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Respiratory metabolism in two species of carabid beetle from the sub-Antarctic island of South Georgia

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Abstract The influence of feeding state on cold-adapted metabolism was investigated in the adults of two carabid beetles, *Trechisibus antarcticus* and *Oofterus soledadinus* (Coleoptera: Carabidae), which have been introduced to sub-Antarctic South Georgia. The metabolic rates in both fed and starved *O. soledadinus* and *T. antarcticus* were determined at eight temperatures ranging from 0 to 35°C, using a Servomex 570A oxygen analyser. There was no significant difference in the metabolic rates between the fed and starved animals of each species. In *T. antarcticus* this ranged from 0.28 to 3.84 ml O₂ g⁻¹ h⁻¹, and in *O. soledadinus* from 0.19 to 2.80 ml O₂ g⁻¹ h⁻¹ at 0 and 35°C, respectively. In each of the four experimental groups there was a strong positive correlation between metabolic rate and temperature, with the highest increase occurring between 0 and 5°C. In contrast, the metabolic rate was significantly negatively correlated with initial live weight of the beetles at most temperatures. The results are discussed comparatively with other species and against a background of the ecology of the two carabids at South Georgia.

Introduction

In the past it was thought that most insects exhibited little respiratory adaptation to temperature (Scholander et al. 1953; Remmert 1980), but this has not proved to be the case in polar arthropods; for example, Crafford and Chown (1993) have shown Coleoptera, Lepidoptera and Diptera from the sub-Antarctic to be capable of respiratory adaptation to temperature. Also, Block

and Young (1978) concluded that some Antarctic mites had elevated metabolic rates over the normal environmental temperature range.

Polar arthropods increase their metabolic rates in order to compensate for low temperatures, for example Collembola (Block 1979, 1984) and terrestrial mites (Block and Young 1978). Also, Bullock (1955) and Kestler (1984) found that in cold environments, ectotherms can compensate for the effects of low temperatures by raising their metabolic rates compared with temperate species. Elevation of metabolic rate in both alpine and polar invertebrates has been shown to be an adaptation to low temperatures and short growing seasons (Strømme 1989), whilst increased oxygen consumption has demonstrated an increase in metabolism in Arctic and Antarctic arthropods (Sømme et al. 1989). Elevated metabolic rates were found in spiders, mites, Collembola and beetles from Spitsbergen in the high Arctic by Aunaas et al. (1983) and Strømme et al. (1986).

In contrast, neither the Antarctic midge *Belgica antarctica* (Diptera: Chironomidae) nor the Antarctic tick *Ixodes uriae* (Acari: Metastigmata) showed elevated respiration rates compared with temperate species (Lee and Baust 1982a,b), and Kevan and Danks (1986) found that many Arctic insects remained active at temperatures below the threshold temperatures of temperate species although increased metabolic rates were not common.

There have been a number of studies on respiration in sub-Antarctic invertebrates, e.g. Block (1981), Sømme et al. (1989), Crafford and Chown (1993) and Chown (1997). However, few studies have been carried out on carnivores from sub-Antarctic islands, which being predatory are faster moving, and therefore generally have a higher metabolism than herbivores.

The sub-Antarctic island of South Georgia occupies an isolated position, 53°S and 34°W, well inside the Antarctic Convergence in the South Atlantic Ocean. It is a mountainous island and half its land surface area is covered by permanent snow and ice. The climate is

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characterised by relatively mild winters and very short, cool summers (mean summer temperature is 5°C), and there is an impoverished insect fauna (Gressitt 1970; Block 1988; Block et al. 1988).

The two Coleoptera investigated were *Ooapterus soledadinus* Guérin-Ménéville, 1830, first reported on South Georgia at King Edward Point in 1963 (Darlington 1970), and *Trechisibus antarcticus* (Dejean, 1831), first recorded in the Husvik Harbour area in 1982 (Vogel 1985). They belong to the family Carabidae and both species are common in the Falkland Islands (Roux and Voisin 1982) and were probably introduced from there to South Georgia during whaling operations. *O. soledadinus* is the slightly larger beetle of the two, being up to 0.7 cm in body length and up to 12 mg in live weight, whereas *T. antarcticus* is up to 0.5 cm long and 10 mg live weight. These species co-exist in the Husvik and Stromness Bay area of South Georgia, but *O. soledadinus* is more restricted in its distribution (Block et al. 1988). The latter species is found in certain areas of the Husvik whaling station, and was recorded up to the Karrakatta River and at Jason Harbour in the 1995–1996 season (Brandjes 1996). *T. antarcticus* is more widely distributed in the area (P.S. Ottesen personal communication). Both species are carnivorous, feeding on various mites and springtails and *T. antarcticus* also preys on the larvae of the herbivorous beetle *Hydromedion sparsutum* Müller (Coleoptera: Perimylopidae).

In this study, the metabolic rates of the two introduced carabid beetles were compared between and within the two species, in the satiated and unfed state, for up to 5 days. The results were compared with published data on metabolic rates of other arthropods from polar and other cold environments.

Materials and methods

The study was carried out between January and April 1994 at the British Antarctic Survey summer field station at Husvik, in the Stromness Bay area of South Georgia. Measurements were made only on adults of *T. antarcticus* and *O. soledadinus* (due to the difficulty in locating larvae of both species). *T. antarcticus* adults were collected in lowland areas, from tussock grass litter and from the soil surface under rocks and pieces of timber (from the whaling station buildings) in the Husvik area, whilst *O. soledadinus* adults were sampled from very specific sites within the whaling station, again under stones and timber on the soil surface. A fresh sample of beetles was collected for each set of experiments, which were conducted as soon as possible afterwards. Beetles were collected individually using an electrically-powered aspirator. For each set of experiments, conducted at one of eight temperatures, two sets of petri dishes were set up per species. One set had damp filter paper plus an adequate food supply (Col-

lembola, collected from tussock grass litter) and the other set had only damp filter paper. Five individuals were placed in each of the prepared dishes. The dishes were placed at 10°C for 3–5 days prior to the measurement of respiration, and feeding was observed during this time in the dishes with prey.

The experimental procedure was identical for the two species whether starved or fed. Experiments were carried out at four main temperatures, 0, 10, 20 and 30°C, and four intermediate temperatures, 5, 15, 25 and 35°C for comparative purposes. Twenty individuals were used per species and feeding regime at the main temperatures, whereas ten individuals were used at the intermediate temperatures. For each experiment beetles of both species and feeding regime were weighed on a battery-operated Cahn microbalance (accurate to $\pm 1 \mu\text{g}$) and placed individually in 5-ml vac-u-test R vials (see Crafford and Chown 1993). There were also two (empty) control vials per experiment. All vials were acclimated at the required temperature in a water bath for 1 h. The tubes were then sealed with a rubber bung, and left in the water bath for varying lengths of time depending on the temperature of the experiment: at 0°C, 11 h; at 5°C, 10 h; at 10°C, 9 h; at 15°C, 8.5 h; at 20°C, 7.5 h; at 25°C, 5 h; at 30°C, 5 h and at 35°C, 2 h. A vacuum was introduced into a Servomex 570A oxygen analyser (Crafford and Chown 1993) and a sample of air from each of the tubes was drawn up into the vacuum and analysed individually. The oxygen content (%O₂) of each air sample was determined. The difference between the oxygen content of the vial before and after respiration by the insect was calculated, and the oxygen consumption expressed as ml O₂ g⁻¹ h⁻¹.

Results

Table 1 compares the oxygen uptake, or metabolic rate (corrected to standard temperature and pressure – STP) in fed and starved beetles of each species and at each temperature. There is no significant difference between the metabolic rate of fed and starved animals of both species at most temperatures, the exceptions being at 0 and 15°C in *O. soledadinus* and at 0 and 35°C in *T. antarcticus*. At each of the lower temperatures in each species the metabolic rate was highest in the starved animals and conversely, at the higher temperature, the metabolic rate was lower in starved animals.

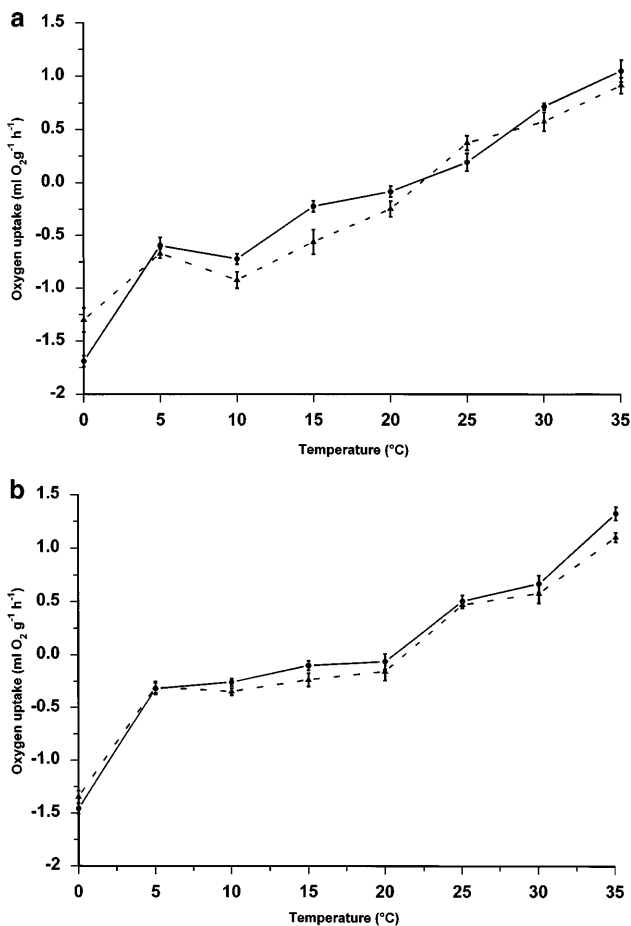
Figure 1 shows the log-transformed metabolic rate against temperature for *O. soledadinus* and *T. antarcticus* respectively. Regression equations are given in the legend, and indicate a very strong correlation overall, over the whole temperature range, between metabolic rate and temperature for both species.

An ANOVA was used to test for differences in the metabolic rate between temperatures in each species on each treatment. For fed *O. soledadinus* $F_{7,109} = 237.54$, $P < 0.001$, which showed that significant differences

Table 1 Metabolic rate ($\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ($\pm \text{SE}$)) corrected to STP of two South Georgian carabid beetles *Oopterus soledadinus* and *Trechisibus antarcticus*, n being the number of beetles

Temperature (°C)	<i>Oopterus soledadinus</i>			<i>Trechisibus antarcticus</i>		
	Fed	Starved	t	Fed	Starved	t
0	0.1892 ± 0.0106 18	0.3093 ± 0.0506 17	2.36 *	0.2363 ± 0.0119 15	0.2685 ± 0.0159 20	2.19 *
5	0.5668 ± 0.0457 10	0.5153 ± 0.0207 10	1.02 <i>ns</i>	0.7361 ± 0.0438 10	0.7457 ± 0.0158 10	0.15 <i>ns</i>
10	0.4961 ± 0.0280 19	0.4181 ± 0.0290 20	1.94 <i>ns</i>	0.7784 ± 0.0259 20	0.7134 ± 0.0243 20	1.80 <i>ns</i>
15	0.8538 ± 0.0501 10	0.5996 ± 0.0650 9	3.10 **	0.9106 ± 0.0414 10	0.8022 ± 0.0521 9	1.63 <i>ns</i>
20	0.8138 ± 0.0509 20	0.9432 ± 0.0454 20	1.86 <i>ns</i>	0.9023 ± 0.0585 20	0.9896 ± 0.0729 20	0.91 <i>ns</i>
25	1.2528 ± 0.1094 10	1.4878 ± 0.1112 10	1.51 <i>ns</i>	1.6769 ± 0.0981 10	1.6058 ± 0.0547 10	0.63 <i>ns</i>
30	1.8677 ± 0.1441 20	2.1018 ± 0.0616 19	1.26 <i>ns</i>	1.8599 ± 0.1247 20	2.0877 ± 0.1295 19	1.07 <i>ns</i>
35	2.8086 ± 0.2035 10	2.5625 ± 0.1757 10	0.92 <i>ns</i>	3.8462 ± 0.2226 10	3.0558 ± 0.1366 20	3.03 **

ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$



existed between the metabolic rates at each temperature, and the Tukey HSD test revealed that the metabolic rate at each temperature was significantly higher (at $P < 0.05$ level) than the metabolic rate at the immediately preceding temperature (except between 5 and 10°C, and 15 and 20°C). For starved *O. soledadinus* $F_{7,108} = 74.24$, which again showed that there were significant differences between the metabolic rates at the eight temperatures. The Tukey HSD test showed that the only significant differences in the metabolic rate at subsequent temperatures were between 0 and 5°C, and 20 and 25°C, where the rate was faster at the higher temperature in each case. For fed *T. antarcticus* there were differences in the metabolic rate at subsequent temperatures, $F_{7,108} = 155.19$, $P < 0.001$. The Tukey HSD test revealed that at 5, 25 and 35°C, the metabolic rates were significantly higher than at the preceding temperature. There were also differences in the metabolic rate and temperature in starved *T. antarcticus*, $F_{7,111} = 112.36$, $P < 0.001$, where significant differences

Fig. 1 a Relationship between log. metabolic rate and temperature in adults of *Oopterus soledadinus* for fed (●—●) and starved (▲--▲) animals. Regression equations: fed animals, $y = 0.068x - 1.364$, $r = 0.97$, $P < 0.001$; starved animals: $y = 0.062x - 1.312$, $r = 0.97$, $P < 0.001$. b Relationship between log. metabolic rate and temperature in adults of *Trechisibus antarcticus* for fed (●—●) and starved (▲--▲) animals. Regression equations: fed animals, $y = 0.064x - 1.080$, $r = 0.95$, $P < 0.001$; starved animals: $y = 0.058x - 1.037$, $r = 0.94$, $P < 0.001$

existed between 0 and 5°C, 20 and 25°C, and 30 and 35°C.

Comparison by analysis of covariance (ANCOVA) of the slopes of the lines from fed and starved individuals of *O. soledadinus* (Fig. 1a) and *T. antarcticus* (Fig. 1b) showed that there was no significant difference ($F_{7,217} = 2.24, P > 0.05$ and $F_{7,219} = 3.44, P > 0.05$ respectively). However, when comparisons are carried out by ANCOVA between species/feeding regimes, the slopes of the lines are seen to differ significantly: between fed *O. soledadinus* and fed *T. antarcticus*, $F_{7,217} = 40.31, P < 0.001$; between starved *O. soledadinus* and starved *T. antarcticus*, $F_{7,219} = 21.17, P < 0.001$; between fed *O. soledadinus* and starved *T. antarcticus*, $F_{7,220} = 15.99, P < 0.001$ and between starved *O. soledadinus* and fed *T. antarcticus*, $F_{7,216} = 41.05, P < 0.001$. These results indicate that in each comparison *T. antarcticus* had the higher respiratory metabolism over the temperature range 0–35°C.

In both species the greatest increase in metabolic rate between any two adjacent temperatures was between 0°C and 5°C after which, particularly in *T. antarcticus* (Fig. 1b), there was a period of thermal neutrality up to approximately 20°C, when increasing temperature had little effect on the rate of metabolism. Table 2 gives the Q_{10} values over three ranges of temperature for fed and starved *O. soledadinus* and *T. antarcticus*. Fed individuals of both species had $Q_{10} > 3$ over 0–5°C. A similar pattern of Q_{10} values was found in each species and feeding regime. The highest Q_{10} in each case was over the 20–35°C range and the values between 0 and 5°C were higher than those between 5 and 20°C (apart from starved *O. soledadinus*).

The relationship between metabolic rate and the initial weight of *O. soledadinus* and *T. antarcticus* at the eight experimental temperatures is given for fed animals (Table 3) and for starved animals (Table 4). In both species it is clear that the metabolic rate appears to be significantly negatively correlated with initial weight at the majority of temperatures (at temperatures where this is not the case, the correlation coefficient is not significant).

Table 2 Q_{10} values over three ranges of temperature (°C) for fed and starved adults of *Oopterus soledadinus* and *Trechisibus antarcticus*

Temperature range (°C)	<i>O. soledadinus</i>		<i>T. antarcticus</i>	
	Fed	Starved	Fed	Starved
0–5	3.04	1.68	3.18	2.79
5–20	1.53	1.94	1.30	1.41
20–35	3.60	2.85	4.44	3.22

Discussion

Overall there was no difference in the metabolic rate between fed and starved individuals of either *O. soledadinus* or *T. antarcticus* over the temperature range 0–35°C. This indicates that short-term starvation had no significant effect on metabolic rate. Individual beetles could survive 3–5 days without capturing prey, apparently with no detriment to their respiratory metabolism. The surface temperatures encountered by these beetles during a South Georgian summer range from 0.7 to 25°C (H.E. McAlister unpublished work), but extreme high temperatures up to 35°C can occur in sheltered microsites in grassland areas.

In both species the metabolic rate increased at progressively higher temperatures, with highly significant correlation coefficients, in fed and starved beetles. The oxygen consumption did not decline at high temperatures (> 30°C) and this is probably a characteristic of surface-active species. The majority of metabolic rates at a particular temperature were significantly higher than at the immediately preceding temperature. There was no difference in each species between the slopes of the regression lines for fed and starved individuals, indicating that the trend for individuals of the same species is similar on either feeding regime. However, between species and feeding regimes, there were significant differences between the slopes of the regression lines, which indicated that in each comparison, *T. antarcticus* generally had the faster metabolic rate at each

Table 3 Regression equations of metabolic rate ($\text{ml O}_2 \text{g}^{-1} \text{h}^{-1}$) on initial live weight (mg) at each of eight temperatures for fed *Oopterus soledadinus* and fed *Trechisibus antarcticus*

Temperature (°C)	Species	Regression equation	<i>n</i>	<i>r</i>	<i>P</i>
0	<i>O. soledadinus</i>	$y = -0.027x + 0.375$	18	0.97	<0.05
	<i>T. antarcticus</i>	$y = -0.048x + 0.495$	15	0.97	<0.01
5	<i>O. soledadinus</i>	$y = -0.080x + 1.110$	10	0.76	<0.05
	<i>T. antarcticus</i>	$y = -0.190x + 1.630$	10	0.99	<0.01
10	<i>O. soledadinus</i>	$y = -0.046x + 0.842$	19	0.51	<0.05
	<i>T. antarcticus</i>	$y = 0.016x + 0.674$	20	0.16	>0.05
15	<i>O. soledadinus</i>	$y = -0.001x + 0.858$	10	0.01	>0.05
	<i>T. antarcticus</i>	$y = 0.043x + 0.665$	10	0.32	>0.05
20	<i>O. soledadinus</i>	$y = -0.103x + 1.720$	20	0.48	<0.05
	<i>T. antarcticus</i>	$y = 0.001x + 0.891$	20	0.01	>0.05
25	<i>O. soledadinus</i>	$y = 0.092x + 1.180$	10	0.18	>0.05
	<i>T. antarcticus</i>	$y = -0.349x + 3.500$	10	0.85	<0.01
30	<i>O. soledadinus</i>	$y = -0.104x + 2.820$	20	0.55	<0.05
	<i>T. antarcticus</i>	$y = -0.221x + 3.280$	20	0.52	<0.05
35	<i>O. soledadinus</i>	$y = -0.616x + 7.430$	10	0.70	<0.05
	<i>T. antarcticus</i>	$y = 0.275x + 2.280$	10	0.40	>0.05

Table 4 Regression equations of metabolic rate ($\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) on initial live weight (mg) at each of eight temperatures for starved *Ooapterus soledadinus* and starved *Trechisibus antarcticus*

Temperature ($^{\circ}\text{C}$)	Species	Regression equation	<i>n</i>	<i>r</i>	<i>P</i>
0	<i>O. soledadinus</i>	$y = 0.046x + 0.005$	17	0.27	>0.05
	<i>T. antarcticus</i>	$y = -0.017x + 0.368$	20	0.51	<0.05
5	<i>O. soledadinus</i>	$y = 0.017x + 0.412$	10	0.17	>0.05
	<i>T. antarcticus</i>	$y = -0.173x + 1.540$	10	0.97	<0.01
10	<i>O. soledadinus</i>	$y = -0.030x + 0.627$	20	0.59	<0.05
	<i>T. antarcticus</i>	$y = 0.001x + 0.711$	20	0.01	>0.05
15	<i>O. soledadinus</i>	$y = 0.022x + 0.540$	9	0.09	>0.05
	<i>T. antarcticus</i>	$y = -0.063x + 1.170$	9	0.74	<0.05
20	<i>O. soledadinus</i>	$y = 0.042x + 0.531$	20	0.22	>0.05
	<i>T. antarcticus</i>	$y = 0.077x + 0.910$	20	0.19	>0.05
25	<i>O. soledadinus</i>	$y = -0.131x + 2.430$	10	0.68	<0.05
	<i>T. antarcticus</i>	$y = 0.001x + 1.601$	10	0.01	>0.05
30	<i>O. soledadinus</i>	$y = 0.042x + 2.000$	19	0.07	>0.05
	<i>T. antarcticus</i>	$y = -0.238x + 3.280$	19	0.49	<0.05
35	<i>O. soledadinus</i>	$y = -0.237x + 4.280$	10	0.68	<0.05
	<i>T. antarcticus</i>	$y = -0.527x + 6.060$	10	0.95	<0.01

of the eight temperatures. Within each species the smaller adults also generally had the highest metabolic rates.

P.S. Ottesen (personal communication) also found that *T. antarcticus* had a higher respiratory metabolism than *O. soledadinus* at a given temperature, coupled with a lower chill coma point, and suggested that *T. antarcticus* was the most cold-adapted species. This could also explain the success of *T. antarcticus* in colonising a wider range of terrestrial habitats on South Georgia. *T. antarcticus* is the smaller of the two species and in both studies the size difference could explain the variations in metabolic rates. That individuals have lower body weights than other species could partly explain their higher metabolic rate (Sømme et al. 1989). The metabolic rate per unit body mass is known to be lower in larger animals than in smaller animals: metabolic rate to body mass in poikilotherms and homeotherms increases with an exponent of 0.75 (Hemmingen 1960).

Obviously it would be advantageous for both species to avoid very high temperatures, particularly the smaller individuals. They may adapt behaviourally by occupying habitats where the temperature would be more stable, i.e. under rocks and in the litter layer of higher plants.

The higher increase in rate of metabolism at 5°C (from 0°C) may be an adaptation to living in an extreme environment, as this would permit a rapid acceleration of metabolism as the temperature rose after a cold period, and conversely would permit a fast deceleration as temperature declined.

The results from this study were compared with metabolic rates obtained for Coleoptera from other cold environments in comparable seasons, mostly made on summer-acclimatised insects. Comparative respiration studies are complicated by the fact that the metabolic rate is strongly affected by factors such as body size (Schmidt-Nielsen 1972) and phylogeny (Zachariassen et al. 1987). The metabolic rates for *O. soledadinus* and *T. antarcticus* in both treatments were higher than for the herbivorous *Otiorrhynchus dubius* (Coleoptera:

Curculionidae) and *Melasoma collaris* (Coleoptera: Chrysomelidae) from Finse (Hågvar and Ostbye 1974; Meidell 1983). This is in contrast to Block (1981) who found that the metabolic rate of *O. soledadinus* fell within the range of these two species. The metabolic rates in the present study were generally lower than those of a Spitsbergen weevil *Rhynchaenus flagellum* (Coleoptera: Curculionidae) (Strømme et al. 1986) but this may be due to the difference in size as *R. flagellum* had a much lower body weight.

The metabolic rates found for *O. soledadinus* and *T. antarcticus* were approximately double those of the South Georgian herbivores, *H. sparsutum* and *Perimylops antarcticus* (Sømme et al. 1989) over similar temperature ranges. Compared with the limited data on metabolic rates of *O. soledadinus* and *T. antarcticus* collected previously (P.S. Ottesen personal communication), the rates obtained in the present study are higher for each species. According to the energy content of their food, herbivores and carnivores have very differing metabolic rates.

Additional data on metabolic rate of cold-climate carabid beetles have also been collected by Conradi-Larsen and Sømme (1973), Strømme (1989) and Nylund (1991). Although wide variations in metabolic rates of *O. soledadinus* and *T. antarcticus* are evident in this study, they generally fit well into the middle range of the rates given for the northern carabids.

As increasing the temperature (to $> 5^{\circ}\text{C}$) has the effect of increasing their metabolic rates, these beetle species would become more active, thereby leading to higher feeding rates and colonisation rates. This in turn would have an effect on their prey species numbers. This could be particularly relevant to *T. antarcticus* as, overall, this species has a slightly higher metabolic rate than *O. soledadinus* at the temperatures investigated. Higher temperatures could cause greater expansion of the beetle's range and, in particular, a greater impact on one of its prey species, the larvae of the endemic herbivore *H. sparsutum*, upon which it has already had a marked effect (Ernsting et al. 1995).

It is proposed that, as such carabid beetles are active on South Georgia within the temperature range 0–35°C, starvation, at least for short periods, will not seriously affect their metabolic rates. Their metabolism will increase significantly at a few degrees above 0°C (found to be ca. 5°C in this study), allowing individuals to be active and to forage at low habitat temperatures. Further studies to determine the precise temperature (between 0 and 5°C) at which the increase in metabolism occurs are required and the results linked to the behavioural ecology of the species.

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