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Elevation and climatic tolerance: a test using dung beetles

Kevin J. Gaston and Steven L. Chown

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An increase in the altitudinal range of occurrence of species in an assemblage with increasing elevation has been explained as a consequence of individual organisms having to be able to withstand a broader range of climatic conditions at higher elevations; the climatic variability hypothesis. Here we show that for scarab dung beetles (26 species) across an elevational transect (approx. 2500 m) in southern Africa thermal tolerance range does increase with increasing elevation across individuals and across species. The maximal thermal tolerance range exhibited increases slowly with elevation and the minimum range increases more rapidly. The mechanistic basis of the change appears to be one of rapidly changing critical thermal minimum (CT_{min}) with elevation and only small changes in critical thermal maximum (CT_{max}). Of course, even if the pattern of tolerance of species assumed by the climatic variability hypothesis is correct, an increase in altitudinal range with increasing elevation need not necessarily follow. However, although sampling has been limited, there does appear to be an elevational increase in altitudinal range for this species assemblage.

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Stevens (1992) has shown for a number of data sets that for a given taxon there is a positive relationship between the altitudinal range over which species occur and elevation. That is, species at higher elevations occur across a broader span of altitudes than do species at lower elevations (see also Fleishman et al. 1998, Ruggiero and Lawton 1998). This pattern has been associated with a decline in the species richness of a taxon with increasing elevation, and is analogous to the decline in the latitudinal extents of species towards lower latitudes which has been documented for some groups ('Rapoport's rule'; Rapoport 1982, Stevens 1989; but see Gaston et al. 1998). Indeed, Stevens (1992) argues that trends in altitudinal and latitudinal range may both result if species in which individual organisms have to be able to withstand a broad range of local climatic conditions are as a result enabled to become more widely distributed; the 'climatic variability' or 'seasonality' hypothesis. Towards higher latitudes and elevations, climatic conditions become more variable (Sømme and Block 1991, Ferguson and Messier 1996), and individuals of resident species (as

opposed to migratory ones) must be able to withstand these wide extremes (but see Gaston and Chown 1999 regarding latitudinal patterns). The general idea that if individual organisms are able to withstand wider climatic variability the species as a whole will be able to become more widespread has deep historical roots (e.g. Allee et al. 1949, Dobzhansky 1950, Janzen 1967).

Whilst intuitively appealing, from an empirical perspective the chain of causality underlying the climatic variability hypothesis as it pertains to elevational gradients is incomplete. Stevens (1992) has shown that climates are more variable towards higher elevations and that altitudinal ranges increase towards higher elevations. However, tests of the relationship between the elevations at which species in a taxon occur and the climatic tolerances of individuals of those species essentially remain lacking. Thus, Brattstrom (1968) provided data on critical thermal minima and maxima for species of amphibians at different altitudes, but comparisons are limited by variation in latitude and acclimation temperatures from which the information derives.

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In this paper, we use data on scarab dung beetles (Coleoptera, Scarabaeidae) across an elevational transect in southern Africa to test whether elevational patterns in the climatic tolerances of species are as assumed by the climatic variability hypothesis. Temperature is generally acknowledged to be an important climatic parameter influencing the distributions of dung beetles (Davis 1997), and thermal tolerance is used as a measure of climatic tolerance.

Methods

Beetles were sampled across a single gradient at six localities, at altitudes from 500 to nearly 3000 m at approximately 500-m intervals, from Vernon Crookes Nature Reserve close to Umzinto on the Kwazulu-Natal coast to the South Africa-Lesotho border at the top of Sani Pass (Table 1) [this transect embraces a similar set of elevations to those of several of Stevens' (1992) data sets]. Between 3 and 9 December 1997, pitfall traps were set at each site, baited with 500 g of cattle dung, and cleared and reset on a regular basis.

Beetles (species list in Table 2) were taken to the laboratory after a maximum of seven days, where they were maintained at 20°C (14 L:10 D) for a minimum of four days. Critical temperature tolerances were determined using dynamic (CT_{min} , CT_{max}) methods similar to those of Klok and Chown (1997) (see Lutterschmidt and Hutchison 1997a, b for general review), using a Grant LTD6 waterbath. Beetles were kept separately in 20-ml plastic containers lined with a small amount of fine sand. They were first held at a temperature of 15°C for 10 min. The temperature was then lowered at 0.5°C min⁻¹ to 6°C for beetles collected between 500 and 1900 m, or to 4.5°C for those collected at higher elevations. It was held at this point for a further 10 min and then increased at the same rate. The critical thermal minimum (CT_{min}) (cold coma) point was recorded as that at which beetles could right themselves and

Table 2. Dung beetle species (Coleoptera: Scarabaeidae: Scarabaeinae) used for CT_{min} and CT_{max} determinations in this study. A full species list for the transect sampled here is provided by Davis et al. (in press).

Tribe	Species
Canthonini	<i>Epirinus relictus</i> Scholtz & Howden <i>Epirinus sulcipennis</i> Boheman <i>Epirinus validus</i> Péringuey
Coprini	<i>Copris caelatus</i> Fabricius <i>Copris corniger</i> Sahlberg
Dichotomiini	<i>Xinidium dentilabris</i> Harold
Gymnopleurini	<i>Gareta unicolor</i> (Fahraeus)
Oniticellini	<i>Euoniticellus triangulatus</i> (Harold) <i>Liatongus militaris</i> (Castelnau)
Onitini	<i>Onitis pecuarius</i> Lansberge
Onthophagini	<i>Caccobius obtusus</i> Fahraeus <i>Digitonthophagus gazella</i> (Fabricius) <i>Onthophagus asperulus</i> (d'Orbigny) <i>Onthophagus</i> nr. <i>Asperulus</i> sp. 1 <i>Onthophagus</i> nr. <i>Asperulus</i> sp. 2 <i>Onthophagus binodis</i> Thunberg <i>Onthophagus</i> nr. <i>Sugillatus</i> <i>Onthophagus</i> nr. <i>Tuberculatus</i> sp. 1 <i>Onthophagus</i> nr. <i>Tuberculatus</i> sp. 2 <i>Onthophagus</i> nr. <i>Tuberosus</i> <i>Onthophagus</i> nr. <i>Vigens</i> <i>Proagoderus brucei</i> Reiche
Scarabaeini	<i>Scarabaeus westwoodi</i> Harold
Sisyphini	<i>Neosisyphus muricatus</i> Olivier <i>Neosisyphus spinipes</i> (Thunberg) <i>Sisyphus costatus</i> Thunberg

maintain coordinated leg movements, and the critical thermal maximum (CT_{max}) (heat stupor) temperature as that at which they lost coordination (showed spasms) (Klok and Chown 1997). CT_{min} and lower lethal temperature tend to be correlated for many arthropods (Sømme 1989, Block 1990), as do CT_{max} and upper lethal temperature (Lutterschmidt and Hutchison 1997a, b). The tolerances of different species were determined at each of the elevations, avoiding any spatial non-independence in subsequent analyses, and the sequence in which the thermal tolerances of species were determined was randomised such that there was no systematic tendency for species from high or low elevations to be maintained under laboratory conditions for longer periods. All determinations were made three hours after the onset and three hours before the end of photophase.

Climatic variation across the transect was examined by subtracting mean air temperature of the warmest month from mean air temperature of the coldest month at each site on the transect. These values were obtained for each of the sampling sites from interpolated climate surfaces generated by the Computing Centre for Water Research (CCWR, University of Natal) using recorded meteorological data from the past 70 years. Whilst the thermal environments (e.g. dung and soil surface) occupied by dung beetles will be rather different from these values, they serve as reasonable surrogates over the broad range of elevations of concern. In the absence of

Table 1. Location (decimal degrees) and elevation of the study sites (site names following Davis et al. in press).

Study site and nearest town/feature	Grid reference	Elevation (m)
Scarp-top (Sani Pass)	29°35.16'S, 29°17.22'E	2865
Mid-slope (Sani Pass)	29°35.68'S, 29°18.13'E	2400
Drakensberg Foothills (Sani Pass)	29°36.42'S, 29°21.19'E	1900
Farm "Sunrise" (Underberg)	29°50.31'S, 29°38.75'E	1400
Farm "Herdstown" (Ixopo)	30°10.59'S, 30°06.41'E	1000
Vernon Crookes Nature Reserve (Umzinto)	30°16.17'S, 30°37.46'E	500

snow, reasonably strong relationships between soil surface temperatures and temperatures above the surface (up to 1.5 m) have been found elsewhere (Rosenberg et al. 1983, Chown and Crafford 1992, Klok and Chown 1998a).

Results

Treating individual beetles as independent data points, the range of thermal tolerances increased with elevation, although the variance in this range declined (Fig. 1a; Spearman rank correlation $r_s = 0.554$, $n = 229$, $p < 0.001$). The thermal tolerance range of individuals at the highest elevations was approximately 10°C greater than those at the lowest elevations. Both CT_{min} and CT_{max} declined with elevation, with the former being more steeply related and strongly correlated with altitude than the latter (Fig. 2; CT_{min} : $r_s = -0.748$, $n = 229$, $p < 0.001$; CT_{max} : $r_s = -0.354$, $n = 229$, $p < 0.001$). Thus, thermal tolerance range changed more as a consequence of the steep decline in CT_{min} ($r_s = -0.755$, $n = 229$, $p < 0.00001$) than the much shallower increase in CT_{max} ($r_s = 0.235$, $n = 229$, $p < 0.0004$). Of the 26 species, individuals of only one exhibited a significant correlation between tolerance

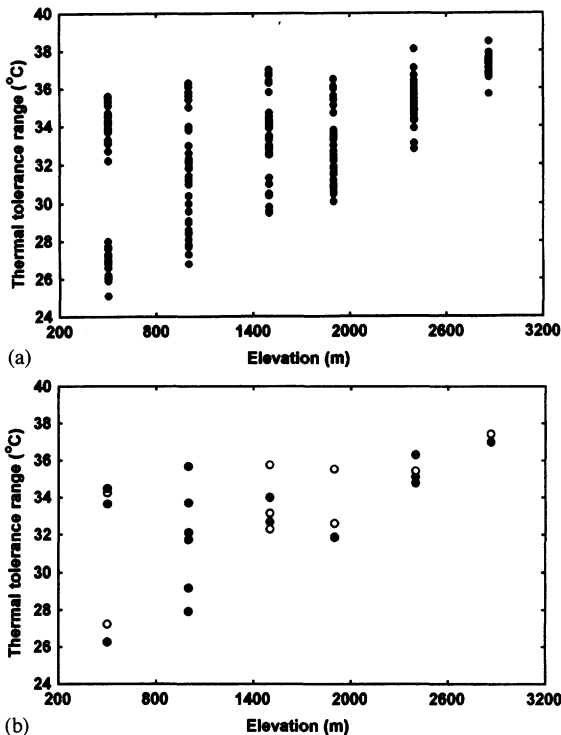


Fig. 1. The relationship between elevation and thermal tolerance range ($CT_{max} - CT_{min}$) for (a) individuals ($n = 229$), and (b) species ($n = 26$) of dung beetles collected at six localities across a 2500-m elevational range in southern Africa (species of the genus *Onthophagus* are indicated by open circles).

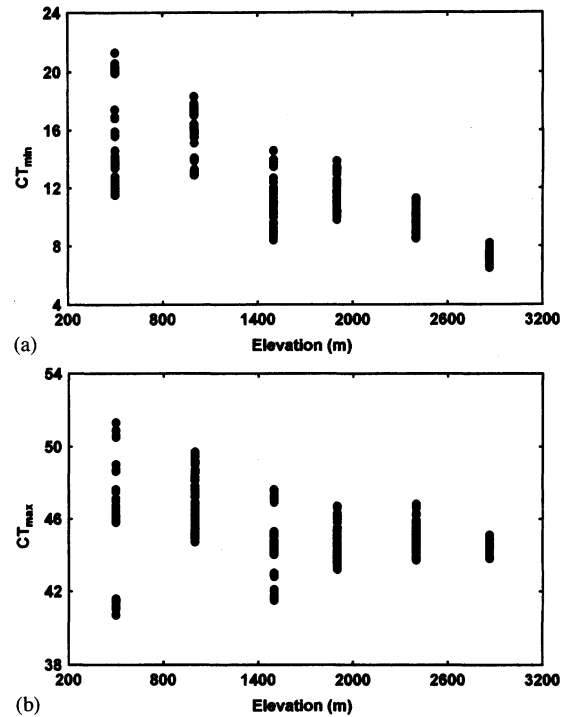


Fig. 2. The relationship between elevation and (a) critical thermal minimum (CT_{min}), and (b) critical thermal maximum (CT_{max}) for individual ($n = 229$) dung beetles collected at six localities across a 2500-m elevational range in southern Africa.

range and body mass (*Proagoderus brucei*; $r_s = -0.631$, $n = 10$, $p < 0.05$).

Treating species as independent data points and averaging across individuals, essentially the same pattern of relationship between thermal tolerance range and elevation was revealed as for individuals (Fig. 1b; Spearman rank correlation $r_s = 0.557$, $n = 26$, $p < 0.01$). In this case, the steep decline in CT_{min} continued to contribute to the change in thermal tolerance range ($r_s = -0.709$, $n = 26$, $p < 0.0001$), whereas changes in CT_{max} did not contribute significantly ($r_s = 0.117$, $n = 26$, $p = 0.568$). There was no significant relationship between log mean body mass and mean tolerance range ($r_s = 0.055$, $n = 26$, NS), mean CT_{min} ($r_s = -0.050$, $n = 26$, NS) or mean CT_{max} ($r_s = -0.006$, $n = 26$, NS).

Thermal tolerances were determined for species of the genus *Onthophagus* from every locality sampled, except that at 1000 m (nine species in all). Extracting these data separately, treating them as independent data points and averaging across individuals, there was no significant relationship between tolerance range and elevation, although the correlation coefficient was positive ($r_s = 0.557$, $n = 9$, NS) and the species with the broadest tolerance range occurred at the highest elevation and the one with the narrowest range occurred at the lowest elevation (Fig. 1b). There was a significant decline in CT_{min} with elevation ($r_s = -0.889$, $n = 9$, $p < 0.001$), though not CT_{max} ($r_s = -0.137$, $n = 9$, $p < 0.001$).

In the absence of an accepted phylogeny for the Scarabaeidae, the best available systematic classification provided only eight separate nodes for Comparative Analysis by Independent Contrasts (CAIC; Purvis and Rambaut 1995), to control for the phylogenetic non-independence of data points. Using ordinary least squares regression, with no model constant, there was no relationship between contrasts of elevation (predictor variable) and mean tolerance range ($r = 0.520$, $n = 8$, NS) or mean CT_{\max} ($r = -0.134$, $n = 8$, NS). However, there was a significant relationship between contrasts of elevation (predictor variable) and mean CT_{\min} ($r = -0.700$, $n = 8$, $p < 0.05$).

The thermal tolerance ranges of individuals, and the mean values for species, at the lowest elevation (500 m) appear bimodal, with three species having reasonably high values and two very low ones (Fig. 1). This was the only elevation at which samples came from two habitats, namely forest and grassland (elsewhere they came solely from grasslands). The three species with high values of thermal tolerance range all derive from the grassland samples, whilst one of the other species derives from the grassland samples and one from the forest.

Data from the interpolated climate surface for each of the six altitudinal sites indicated a sharp rise in temperature range between 500 and 1500 m, and a more variable pattern above this altitude, but nonetheless with the largest temperature range at 2865 m (Fig. 3). The inconsistent patterns in the mid- to high-elevation range may be due in most part to poor performance of the climate interpolations in areas of great topographic complexity (B. Erasmus pers. comm.), thus possibly accounting for the fact that the relationship between altitude and temperature range was only on the verge of statistical significance (Fig. 3).

The elevational occurrence of dung beetles had been assessed across the same transect as used here, over four days in January 1997 (Davis et al. in press). At

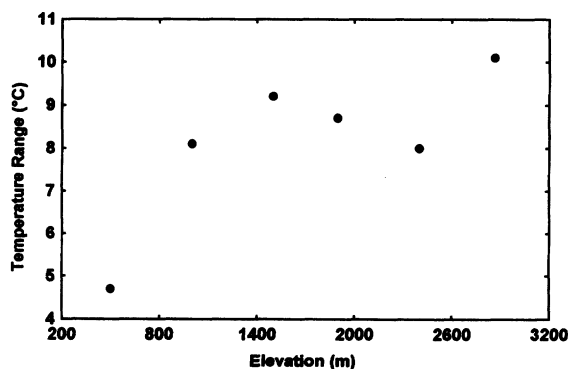


Fig. 3. The relationship between elevation and annual temperature range at six localities across a 2500-m elevational range in South Africa ($r^2 = 0.590$, $n = 6$, $p = 0.075$). The data were derived from an interpolated climatic surface for South Africa.

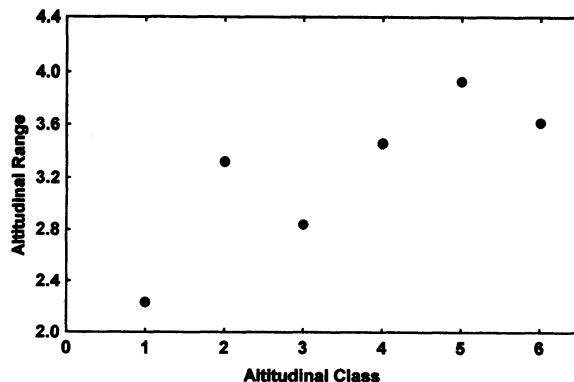


Fig. 4. The relationship between elevational class and mean altitudinal range for dung beetle species (total $n = 73$) sampled across a 2500-m elevational transect in southern Africa. Given their relatively small number and slightly uneven spacing, the six elevations sampled were ordered 1 to 6 (from lowest to highest), the altitudinal range is the mean number of classes spanned by the species occurring in each class (the numbers of species in each class are: 1 – 43, 2 – 28, 3 – 37, 4 – 24, 5 – 14, 6 – 13, and there is a significant positive relationship between altitudinal class and altitudinal range: $r_s = 0.89$, $p = 0.019$).

each locality three trap sites consisting of four pitfall traps were established. Traps were baited with 500 g of cattle dung and cleared every 12 h. Combining these occurrence data with those from the present trapping, carried out to obtain specimens for measuring tolerances, generated a broadly positive relationship between altitudinal range and elevation (Fig. 4). Whilst the sampling program was not sufficient to demonstrate whether all the species occurring at each elevation had been collected, it seems unlikely that this pattern would be radically altered by continued efforts.

Discussion

There is evidence for a general increase in the temperature tolerance range of dung beetles across an elevational gradient of approximately 2500 m in southern Africa. The pattern is exhibited when individuals or species are treated as separate data points. It is only possible to conduct a weak test controlling for the effects of phylogenetic non-independence, and whilst this does not yield a significant result the correlation coefficient between contrasts on elevation and tolerance range remains positive. This lack of significance in the independent contrasts analysis is plausibly due largely to poor taxonomic resolution within the Scarabaeidae (a classification is available at tribal level only). In consequence, the following discussion relies more heavily on the results of the analysis where species were regarded as independent, but bearing the potentially marked effects of non-independence in mind.

Broadly our findings therefore conform to the assumptions of the climatic variability hypothesis. This hypothesis assumes that species occurring in areas of low climatic variability will not have wide climatic tolerance ranges. However, this need not be the case, and indeed some dung beetle species occurring at all elevations in southern Africa have wide thermal tolerance ranges. This is reflected in a shallow increase in the maximum thermal tolerance range exhibited at different elevations, and a steep increase in the minimum thermal tolerance range, and hence the reduced variance in tolerance ranges towards higher elevations (Fig. 1). Nonetheless, the overall pattern is one of increasing thermal tolerance range with elevation.

The mechanistic basis of this change appears to be one of rapidly changing CT_{min} with elevation (also found when phylogenetic non-independence is crudely controlled for) and only small changes in CT_{max} . Thus, CT_{min} appears to be a more labile trait than CT_{max} . Indeed, an examination of the literature on insect thermal biology suggests that lower thermal tolerances tend to be more variable than upper thermal ones. While in most terrestrial arthropods the latter tend to remain in the region of 35–50°C (see e.g. Mellanby 1932, Edney 1971, Roberts et al. 1991, Mitchell et al. 1993, Hodgkinson et al. 1996, Klok and Chown 1997, 1998b), lower thermal tolerances assume a much wider variety of values (Block 1982, Miller 1982, Sømme 1982, Lee 1991, Mitchell et al. 1993, Klok and Chown 1997). Lutterschmidt and Hutchison (1997a: 1567) made the same point with regard to ectotherms in general and Stanley et al. (1980) argued that increased cold stress resistance appears to allow the penetration of temperate areas by cosmopolitan *Drosophila* species. Although these lower thermal tolerances are likely to be affected by the cold hardiness strategy adopted by different insect species (freeze tolerant as opposed to freeze avoiding) (Block 1990), this influence is unlikely to be consistent. Experimental evidence which indicates that the relationship between evolutionary changes in upper and in lower thermal tolerances may be complex is pertinent in this regard (see Huey and Berrigan 1996, Mongold et al. 1996).

Nonetheless, at least some authors have documented a close relationship between temperature tolerance and environmental temperatures (e.g. Snyder and Weathers 1975, Klok and Chown 1997, 1998b), and this may serve as a proximal explanation both for the pattern observed in this study, and for general differences in the lability of upper and lower thermal tolerances. Indeed, Fig. 5 shows clearly that while absolute maximum temperatures differ only marginally with latitude (except at the very highest of latitudes) across the New World – latitudinally the most continuous landmass – absolute minimum temperatures vary considerably, especially in the more continental northern hemisphere (see also Gaston and Chown 1999). Fig. 3 demon-

strates similar altitudinal variation in temperature ranges across the Kwazulu-Natal transect.

Ultimately, differences in the lability of upper and lower thermal tolerances must, however, be a consequence of differences in the mechanistic bases of biochemical adaptation to heat and cold stress (see Hochachka and Somero 1984, Johnston and Bennett 1996, Storey and Storey 1996 for overviews), and environmentally mediated differences in their interactions. Mongold et al. (1996) suggested that traits important for performance of *Escherichia coli* at low temperatures are functional across the entire temperature spectrum, and that adaptation to low temperatures tended to lower both upper and lower thermal tolerance temperatures. In addition, they suggested that a different set of traits might be involved in adaptation to high temperatures. Our data certainly show that upper thermal tolerance (in this case CT_{max}) declines with an improvement in ability to tolerate low temperatures (i.e. a declining CT_{min}), but that the decline in CT_{max} is much shallower than that in CT_{min} . The asymmetric evolutionary response to low and high temperatures identified by Mongold et al. (1996) provides a potential mechanistic basis for this pattern. Such a partial decoupling of resistance to high and low temperatures, in conjunction with steep altitudinal gradients in absolute minima but more shallow gradients in absolute maxima, go some considerable way towards accounting for our finding that it is mostly changes in CT_{min} that are responsible for the broadening of climatic tolerance with elevation. However, over larger climatic gradients, such as those associated with latitude, the biochemistry of reasonably constant CT_{max} values but widely varying CT_{min} ones may be rather different. In this case, differences in tolerance may be due largely to coupled heat and cold shock responses in more tropical species, while temperate/polar species do not show so much a shock response to cold stress as an alteration in metabolism to

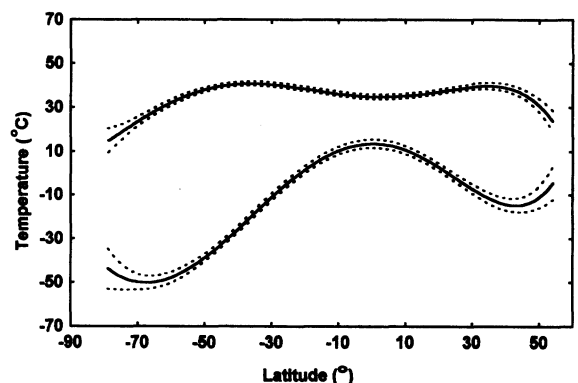


Fig. 5. Best fit polynomial regression lines ($\pm 95\%$) showing the relationship between latitude and absolute maximum (top line) and absolute minimum (bottom line) temperatures across the New World (negative latitudes are north of the equator) (data from Müller 1982).

accommodate survival under low temperature conditions (Denlinger et al. 1991, Storey and Storey 1996). Nonetheless, the whole-animal pattern remains the same: widely varying lower thermal tolerances and reasonably constant upper ones.

In this context, experimental work demonstrating that both upper and lower tolerances respond significantly to acclimation (and seasonal acclimatization) (see e.g. Huey and Berrigan 1996, Lutterschmidt and Hutchison 1997a, Klok and Chown 1998b), and that the thermal history of the population can influence later responses to temperature, often in an unpredictable fashion (Hoffmann 1995, Mongold et al. 1996, Bennett and Lenski 1997), is significant. Although the effects of acclimation (or seasonal acclimatization) have not been investigated here, we do not suspect that a full investigation of thermal tolerances (see e.g. Huey and Berrigan 1996) will significantly alter our major conclusions. However, we suggest that such work, and the broader application of the findings of experimental acclimation studies (e.g. Mongold et al. 1996, James et al. 1997), are sorely needed to provide a more rigorous test of the major physiological mechanisms that have been invoked to account for a variety of macroecological patterns (Chown and Gaston 1999).

Of course, if the pattern of climatic tolerance of species is as assumed by the climatic variability hypothesis, it does not necessarily mean that an increase in altitudinal range with increasing elevation will follow. However, although the sampling has been limited, there does appear to be an elevational increase in altitudinal range for the present dung beetle assemblage, along with an altitudinal gradient in thermal tolerance range (see Fig. 4).

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