni*, whereas the opposite was true in *B. parvulus* and *E. similis* (Table 2). No significant differences in winter and summer SCPs were found in *B. randi* and *B. elongatus*. Lower lethal temperatures were remarkably similar in all of the species and did not show large seasonal variation, although declines in the lowest temperature that 100% of the samples could survive were evident in *P. eatoni* and *B. randi*. Similarly, survival of exposure to constant −8°C showed some variation between species, and within species between seasons in most cases (Table 3). However, this was not the case in *P. eatoni* and to a lesser extent in *B. elongatus*. In *P. eatoni*, time to 50% mortality was almost 4 times longer in the winter- than in the summer-acclimatized individuals.

Table 2 Mean ± SE supercooling point (SCP) (sample size in parentheses) and lower lethal temperatures (LLT) of the six weevil species from Marion Island during winter and summer. Results of single classification analyses of variance of SCP on season are indicated. In the LLT column, the first value represents the lowest temperature at which 100% of the sample survived, whereas the second value indicates 100% mortality (n = 5–10 per temperature per trial)

Species and Season	SCP (°C)	LLT (°C)
Palirhoeus eatoni Winter	−15.5 ± 0.94 (9)	−9, −10
P. eatoni Summer	−11.8 ± 0.98 (10)	−7, −12
ANOVA	F = 7.75, P = 0.013	
Bothrometopus randi Winter	−4.8 ± 0.19 (10)	−9, −12
B. randi Summer	−5.6 ± 0.39 (10)	−7, −12
ANOVA	F = 3.41, P = 0.08	
B. parvulus Winter	−4.8 ± 0.19 (10)	−8, −12
B. parvulus Summer	−8.3 ± 0.44 (10)	−9, −12
ANOVA	F = 51.8, P = 0.0001	
B. elongatus Winter	−6.4 ± 0.49 (10)	−8, −15
B. elongatus Summer	−5.8 ± 0.28 (10)	−7, −12
ANOVA	F = 0.99, P = 0.34	
Ectemnorhinus marioni Winter	−7.4 ± 0.62 (10)	−9, −12 (20)
E. marioni Summer	−5.5 ± 0.34 (10)	−9, −11
ANOVA	F = 6.85, P = 0.017	
E. similis Winter	−4.3 ± 0.25 (10)	–
E. similis Summer	−5.7 ± 0.18 (10)	−10, −11
ANOVA	F = 19.11, P = 0.0004	

Table 3 Time at which mortality exceeded 50% of the sample (n = 5), when individuals of each of the six weevil species were held at a constant temperature of −8°C

Species and Season	Time (h)
Palirhoeus eatoni Winter	27–30
P. eatoni Summer	6–9
Bothrometopus randi Winter	12–15
B. randi Summer	18–21
B. parvulus Winter	27–30
B. parvulus Summer	21–24
B. elongatus Winter	15–18
B. elongatus Summer	9–12
Ectemnorhinus marioni Winter	9–12
E. marioni Summer	9–12
E. similis Winter	–
E. similis Summer	15–18

Table 4 Summer upper lethal temperature (ULT) and time at which mortality exceeded 50% of the sample when individuals of each of the six weevil species from Marion Island were held at a constant temperature of 33°C. In the ULT column, the first value represents the lowest temperature at which 100% of the sample survived, whereas the second value indicates 100% mortality. (n = 5–10 per temperature per trial)

Species	ULT (°C)	Time (h)
Palirhoeus eatoni	32, 36	12–15
Bothrometopus randi	31, 37	6–9
B. parvulus	32, 37	12–15
B. elongatus	31, 36	18–21
Ectemnorhinus marioni	34, 38	12–15
E. similis	34, 36	15–18

In the case of upper lethal temperature, all of the species showed 100% survival of temperatures up to, and including, 31°C. Percentage mortality increased upwards of this temperature and reached 100% at ca. 37°C (Table 4). No marked differences in upper lethal temperature were found between the species, although it appeared that the two *Ectemnorhinus* species could tolerate somewhat higher temperatures than those in the genera *Bothrometopus* and *Palirhoeus*. However, this was not reflected in their tolerance of prolonged exposure to 33°C (Table 4). Most of the species could tolerate 33°C for at least 12 h, although this was not the case in *B. randi*.

Discussion

With regard to the lower temperature limits of the adult weevils found on Marion Island, it is clear that the *Bothrometopus* and *Ectemnorhinus* species are freeze tolerant, whereas *Palirhoeus eatoni* avoids freezing. However, the extent of the freeze tolerance in the former species is not pronounced, and their lower lethal temperatures are considerably higher than those found in freeze-tolerant beetles from the high Arctic (e.g. Miller 1982; Ring 1982; Lee 1991) and more temperate northern latitudes (Vernon et al. 1996). If the microhabitat temperatures that these species are liable to encounter are taken into consideration (Table 1) this is not surprising. Most sub-zero thermal events on Marion Island are not extreme and are usually short-lived, particularly at lower altitudes (Schulze 1971; Chown and Crafford 1992; Blake 1996). Hence a limited degree of freeze tolerance, which would enable adults of these species to endure relatively high sub-zero temperatures for a few hours at most, would be sufficient for their survival. This limited degree of freeze tolerance appears to be retained in the species in both summer and winter, probably because freezing events occur at any time of the year (Schulze 1971; Chown and Crafford 1992; Blake 1996). However, the extent of freeze tolerance appears to decline from winter to summer in *B. parvulus* and *E. similis*, and to a certain degree also in *B. randi*. This is the situation more usually found in insects (Van der Laak 1982; Lee 1991). Storey and Storey (1996) suggested that in vertebrates "ecologically relevant freeze-tolerance" refers only to those situations where individuals endure long periods in the frozen state. The data presented here suggest that this restriction is not broadly applicable, but do support Klok and Chown's (in press) suggestion that in arthropods the "freeze tolerant" category may merit the scrutiny recently applied to freeze susceptibility (see also Bale 1996).

Although the SCP and lower lethal temperatures of *Palirhoeus eatoni* suggest that this species is not cold tolerant (e.g. Zachariassen 1985; Block 1990), the pronounced decline in its winter SCP, and increase in its tolerance to constant low temperatures indicate that it possesses a limited degree of cold tolerance at this time. In addition, the pronounced difference in cold hardiness between this species and the others could be a consequence of its occurrence in the supra-littoral zone (see Chown 1989). Chown and Van Drimmelen (1992) showed that the larvae of this species are able to osmoregulate in both fresh and seawater and maintain elevated haemolymph osmolalities compared with the larvae of *B. randi* and *E. similis*, and it seems likely that the syntopic adults will show similar adaptations. Increased desiccation resistance is also characteristic of the adults of this species (Chown 1993a). Ring and Danks (1994) suggested that the physiological characteristics that enable species to survive desiccation may promote cold tolerance. Due to its osmoregulation demands, *P. eatoni* may be forced to adopt a "supercooling" strategy to survive low winter temperatures. This deserves further attention, particularly because Storey and Storey (1996) have argued that freeze tolerance may be the more common strategy in intertidal invertebrates.

The data presented here indicate that, with the exception of the supra-littoral zone, habitat had little influence on cold hardiness strategy of the weevils studied. Although unexpected (see Chown 1993a), this result may be a consequence of the fact that adult weevils in fellfield and rock face habitats tend to seek shelter in wet moss cushions during dry periods (Chown 1993a,b). Hence they may be continually exposed to water. Furthermore, the results suggest that freeze tolerance has evolved in *Bothrometopus* and *Ectemnorhinus* from a condition of freeze susceptibility in *Palirhoeus eatoni*. However, given that *Disker*, the adelphotaxon to all three genera, occupies fellfield habitats (Kuschel and Chown 1995), the latter suggestion seems unlikely.

Freeze tolerance in insects appears to be more frequent in the higher insect orders and is common in adult Coleoptera (Block 1982). Therefore it is not surprising that adults of most of the weevil species on Marion Island are freeze tolerant, especially as they may regularly be exposed to water in their environments (see above) and actively feed throughout the year (Chown 1989; Chown and Scholtz 1989b,c). Duman et al. (1991) argued that frequent exposure to ice nucleators, such as ice crystals and food particles, may select for freeze tolerance in insects. However, they also suggested that regular freeze-thaw cycles, such as those occurring on Marion Island (Blake 1996), should select for supercooling enhancement. Perhaps the limited degree to which temperature is depressed below freezing point (Chown and Crafford 1992; Blake 1996), and the fact that the weevil adults must resume feeding as soon as conditions permit (see Chown and Scholtz 1989c; Chown 1993a,b), preclude the latter strategy and favour freeze tolerance. A similar, limited degree of freeze tolerance is also characteristic of other sub-Antarctic insects, including perimylopid beetles from South Georgia (Worland et al. 1992) and the larvae of *Pringleophaga marioni* (Lepidoptera) from Marion Island (Klok and Chown in press). In fact, this trend towards limited freeze tolerance is common in a number of high-latitude, southern hemisphere insects (e.g. Ramløv et al. 1992; Block and Convey 1996). Hence the data presented here add some support to Klok and Chown's (in press) hypothesis that freeze tolerance may be more common in high southern latitudes than in similar northern ones.

The upper lethal limits found in these species correspond closely with those recorded in their microhabitats (Table 1), and the short period of survival at constant high temperature (33°C) also matches the pattern of occurrence of high temperatures at Marion Island. These are sporadic and are associated with calm, sunny days, which tend to be rare (Schulze 1971; Smith and Steenkamp 1990; Chown and Crafford 1992; Blake 1996). However, Smith and Steenkamp's (1990) finding that mean air temperature has risen by 1°C at Marion Island since the late 1940s, and their suggestion that insolation may increase, are cause for concern, especially if this is accompanied by a general drying of habitats (Chown and Smith 1993). A combination of high temperatures and low humidities may reduce the survival of these weevil species (see also Chown 1993a). Klok and Chown (in press) argued that increasing temperatures may compromise the survival of the endemic *Pringleophaga marioni* at Marion Island as a consequence of interactions between its physiological tolerances and predation by feral house mice. Chown and Smith (1993) demonstrated that weevils are forming an increasing component of the house mouse's diet at Marion Island and a similar interaction can be expected.

In conclusion, this study shows that the adults of weevils from Marion Island have thermal tolerance limits that closely match the microhabitat conditions they are liable to encounter. It also provides some support for Klok and Chown's (in press) idea that freeze tolerance may be more common in wetter, high southern hemisphere latitudes than in drier northern ones. Nonetheless, evaluations of the cold tolerance strategies of the larvae of these species are also required, as well as an expansion of the adult work to include the influence of freezing events on the F1 generation (Block 1990; Bale 1993), and the differences between populations occurring at different altitudes (see Chown et al. 1997). Such investigations may shed considerable light on the interactions between tolerances to abiotic factors and introduced predators during climate change.

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