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Addo-Bediako, A., Chown, S.L. and Gaston, K.J. (2000) Thermal tolerance, climatic variability and latitude. Proceedings of the Royal Society B: Biological Sciences, 267 (1445). pp. 739-745. ISSN 1471-2954

DOI:10.1098/rspb.2000.1065

THE ROYAL
SOCIETY

Thermal tolerance, climatic variability and latitude

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The greater latitudinal extents of occurrence of species towards higher latitudes has been attributed to the broadening of physiological tolerances with latitude as a result of increases in climatic variation. While there is some support for such patterns in climate, the physiological tolerances of species across large latitudinal gradients have seldom been assessed. Here we report findings for insects based on published upper and lower lethal temperature data. The upper thermal limits show little geographical variation. In contrast, the lower bounds of supercooling points and lower lethal temperatures do indeed decline with latitude. However, this is not the case for the upper bounds, leading to an increase in the variation in lower lethal limits with latitude. These results provide some support for the physiological tolerance assumption associated with Rapoport's rule, but highlight the need for coupled data on species tolerances and range size.

Keywords: cold hardiness; physiological tolerance; Rapoport effect; upper lethal limits

1. INTRODUCTION

Rapoport's rule, the increase in the latitudinal extents of occurrence of species towards higher latitudes, has attracted increasing interest recently (Roy *et al.* 1994, 1998; Blackburn & Gaston 1996; Rohde 1996; Fleishman *et al.* 1998; Gaston *et al.* 1998; Johnson 1998; Ruggiero & Lawton 1998; Santelices & Marquet 1998; Gaston & Chown 1999*a*). According to Stevens (1989), the mechanism largely responsible for producing this macroecological pattern is straightforward. To survive at higher latitudes individual organisms need to be able to withstand greater temporal variability in climatic conditions than at lower latitudes. In consequence, the species to which these individuals belong can attain wider latitudinal extents at higher latitudes. This climatic variability hypothesis has a distinguished history (for a review, see Gaston & Chown 1999*a*) and Stevens (1989) argued that it actually applies to the distributions of species across most environmental gradients (e.g. Stevens 1992; but see Rohde 1992; Roy *et al.* 1998).

Two assumptions are critical to the climatic variability hypothesis. It requires first that there is indeed an appropriate gradient (latitudinal, altitudinal or otherwise) in climatic variability and, second, that there is a matching cline in the physiological tolerances of species, probably most significantly in thermal tolerances (Gaston *et al.* 1998). Although there is substantial evidence in support of the former assumption (Stevens 1989, 1992; Gaston & Chown 1999*a*), the latter has seldom been assessed (Gaston *et al.* 1998; Spicer & Gaston 1999). The only study which explicitly set out to investigate both assumptions, for dung beetles on an altitudinal gradient, concluded that there was some support for both (Gaston & Chown 1999*b*). These authors also demonstrated that the variation in the thermal tolerances of the species concerned was due more to a cline in lower than upper thermal limits and argued that this may be true for latitudinal clines too (see also Lutterschmidt & Hutchinson 1997; Goto & Kimura 1998).

Despite the obvious importance of doing so, variation in the thermal tolerances of species across a large latitudinal gradient has to date been little investigated (see Scholander *et al.* (1953) for pioneering attempts and Spicer & Gaston (1999) for a further review). Clearly, a field investigation such as that undertaken by Gaston & Chown (1999*b*) could be performed on larger scales to address this problem. However, synthetic analyses of available physiological information provide an alternative first step.

Here we report the results of a synthetic, quantitative analysis of the latitudinal patterns of variation in insect cold hardiness or lower lethal temperature limits (both the lower lethal temperature (LLT) and crystallization temperature or supercooling point (SCP)) (see Block 1990; Lee & Denlinger 1991; Bale 1993; Sømme 1999) and insect upper thermal limits (both the critical thermal maxima (CT_{max}) and upper lethal temperature (ULT)) (see Lutterschmidt & Hutchison 1997) based on the published literature. We determine the extent of such variation for both the upper and lower lethal limits and whether this provides support for the physiological tolerance assumption of the climatic variability hypothesis. We also (i) determine whether the classification scheme presently used for patterns in insect cold hardiness (Block 1990; Bale 1993; Sinclair 1999; Sømme 1999) has substantial quantitative support, because the outcome of such an analysis would, to a large extent, determine the approach adopted in all subsequent analyses, (ii) examine variation in the cold hardiness strategy (freezing tolerant or intolerant, see § 2) between life stages because this determines whether all stages can be included in the broad-scale analyses of the lower lethal limits (the bulk of the upper lethal limit data are for adult insects), and (iii) determine the partitioning of variation in the LLT, SCP, CT_{max} and ULT amongst taxonomic levels, because such partitioning of physiological variation has been poorly documented in animal groups (Spicer & Gaston 1999) and again has implications for the interpretation of other results.

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Received 9 December 1999 *Accepted* 27 January 2000

2. METHODS

We chose to study the upper and lower lethal limits in insects mostly because these limits have been studied in many taxa and because the physiological principles underlying thermal tolerance have been comprehensively assessed at several levels of organization. Insect lower lethal limits have been widely investigated over the past 50 years (Sømme 1982, 1999; Block 1990; Duman *et al.* 1991; Lee & Denlinger 1991; Danks 1996; Sinclair 1999) and their physiological basis is well known (Zachariassen 1985; Storey & Storey 1996; Sømme 1999). The same is generally true of insect upper lethal limits (e.g. Vannier 1994; Lutterschmidt & Hutchison 1997), although a full appreciation of the importance of heat-shock proteins in promoting tolerance of heat stress in insects is more recent (for a review, see Feder & Hofmann 1999).

The relevant literature on insect cold hardiness, excluding a number of Russian studies which could not readily be obtained, was assessed as far back as 1900 (1928–1998), but with major emphasis placed on the last 50 years. Over 400 published papers were examined. We excluded the following studies from the analyses: (i) those dealing with insects treated with bacteria or liquid nitrogen and those where insects were pierced with the thermocouples used for the investigation, because SCPs and LLTs are altered by such treatments (Sømme 1982; Lee *et al.* 1993), and (ii) studies of insects collected in their summer activity period and those using insects from laboratory colonies. It has been shown that summer acclimatized (or acclimated) insects are generally not cold hardy (Block 1990; Lee & Denlinger 1991; Storey & Storey 1996; Sømme 1999). Following this selection a second, iterative protocol was employed. Where a species was examined more than once, either in a single paper or by different authors, the record with the lowest SCP was selected and the other records were set aside. If a species was encountered twice or more with the same SCP, then the record from the geographical location which was least represented in the database was selected. However, if different development stages had been investigated, data from each of these stages were included, but assessed in the same manner. Thus, data on 250 species belonging to 87 families and ten orders were extracted from a total of 175 published papers.

From each of these studies the following information was obtained: the SCP, LLT, geographical location, season, stage of development and whether the authors considered the insect to be freezing tolerant or freezing intolerant. Until fairly recently, most cold-hardy insects were classified as either able to tolerate freezing of water in their extracellular spaces (freezing tolerant) or as unable to do so (freezing intolerant) (Block 1990; Lee & Denlinger 1991; Storey & Storey 1996; but see Bale 1996). In those studies where the LLT was not reported, only the SCP was used. No assumption of equivalence of the SCP and LLT was made (see Bale (1993, 1996) for the rationale). For the purpose of analysis the mean SCP and/or LLT reported in a study were used because in some cases authors provided only means, while others included a measure of variation (e.g. range and standard deviation). This assumes that both the SCP and LLT show a normal distribution of values, which is a reasonable assumption for winter-acclimatized individuals (Klok & Chown 1998).

Two major methods of determining upper thermal tolerance are generally employed. For the static or ULT method the time to death at constant test temperatures is determined. The dynamic method, often known as the CT_{max}, involves increasing the test temperatures until an end-point, often the onset of spasms, is reached. Two hundred and seventy-two papers which employed either or both methods were examined (from 1900 onwards; see above). From each of these, the following information was extracted: the ULT and/or CT_{max}, geographical location, season and stage of development. Data were not used from studies where an insect was exposed to high temperatures for more than 24 h because death due to starvation or other factors could not be ruled out. Likewise, data from treatments including modified atmospheres were also discarded. An iterative protocol, similar to that described above, was then employed. Where a species was examined more than once, either in a single paper or by different authors, the record with the highest ULT or CT_{max} was selected. If a species was entered twice or more with the same ULT or CT_{max}, then the record from the geographical location which was least represented in the database was selected. Because data from adult insects predominated ($>70\%$) we excluded immature stages from the analysis (see above). Thus, data from a total of 127 published papers were used.

3. RESULTS AND DISCUSSION

Inspection of the cold-hardiness database revealed that, where cold hardiness in all or most stages of a given species had been investigated ($n = 16$, two for freezing-tolerant insects and 14 for freezing-intolerant insects), the strategy (freezing tolerant or intolerant) generally did not differ between them (94% of the species showed no difference). Thus, we did not distinguish between developmental stage in the initial assessments of the data. All stages of a given species were also included if more than one stage was investigated, because SCPs vary significantly with stage, at least in the freezing-intolerant species (SCP freezing-intolerant species ANOVA, $F_{3,204} = 30.53$ and $p < 0.00001$, SCP freezing-tolerant species ANOVA, $F_{1,129} = 0.008$ and $p > 0.9$ and LLT freezing-tolerant species ANOVA, $F_{1,98} = 0.345$ and $p > 0.5$). However, to avoid problems associated with statistical non-independence, all statistical analyses were undertaken using data for adult insects whenever data for more than one stage were available, but data for the other stages when only these were available (if both the larval and pupal values were available, only one of these was used based on the iterative protocol). This was done because the majority of the studies used concerned adult insects.

A bivariate scatter plot of the SCP and LLT, including a line of equivalence of the two (see Sinclair (1999) for the rationale), was used in conjunction with the conclusions of the authors who undertook a particular investigation, in order to determine the extent to which species could be assigned to one of the two classical cold-hardiness strategies. Freezing-intolerant species are generally well differentiated from freezing-tolerant ones (figure 1). Most species originally identified as freezing intolerant have equivalent SCPs and LLTs (figure 1). Nonetheless, within each of the categories there is clearly considerable variation, including some instances of pre-freeze mortality in freezing-intolerant species and a wide range of SCPs and LLTs in freezing-tolerant species (figure 1). Such variation has been widely discussed (Ring 1982; Bale 1993; Klok & Chown 1997; Sinclair 1999; Sømme 1999) and it encompasses that shown by a small number of species known to

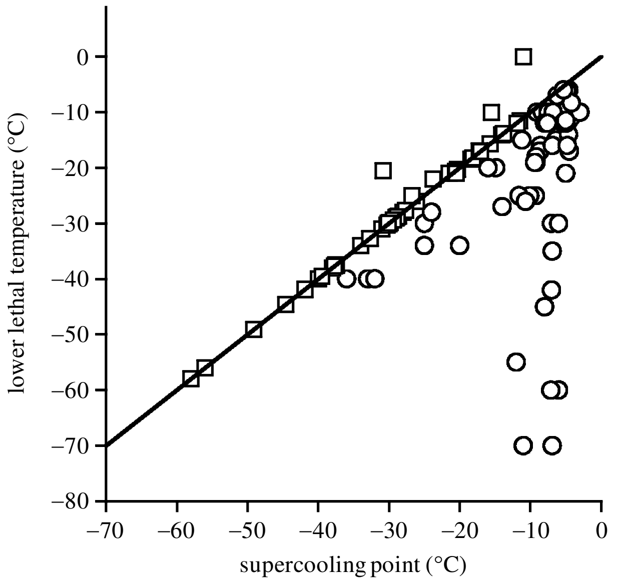

Figure 1. Plot of the LLT against the SCP of both freezing-tolerant (open circles) and freezing-intolerant (open squares) insect species. The line of equivalence is also shown.

survive only partial extracellular ice formation (e.g. Sinclair *et al.* 1999) and at least one species which is known to have switched from being freezing intolerant to freezing tolerant over a period of a year (Kukal & Duman 1989). The importance of pre-freeze mortality in insects has been discussed by a variety of authors (e.g. Knight *et al.* 1986) and forms the basis of a somewhat polemical though useful extended cold-hardiness classification (Bale 1987, 1993, 1996; Sømme 1999). Our analysis suggests that, while the classical distinction between freezing-tolerant and freezing-intolerant species may no longer be sufficient for describing the full range of variation in cold hardiness found in insects, it remains useful as a rule distinguishing the strategies generally adopted by insects because the dichotomy is well supported (Lawton 1999).

To investigate the taxonomic levels at which most variance in cold hardiness was partitioned, the SCP and LLT values for the freezing-tolerant species and SCP values for the freezing-intolerant ones (due to equivalence of the SCP and LLT) (figure 1) were separately subjected to nested analysis of variance using the Satterthwaite approximation for unequal sample sizes. Out of the ten orders investigated, two included freezing-tolerant species only (Blattodea three species examined and Neuroptera one species) and two freezing-intolerant species only (Mecoptera two species and Siphonaptera one species). Both strategies are found in the remaining six orders (Orthoptera eight species examined, Hemiptera 30 species, Coleoptera 91 species, Diptera 33 species, Lepidoptera 42 species and Hymenoptera 39 species). Therefore, the current evidence does not support the idea of a strong phylogenetic constraint with regard to the evolution of these strategies, nor does it support the notion that freezing tolerance is restricted to holometabolous insects (Block 1982, 1990). Nonetheless, within each of the strategies there is evidence of reasonably pronounced phylogenetic constraints on the evolution of the SCP and LLT.

Table 1. *Distribution of the variance in the SCP of the freezing-intolerant and freezing-tolerant insect groups and the LLT of the freezing-tolerant group*

(The tabulated values are the percentages of the total variance accounted for at each successive level. The species level includes the error term in the data.)

trait/level	species	genus	family	order
freezing-intolerant SCP	15.71	33.14**	32.47*	18.68*
freezing-tolerant SCP	1.85	44.12**	40.85**	13.18
freezing-tolerant LLT	32.81	0.06	46.87**	20.26

$^{*}p < 0.05$, $^{**}p < 0.001$.

Table 2. *Distribution of the variance in the* CT_{max} *and ULT*

(The tabulated values are the percentages of the total variance accounted for at each successive level. The species level includes the error term in the data.)

trait/level	species	genus	family	order
CT_{max}	25.86	57.72**	12.62	3.80
ULT	22.78	29.89**	46.61**	0.72

$^{*}p < 0.05$, $^{**}p < 0.001$.

In both the freezing-tolerant and freezing-intolerant groups, the bulk of the variance in the SCP was partitioned equally between families and between genera, with somewhat less between orders and the least between species (table 1). Likewise, for the LLT of the freezing-tolerant species the bulk of the variance was partitioned between families, but in this case a considerably greater proportion of the variance was partitioned between species and much less between genera (table 1). Variance partitioning in the ULTs was examined using the same methods. CT_{max} data were available for six orders and 24 families and ULT data for 11 orders and 37 families. Within each of the data sets, there is evidence of a phylogenetic constraint similar to that found for cold hardiness. For both the CT_{max} and ULT the bulk of the variance was partitioned either at the family or generic level, with less between species and the least between orders (table 2). These findings are not unusual for many life-history variables (Read & Harvey 1989; Harvey & Pagel 1991), although taxonomic variation in physiological traits is less well understood (Chown *et al.* 1999; Spicer & Gaston 1999).

The variation in the SCP in both freezing-intolerant and freezing-tolerant species and the LLT in the latter also has a clear geographical component (figure 2*a*,*b*). In the northern hemisphere, for which most data are available, the minimum SCP recorded declines with latitude and a similar though less well-defined pattern is clear for the LLT. The low values recorded in the temperate to tropical regions are generally representative of studies undertaken at high altitude. Indeed, if the localities at which these studies were undertaken are corrected to sea level using a 4° increase in latitude for every 305 m increase in elevation (Price *et al.* 1998), then it is clear that few studies have been undertaken in the warm tropics (figure 2*c*). Whether these effects of altitude are

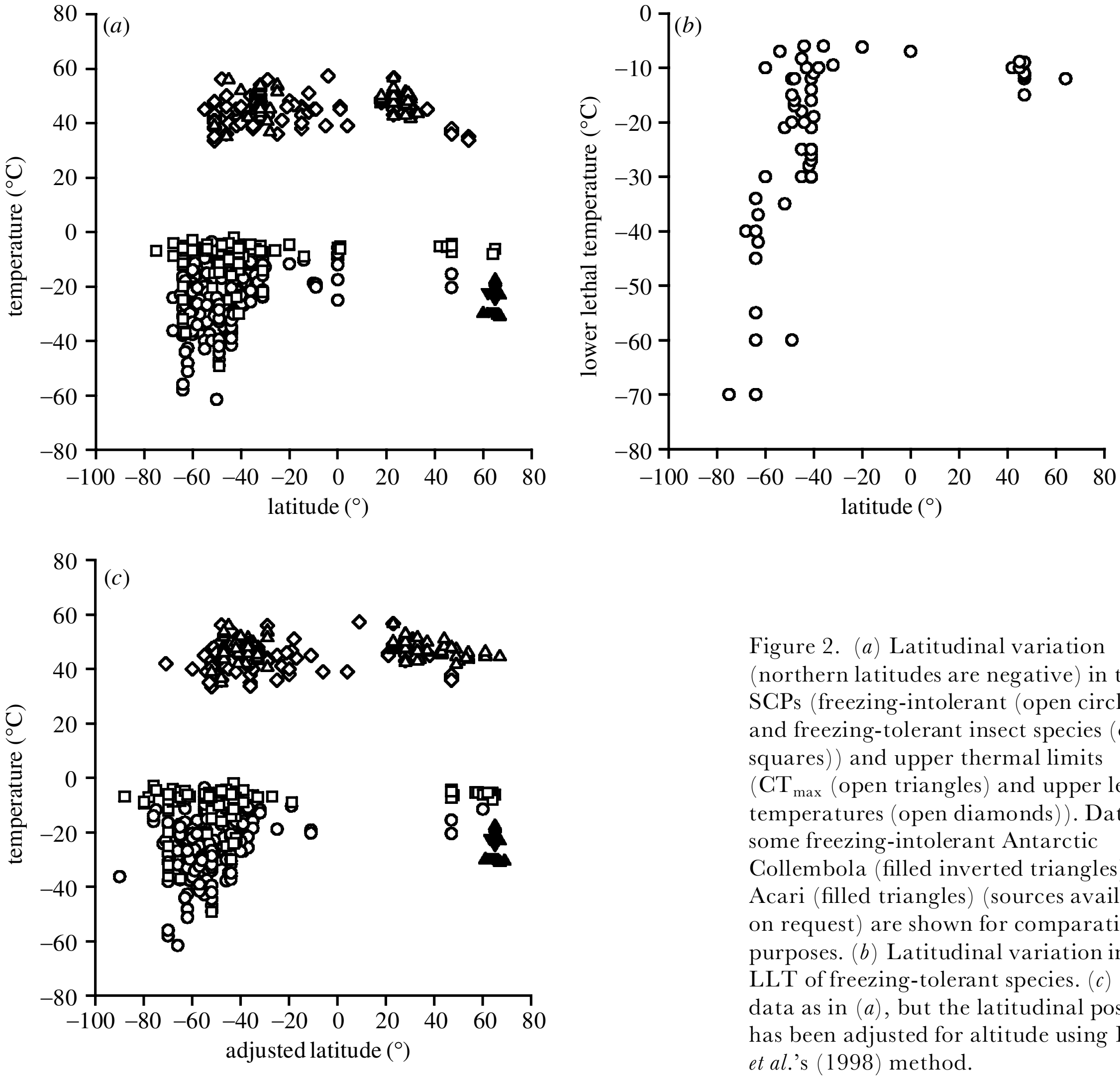

Figure 2. (*a*) Latitudinal variation (northern latitudes are negative) in the SCPs (freezing-intolerant (open circles) and freezing-tolerant insect species (open squares)) and upper thermal limits (CT_{max} (open triangles) and upper lethal temperatures (open diamonds)). Data for some freezing-intolerant Antarctic Collembola (filled inverted triangles) and Acari (filled triangles) (sources available on request) are shown for comparative purposes. (*b*) Latitudinal variation in the LLT of freezing-tolerant species. (*c*) Same data as in (*a*), but the latitudinal position has been adjusted for altitude using Price *et al.*'s (1998) method.

included or ignored makes little difference to the outcome, that is the SCP and LLT tend to increase towards the equator. This latitudinal decline in the SCP remains even when the data are resampled to nine data values per 10° latitudinal bin above 30° N, to take account of the limited SCP data for species from the tropics (figure 3).

Although there were consistent differences between the ULT (mean ± s.e. 44.4 ± 0.34 °C) and CT_{max} (47.4 ± 0.36 °C) ($F_{1,232} = 26.57$ and $p < 0.0001$), the variation in the upper thermal tolerance shows little geographical variation. Indeed, although there appears to be some decline in the ULT at higher latitudes in the Southern Hemisphere, the general trend is towards similar high temperature tolerances across the globe (figure 2*a*), even when the data are adjusted for altitude (figure 2*c*).

These findings provide support for previous conclusions regarding latitudinal variation in insect cold hardiness which were based on limited interspecific (Kukal *et al.* 1991; Kimura *et al.* 1994; Goto & Kimura 1998) and intraspecific comparisons (Kukal & Duman 1989; Heinze *et al.* 1998). They are likewise supportive of the idea that the upper thermal limits show considerably less geographical variation than do the lower ones (Vannier 1994; Lutterschmidt & Hutchison 1997; Goto & Kimura 1998; Gaston & Chown 1999*b*). Thus, there is substantial evidence in favour of the physiological tolerance assumption of the climatic variability hypothesis (Stevens 1989; Gaston *et al.* 1998).

Indeed, a comparison of the absolute maximum and minimum temperatures reported for the New World (figure 4) with the lower bound of the SCP and LLT plots (figure 2) and the upper bound of the ULT plots indicates a close correspondence between the two. However, the decline in the SCP and, to some extent, the LLT is not shown by all species. Rather, the SCP and LLT variation tends to increase with latitude using both the original data (figure 2) (for freezing-intolerant species, standard deviation of the SCP and latitude using 10° latitudinal bins, $r_s = 0.9$ and $p < 0.05$) and the SCP values resampled ten times to nine (all data) data points per 10° latitudinal bin in the Northern Hemisphere (figure 3) (standard deviation of the SCP and latitude using 10° latitudinal bins, mean $r_s = 0.9$, $p < 0.05$ and $n = 9$ per bin). For five data points (freezing-intolerant species only) the relationship is in the same direction, but is not significant (mean $r_s = 0.7$, $p = 0.2$ and $n = 5$ per bin), largely as a consequence of small sample sizes.

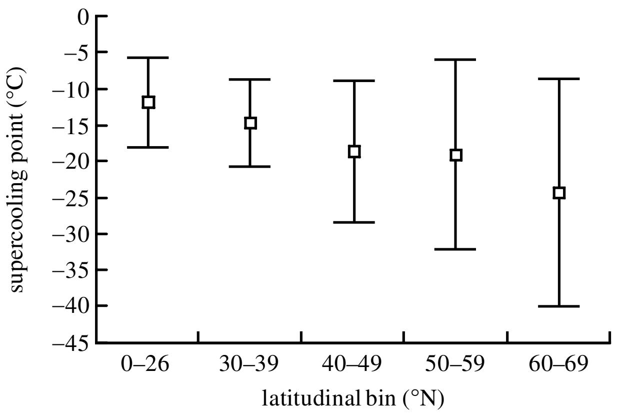

Figure 3. Mean ± s.d. of the SCP for each of five 10° latitudinal bins in the Northern Hemisphere after the original SCP data were resampled to nine data values per 10° bin ten times (SCP and latitudinal bin, mean $r_s = -0.91$, $p < 0.05$ and $n = 9$ per bin). The relationship is in the same direction but not significant if the resampling is based on freezing-intolerant species only (mean $r_s = -0.8$, $p = 0.12$ and $n = 5$ per bin).

A variety of mechanisms could potentially account for this pattern. First, variation in the protocols adopted by researchers will undoubtedly have affected the outcomes of their experiments. Generally, more rapid experimental cooling rates tend to lower insect survival and elevate SCPs (e.g. Kelty & Lee 1999). However, the extent of this variation is considerably less than that documented here. A second, partially artefactual mechanism could be latitudinal variation in researcher effort. The number of studies performed and, hence, the number of taxonomic groups assessed tends to increase with latitude. Hence, the variation in the SCP and LLT should increase because much of it is partitioned at higher taxonomic levels. Although this is the case for the SCP of freezing-intolerant species (for 10° latitude bins there is a positive relationship between the mean latitude and mean number of families examined; $r_s = 0.793$ and $p = 0.033$), such a relationship is not present in the freezing-tolerant species ($p > 0.11$). In addition, this mechanism cannot account for the fact that some insects with apparently high SCPs and LLTs can survive the apparently low temperatures recorded at high latitudes. Rather, the increase in variation with latitude suggests that the variety of temperatures and situations either promoting or reducing the risks of low temperature injury encountered by insects (see Bale 1987) must increase with latitude. For example, at those latitudes where there is a significant accumulation of snow, species overwintering in subnival habitats are likely to encounter less extreme temperatures than those in more exposed habitats (Danks 1996). Finally, some of this variation may be due to the length of time an insect is likely to encounter subzero temperatures and the conditions leading to inoculative freezing, factors which have a pronounced effect on insect cold hardiness (Sømme 1996, 1999; Storey & Storey 1996), but which were not explicitly controlled for in this study. Pronounced low temperature tolerance may develop in response to chronic exposure to moderately low temperatures, rather than as a response to an acute bout of extremely low temperature.

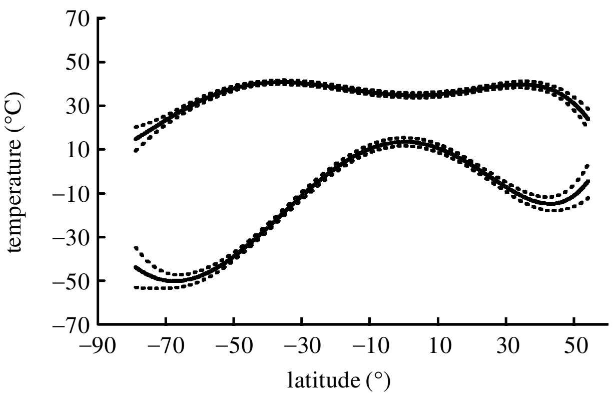

Figure 4. Best fit polynomial regression lines (± 95%) showing the relationship between latitude and the absolute maximum (top line) and absolute minimum (bottom line) temperatures across the New World (negative latitudes are north of the equator) (data from Müller (1982), redrawn from Gaston & Chown (1999*b*)).

Nonetheless, the general pattern of upper and lower temperature tolerances is supportive of the physiological tolerance assumption and particularly so in the Northern Hemisphere above *ca.* 20–30° N. The latter finding provides additional, strong evidence for the physiological tolerance assumption because it is in this region that the Rapoport effect is most evident and consistent across taxa (Rohde 1996; Gaston *et al.* 1998; Gaston & Chown 1999*a*).

An additional pattern which emerged from the analysis of geographical variation in the SCP and LLT was north–south asymmetry in this variation, even when data for freezing-intolerant Antarctic mites and collembolans were included because of the almost complete absence of insects from this continent (figure 2). This variation also clearly paralleled the north–south variation in absolute minimum temperatures (figure 4), which in turn is undoubtedly a consequence of the vast extent of the southern oceans and the large area covered by the northern land masses (Klok & Chown 1997; Gaston & Chown 1999*a*,*b*). It has also been suggested that the generally oceanic nature of the Southern Hemisphere may promote the evolution of freezing tolerance because of the enhanced potential for inoculative freezing in moist habitats (Klok & Chown 1997). The current analysis certainly bears out this suggestion, but the paucity of the data for the Southern Hemisphere leaves some doubt as to its generality. Nonetheless, north–south asymmetry in LLTs and cold-hardiness strategy is an important macrophysiological pattern which seems to vary in a way similar to temperature. The latter may well account for the general lack of a Rapoport effect in vertebrates and plants in the Southern Hemisphere (Gaston & Chown 1999*a*) and its effect on insect cold hardiness might well be expected to result in a similar effect.

Whilst ignoring a variety of factors known to affect the lower and upper lethal temperature limits, this assessment of geographical variation in insect thermal tolerances reveals several important patterns. First, despite many statements that tropical insects cannot tolerate low temperatures, the data are largely lacking. Second, freezing tolerance appears to predominate in the Southern Hemisphere, but here too data are scarce.

Third, the upper lethal limits show much less variation than do the lower lethal limits. Finally and most significantly, there is considerable though qualified support for the physiological tolerance assumption of the climatic variability hypothesis proposed to account for Rapoport's rule, particularly above 20–30° N. Indeed, the substantial variation found in insect lower lethal temperatures within latitudinal bands suggests that, while physiological tolerances in some species vary in the direction predicted by this assumption, others do not. Stevens (1989) implied that the physiological tolerance assumption might not apply to insects which effectively escape the extremes of climate in the overwintering stage. To some extent this does appear to be the case. However, the more crucial question is whether this variation in physiological tolerance translates to variation in range size. To date few studies have systematically examined geographical variation in insect latitudinal extents and the few that have did not usually include any information on physiological tolerances.

We thank Brent Sinclair for a pre-print of his now published work and Melodie McGeoch, Jaco Klok and two anonymous referees for useful comments on an earlier draft of the manuscript. A.A.B. and S.L.C are supported by the South African National Research Foundation and the University of Pretoria. K.J.G. is a Royal Society university research fellow.

REFERENCES

Bale, J. S. 1987 Insect cold hardiness: freezing and supercooling—an ecophysiological perspective. *J. Insect Physiol.* **33**, 899–908.

Bale, J. S. 1993 Classes of insect cold hardiness. *Funct. Ecol.* **7**, 751–753.

Bale, J. S. 1996 Insect cold hardiness: a matter of life and death. *Eur. J. Entomol.* **93**, 369–382.

Blackburn, T. M. & Gaston, K. J. 1996 Spatial patterns in the geographic range sizes of bird species in the New World. *Phil. Trans. R. Soc. Lond.* B **351**, 897–912.

Block, W. 1982 Cold hardiness in invertebrate poikilotherms. *Comp. Biochem. Physiol.* A **73**, 581–592.

Block, W. 1990 Cold tolerance of insects and other arthropods. *Phil. Trans. R. Soc. Lond.* B **326**, 613–633.

Chown, S. L., Le Lagadec, M. D. & Scholtz, C. H. 1999 Partitioning variance in a physiological trait: desiccation resistance in keratin beetles (Coleoptera, Trogidae). *Funct. Ecol.* **13**, 838–844.

Danks, H. V. 1996 The wider integration of studies on cold hardiness. *Eur. J. Entomol.* **93**, 383–403.

Duman, J. G., Wu, D. W., Xu, L., Tursman, D. & Olsen, T. M. 1991 Adaptations of insects to subzero temperatures. *Q. Rev. Biol.* **66**, 387–410.

Feder, M. E. & Hofmann, G. E. 1999 Heat-shock proteins, molecular chaperones, and the stress response—evolutionary and ecological physiology. *A. Rev. Physiol.* **61**, 243–282.

Fleishman, E., Austin, G. T. & Weiss, A. D. 1998 An empirical test of Rapoport's rule: elevational gradients in montane butterfly communities. *Ecology* **79**, 2482–2493.

Gaston, K. J. & Chown, S. L. 1999*a* Why Rapoport's rule does not generalise. *Oikos* **84**, 309–312.

Gaston, K. J. & Chown, S. L. 1999*b* Elevation and climatic tolerance: a test using dung beetles. *Oikos* **86**, 584–590.

Gaston, K. J., Blackburn, T. M. & Spicer, J. I. 1998 Rapoport's rule: time for an epitaph? *Trends Ecol. Evol.* **13**, 70–74.

Goto, S. G. & Kimura, M. T. 1998 Heat- and cold-shock responses and temperature adaptations in subtropical and temperate species of *Drosophila*. *J. Insect Physiol.* **44**, 1233–1239.

Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology.* Oxford University Press.

Heinze, J., Foitzik, S., Kipyatkov, V. E. & Lopatina, E. B. 1998 Latitudinal variation in cold hardiness and body size in the arboreal ant species, *Leptothorax acervorum* (Hymenoptera: Formicidae). *Entomol. Gener.* **22**, 305–312.

Johnson, C. N. 1998 Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. *J. Anim. Ecol.* **67**, 689–698.

Kelty, J. D. & Lee, R. E. 1999 Induction of rapid cold hardening by cooling at ecologically relevant rates in *Drosophila melanogaster*. *J. Insect Physiol.* **45**, 719–726.

Kimura, M. T., Ohtsu, T., Yoshida, T., Awasaki, T. & Lin, F.-J. 1994 Climatic adaptations and distributions in the *Drosophila takahashii* species subgroup (Diptera: Drosophilidae). *J. Nat. Hist.* **28**, 401–409.

Klok, C. J. & Chown, S. L. 1997 Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic caterpillar, *Pringleophaga marioni* (Lepidoptera: Tineidae). *J. Insect Physiol.* **43**, 685–694.

Klok, C. J. & Chown, S. L. 1998 Interactions between desiccation resistance, host-plant contact and the thermal biology of a leaf-dwelling sub-Antarctic caterpillar, *Embryonopsis halticella* (Lepidoptera: Yponomeutidae). *J. Insect Physiol.* **44**, 615–628.

Knight, J. D., Bale, J. S., Franks, F., Mathias, S. F. & Baust, J. G. 1986 Insect cold hardiness: supercooling points and prefreeze mortality. *Cryoletters* **7**, 194–203.

Kukal, O. & Duman, J. G. 1989 Switch in overwintering strategy of two insect species and latitudinal differences in cold hardiness. *Can. J. Zool.* **67**, 825–827.

Kukal, O., Ayres, M. P. & Scriber, J. M. 1991 Cold tolerance in relation to the distribution of swallowtail butterflies. *Can. J. Zool.* **69**, 3028–3037.

Lawton, J. H. 1999 Are there general laws in ecology? *Oikos* **84**, 177–192.

Lee, R. E. & Delinger, D. L. 1991 *Insects at low temperature*. New York: Chapman & Hall.

Lee, R. E., Lee, M. R. & Strong-Gunderson, J. M. 1993 Insect cold hardiness and ice nucleating active microorganisms including their potential use for biological control. *J. Insect Physiol.* **39**, 1–12.

Lutterschmidt, W. I. & Hutchison, V. H. 1997 The critical thermal maximum: history and critique. *Can. J. Zool.* **75**, 1561–1574.

Müller, M. J. 1982 *Selected climatic data for a global set of standard stations for vegetation science.* The Hague, The Netherlands: Junk.

Price, P. W., Fernandes, G. W., Lara, A. C. F. & Brawn, J. 1998 Global patterns in local number of insect galling species. *J. Biogeogr.* **25**, 581–591.

Read, A. F. & Harvey, P. H. 1989 Life history differences among the eutherian radiations. *J. Zool. Lond.* **219**, 329–353.

Ring, R. A. 1982 Freezing tolerant insects with low supercooling points. *Comp. Biochem. Physiol.* A **73**, 605–612.

Rohde, K. 1992 Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527.

Rohde, K. 1996 Rapoport's rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. *Biodiv. Lett.* **3**, 10–13.

Roy, K., Jablonski, D. & Valentine, J. W. 1994 Eastern Pacific molluscan provinces and latitudinal diversity gradient: no evidence for 'Rapoport's rule'. *Proc. Natl Acad. Sci. USA* **91**, 8871–8874.

Roy, K., Jablonski, D., Valentine, J. W. & Rosenberg, G. 1998 Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl Acad. Sci. USA* **95**, 3699–3702.

Ruggiero, A. & Lawton, J. H. 1998 Are there latitudinal and altitudinal Rapoport effects in the geographic ranges of Andean passerine birds? *Biol. J. Linn. Soc.* **63**, 283–304.

Santelices, B. & Marquet, P. A. 1998 Seaweeds, latitudinal diversity patterns, and Rapoport's rule. *Divers. Distrib.* **4**, 71–75.

Scholander, P. F., Flagg, W., Walters, V. & Irving, L. 1953 Climatic adaptation in Arctic and tropical poikiliotherms. *Physiol. Zool.* **26**, 67–92.

Sinclair, B. J. 1999 Insect cold tolerance: how many kinds of frozen? *Eur. J. Entomol.* **96**, 157–164.

Sinclair, B. J., Worland, M. R. & Wharton, D. A. 1999 Ice nucleation and freezing tolerance in New Zealand alpine and lowland weta, *Hemideina* spp. (Orthoptera: Stenopelmatidae). *Physiol. Entomol.* **24**, 56–63.

Sømme, L. 1982 Supercooling and winter survival in terrestrial arthropods. *Comp. Biochem. Physiol.* A **73**, 519–543.

Sømme, L. 1996 The effect of prolonged exposures at low temperatures in insects. *Cryoletters* **17**, 341–346.

Sømme, L. 1999 The physiology of cold hardiness in terrestrial arthropods. *Eur. J. Entomol.* **96**, 1–10.

Spicer, J. I. & Gaston, K. J. 1999 *Physiological diversity and its ecological implications.* Oxford, UK: Blackwell Science.

Stevens, G. C. 1989 The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.* **133**, 240–256.

Stevens, G. C. 1992 The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *Am. Nat.* **140**, 893–911.

Storey, K. B. & Storey, J. M. 1996 Natural freezing survival in animals. *A. Rev. Ecol. Syst.* **27**, 365–386.

Vannier, G. 1994 The thermobiological limits of some freezing intolerant insects: the supercooling and thermostupor points. *Acta Oecol.* **15**, 31–42.

Zachariassen, K. E. 1985 Physiology of cold tolerance in insects. *Physiol. Rev.* **65**, 799–832.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.