

Relationship between the minimum and maximum temperature thresholds for development in insects

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Summary

1. The objective of this study was to test the theoretical prediction that the thermal tolerance range for development in insects should be about 20 °C.
2. The data on the thermal requirements for development of 66 species from eight orders of insects was obtained from the literature. The temperatures at which the developmental rates are at their minimum and maximum was obtained for each population by defining the relationship between developmental rate ($1/D$) and temperature, using either Lactin *et al.*'s (1995) or Briere *et al.*'s (1999) model.
3. Thermal windows, i.e. the range in temperature between the minimum and maximum rate of development for individual species, and the relationship between the minimum and maximum temperatures, were examined.
4. The mean thermal window, 19.8 °C with 95% confidence interval 19.1–20.5 and range 13.3–28.6, was influenced by species phylogeny, with the windows narrower for species having a true pupal stage, but not by ecological traits thought to affect species thermal requirements. The relationship between the minimum and maximum temperatures was highly significant and independent of species phylogeny.
5. Theory and this analysis of empirical data indicate that each species of insect can only develop over a limited range of temperatures independent of species traits. In addition, the relationship between the minimum and maximum developmental rates co-vary independent of species phylogeny. This may help identify the precise nature of the physiological mechanism underlying the seasonal development and distribution of insects, and possibly other ectotherms.

Key-words: distribution, insects, thermal requirements for development, thermal window, thermal tolerance range, ectotherms

Introduction

The effect of temperature on the development and growth of ectotherms has been well studied. Nearly three hundred years ago Réaumur (1735, 1736) recognized that organisms cannot develop below certain temperatures and the temperature sum required to complete development is fairly constant – now commonly referred to as degree days. Nearly one hundred years ago Bodenheimer (1927) reported that a northern and a southern species of grain weevil differed in their performance

at high and low temperatures, with the northern species doing better at low temperatures than the southern species and *vice versa* at high temperatures. More recently, many studies have furthered our understanding of the physiological and evolutionary responses of organisms to their thermal environment. Species inhabiting extreme low and high temperature environments must either be able to tolerate or avoid these conditions to survive. The ways in which they avoid the effects of extreme conditions are well documented (see reviews of Bale 2002; Hodkinson 2005). However, little is known about those species that can tolerate these temperatures, like the thermophiles that develop and reproduce at temperatures of

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113 °C around the ‘black smoker’ chimneys on the Mid Atlantic ridge (Blöchl *et al.* 1997). More is known about the thermal requirements of the species that live in the temperate, subtropical and tropical regions. How each species has adapted to particular thermal conditions is of considerable interest and relevant to discussions on the effect of global warming on the distribution and abundance of ectotherms.

It is well established that there is a range of temperatures over which each species can grow and reproduce, its thermal window (van der Have 2002; Jarošík, Honek & Dixon 2002; Jarošík *et al.* 2004). However, it is unknown whether the width of thermal windows is constrained or variable, and if variable whether the width is related to specific life-history or environmental variables. Theoretical studies (Charnov & Gillooly 2003; Gillooly *et al.* 2002) suggest that the width of the thermal window for each species should be about 20 °C. As this prediction is based on a thermodynamic model of development in ectotherms then the mechanism is more likely to be physiological than ecological, and might be independent of phylogenetic relationships. Biological studies have tended to focus on whether ‘warmer is better’ and a trade-off between maximum performance and breadth of performance, using several different measures of performance (Huey & Hertz 1984; Huey & Kingsolver 1989, 1993; Frazier *et al.* 2006). These studies and the general literature appear to favour a variable rather than a constrained thermal window. The conflict between the theoretical prediction of a constrained thermal window and the view that the breadths of thermal windows should evolve in response to an organism’s environment needs to be resolved. For this, a large data set on performance over a range of temperatures of a group of organisms is required. Preferably the performance measure should indicate the organism is tolerating the conditions. One such measure is the rate development, for which there are a lot of data for insects, an ideal group for testing whether the thermal window is constrained or variable.

The objective of this study is to determine whether in insects the difference between the temperatures when development proceeds at the minimum and maximum rates is about 20 °C, whether the width of the thermal window can be modified by environmental and biological traits and species phylogeny, and whether the relationship between the minimum and maximum developmental rate temperatures is dependent on species relatedness.

Material and Methods

In ectothermic organisms, development rate increases with temperature following a sigmoidal curve when measured over the ecologically relevant range of temperatures (e.g. Wagner *et al.* 1984; Wagner, Olson & Willers 1991). A surrogate value for the lower developmental threshold, which has been widely adopted, is to use the value obtained by extrapolating the linear portion of the relationship between rate of development and temperature back to intercept the *x*-axis. This virtual value is referred to in the literature as LDT or basal temperature (t_b) (e.g. Jarošík, Honek & Dixon 2002; Trudgill, Honek & Van Straalen 2005). At the higher temperatures the slope of the curve decreases, reaches a maximum and then decreases. The point of the

maximum development rate is referred to as the optimum temperature (t_o) (Trudgill, Honek & Van Straalen 2005) or maximum temperature ($t_{d\max}$) (Birkemoe & Leinaas 2000). Although at temperatures greater than that at which the maximum development rate is recorded some individuals can still develop they take longer to reach maturity and many die. That is, the thermal window can be defined in terms of the temperatures at which the minimum and maximum developmental rates occur. We favour the use of $t_{d\max}$ over t_o because optimum implies this temperature is the most favourable for the organism concerned. However, in nature organisms are subject to fluctuations in temperature and are unlikely to be adapted to doing best at one particular temperature, but to optimize their performance over the range of temperatures they most frequently experience in the field. For the same reasons and conformity, we prefer $t_{d\min}$ to t_b .

Several models are proposed, which describe the nonlinear relationship between developmental rate and temperature (e.g. Stinner, Gutierrez & Butler 1974; Logan *et al.* 1976; Sharpe & De Michele 1977; Schoolfield, Sharpe & Magnuson 1981; Harcourt & Yee 1982). Nevertheless, only two, relatively recent models (Lactin *et al.* 1995, their eqn 1; Briere *et al.* 1999, their modified 2nd model) are biologically realistic and simple, and enable a simultaneous fitting of a nonlinear developmental response to temperature and assessment of the value of $t_{d\min}$. These models are used in this study to determine $t_{d\min}$ and $t_{d\max}$ and the width of the thermal window, the difference between these two values.

The data on the thermal requirements for development of insects used in this study mainly comes from papers published by Alois Honek and his colleagues (Honek & Kocourek 1990; Honek 1996a; Jarošík, Honek & Dixon 2002; Jarošík & Honek 2007). Developmental times for at least four different constant temperatures (°C) were obtained mainly from this literature for 74 non-dormant (i.e. not in diapause) populations of sixty-six species, belonging to eight orders of insects. To avoid pseudo-replication of the species for which the studies were done on different morphs or genetic strains, or in different atmospheric conditions or on different host plant cultivars, the values of the temperatures for the minimum and maximum developmental rates for the morphs, strains, atmospheric conditions or cultivars were calculated separately for each population of these species, and to obtain one independent data point for each species, the average value for these populations then established. The averages for these species were not calculated directly by first pooling the results for all their populations, because temperature dependent responses usually differed among the populations of each of these species. The species analysed and their estimated lower and upper temperatures for development are listed (before calculating average $t_{d\min}$ and $t_{d\max}$ for those species for which several populations were analyzed) in Appendix S1 in Supplementary Material.

With a few exceptions, for which only data for one developmental stage (egg, larva or pupa) or part of the total development (e.g. larva + pupa) are available, the total pre-imaginal development (egg to adult) for each population of a species was analysed. In those cases where data is available for more than one stage but the developmental time for these stages could not be pooled (usually, data available for egg and pupa, but not for larva), the developmental stages were analyzed separately, but only the result for the stage giving the better overall fit was chosen for analysis. This selection was based on a comparison of the residual sums of squares, total explained variance (r^2) and an inspection of fitted plots of the models. That data for total development is not available for all species should not bias these analyses, as all the developmental stages of an ectotherm species have the same lower developmental threshold (Jarošík, Honek & Dixon 2002; Jarošík *et al.* 2004).

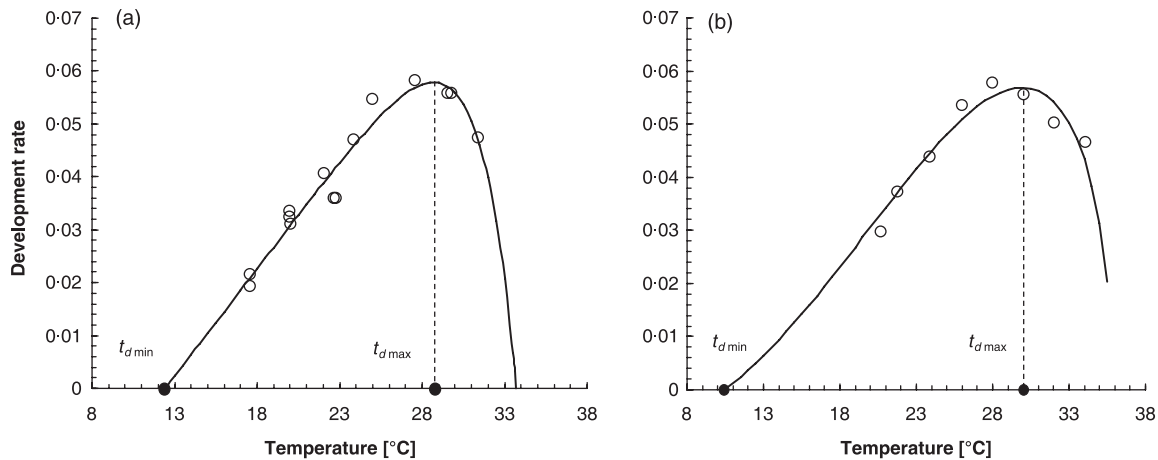


Fig. 1. Least-square nonlinear Levenberg-Marquardt iterative regression fit (a) of Lactin *et al.*'s model (eqn 2) to results for *Bemisia tabaci*, biotype 'B' reared on 'DES119' cotton (Wagner 1995), parameters in Appendix S2, and (b) of Brière *et al.*'s model (eqn 1) to results for *B. tabaci*, biotype 'B' reared on 'Pima S-6' cotton (Wagner 1995), parameters in Appendix S3. Values of $t_{d\max}$, calculated analytically (eqn 4 for Lactin *et al.*'s model A, eqn 3 for Brière *et al.*'s model B) and $t_{d\min}$, assessed as the intersections of the fitted curves with abscissa, are shown. Thermal window is the difference between the $t_{d\max}$ and $t_{d\min}$ values.

To establish the minimum and maximum temperature for development of each population, the relationship between the developmental rates and temperature, with the rate expressed as the reciprocal values of the developmental times in days ($1/d$), was defined using the Lactin *et al.*'s (1995) or Brière *et al.*'s (1999) model. Brière *et al.*'s model for the rate of development, r , which is a positive function of temperature, T ($^{\circ}\text{C}$), needs only three parameters:

$$r(T) = aT(T - T_0)\sqrt{T_L - T} \quad \text{eqn 1}$$

where a is an empirical constant, T_0 is the lower temperature developmental threshold, i.e. $t_{d\min}$, and T_L lethal temperature. On the other hand, Lactin *et al.*'s model needs four parameters:

$$r(T) = e^{\rho T} - e^{[\rho T_{\max} - (T_{\max} - T)/\Delta]} + \lambda \quad \text{eqn 2}$$

where ρ is the maximum developmental rate at $t_{d\max}$, T_{\max} lethal temperature (T_L in Brière *et al.*'s model above), Δ is the width of the high temperature boundary layer (the width of the high temperature decline in developmental rate, over which thermal breakdown becomes the overriding influence), and λ is the intersection of the fitted model curve with abscissa at the lower temperatures, which is used to estimate the minimum temperature for development $t_{d\min}$.

As a consequence of the difference in the number of parameters, to have at least one degree of freedom for the parameter estimates of a fitted model all the populations for which data for only four constant temperatures were available were fitted by Brière *et al.*'s three-parameter model. For the remaining populations, Lactin *et al.*'s model was preferred, because this model gives a better overall fit than that of Brière *et al.* (Kontodimas *et al.* 2004). Both the models were fitted using the least-square nonlinear Levenberg-Marquardt iterative regression method in Statistica 6.0 for Windows (StatSoft, Tulsa), with convergence criterion set to 0.00001. Values for the maximum temperatures for development were calculated analytically from the fitted models; for Brière *et al.*'s model as:

$$t_{d\max} = \frac{2mT_L + (m+1)T_0 + \sqrt{4m^2T_L^2 + (m+1)^2T_0^2 - 4m^2T_0T_L}}{4m+2} \quad \text{eqn 3}$$

for $m = 2$ (Brière *et al.* 1999), and for Lactin *et al.*'s model as:

$$t_{d\max} = \frac{(\rho - 1/\Delta)T_{\max} - \ln(\rho\Delta)}{\rho - 1/\Delta} \quad \text{eqn 4}$$

(Appendix S2). Values of the minimum temperatures for development, $t_{d\min}$, were estimated as the intersections of the fitted curves with abscissa (Fig. 1), but can be also solved numerically, as described in Appendix S2. Parameters of the fitted models are available in Appendices S3 (Lactin *et al.*'s model) and S4 (Brière *et al.*'s model).

The widths of the thermal windows, the differences between $t_{d\max}$ and $t_{d\min}$ for individual species (Fig. 1), were calculated, their distribution presented in a frequency histogram, and the mean value with 95% confidence interval (CI) determined. To reveal how the thermal windows are influenced by species phylogeny and ecological traits, the variation in thermal windows was partitioned into phylogenetic and non-phylogenetic components. First, for all 66 species, a patristic distance matrix (i.e. the sum of branch lengths on a path between a pair of taxa) was derived from the tree of life web site <http://tolweb.org/tree/phylogeny.html> [except for Diptera, for which phylogenetic relationships were extracted from Yeates & Wiegmann (1999), Sæther (2000) and Yeates (2002)], considering each branch length to be equal to one unit (e.g. Prinzing *et al.* 2002). A principal coordinate analysis was then performed on this matrix, using the function *cmdscale* in R Package version 2.3.1 (R Development Core Team 2008). Each principal coordinate (called PC hereafter) of the matrix represents the relative amount of phylogenetic variance, which is proportional to the associated eigenvalue (Diniz-Filho, De Sant'ana & Bini 1998). The PCs were listed in decreasing order of explained variance, from PC1 to PC65. Their order describes decreasing phylogenetic scales, but do not distinguish the exact hierarchical contribution of the individual PCs to the phylogeny.

We then incorporated phylogenetic information encompassed in the PCs into the statistical analysis that simultaneously included ecological traits, following Desdevides *et al.* (2003; Appendix S5). The included ecological traits were as follows: (i) species dry body mass in mg (ln transformed), calculated as mass = (body length)^{2.62} (Rogers, Hinds & Buschbom 1976), (ii) latitude ($^{\circ}\text{N}$ or $^{\circ}\text{S}$) from which the experimental populations originated (a surrogate for the effect of climate; Honek 1996a) and (iii) food specialization according to

Honek (1999) the following: (a) predators, which feed on living animals, i.e. true predators and parasitoids; (b) herbivores, which feed on living plants, i.e. grazers and sap feeders; and (c) 'seed eaters', feeding on dry seeds and dead plant and animal remains, represented mostly by store product pests (Appendix S1). All these traits and latitude are known to affect a species lower developmental threshold and sum of effective temperatures (Honek 1996a,b, 1999; Honek & Kocourek 1990). Body mass (Honek 1996b, 1999) and food specialization (Honek 1999) are known to affect the thermal requirements of insect orders differently, and the effect of food specialization to interact with temperature data for the locations from which the tested species originated (Honek 1996a).

Incorporation of these traits enabled the partitioning of the variance in thermal windows into a part strictly due to: (i) ecological traits (i.e. body size, climate and food), (ii) phylogeny, (iii) joint influence of phylogenetic and ecological traits (i.e. phylogenetically structured variation of ecological traits) and (iv) unexplained variation (see Appendix S5 for details).

The relationship between $t_{d\max}$ and $t_{d\min}$ for individual species was examined by regressing $t_{d\max}$ on $t_{d\min}$. Because $t_{d\max}$ and $t_{d\min}$ were both estimated with error, and on the same scale ($^{\circ}\text{C}$), major axis (MA = model II) was used instead of least square (LS = model I) regression (Sokal & Rohlf 1995); however, for comparison and generality, a LS regression and its statistics (equation, F, df, and explained variance r^2) were also calculated. For MA the regression slope, which is always greater than the LS slope, and its 95% confidence intervals (CI) were calculated, following the method of Sokal & Rohlf (1995, pp. 586–593). After the analysis of the original data, the same analysis was repeated with the variation due to phylogenetic relatedness removed, in which independent contrasts (Felsenstein 1985) for incompletely resolved phylogenies (Harvey & Pagel 1991) were used on the same phylogeny as for the thermal windows. If the slope of the regression for the independent contrasts, forced through the origin, remains significant, it is evidence that the evolutionary independent comparisons yield the same overall pattern between $t_{d\max}$ and $t_{d\min}$ as the cross-species comparison. That is, the variation in the relationship between $t_{d\max}$ and $t_{d\min}$ is, in fact, independent of differences associated with phylogeny (Harvey & Pagel 1991).

Results

RANGE IN THERMAL WINDOWS

The average range of the thermal window between $t_{d\min}$ and $t_{d\max}$ of individual species was 19.8°C , with 95% CI $19.1\text{--}20.5$ and the frequency for individual species concentrated around the predicted value of 20°C (Fig. 2). The range of values was $13\text{--}29^{\circ}\text{C}$ with the extremes 13.3 [*Feltiella acarissuga* (Vallot): Diptera], 13.7 [*Chilocorus bipustulatus* (L.): Coleoptera] and 28.6 [*Aphis spiraeicola* (Patch): Hemiptera] $^{\circ}\text{C}$ (Appendix S1).

The fraction of variation in thermal windows related to ecological traits (i.e. body mass, geographical origin, and food specialization), which include the embedded parts of phylogenetically structured variation (fractions [a + b] in Fig. 3), were significant only if geographical origin is expressed as a geographical zone, i.e. tropical vs. subtropical or temperate species origin ($F = 4.067$; $df = 1, 64$; $P = 0.048$); when the origin of the populations is expressed as latitude in $^{\circ}\text{N}$ or S , the whole model with all the ecological traits and their

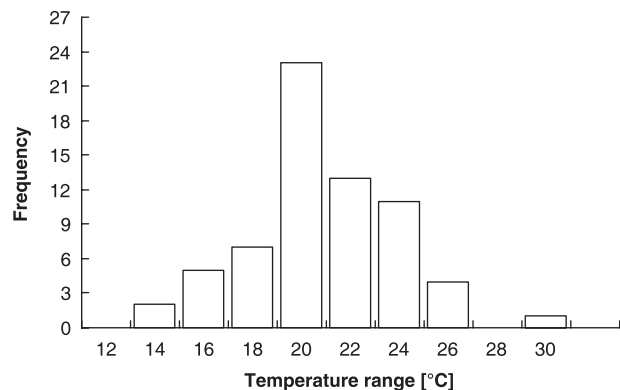


Fig. 2. Frequency histogram of the thermal tolerance ranges (i.e. thermal windows) of the individual species.

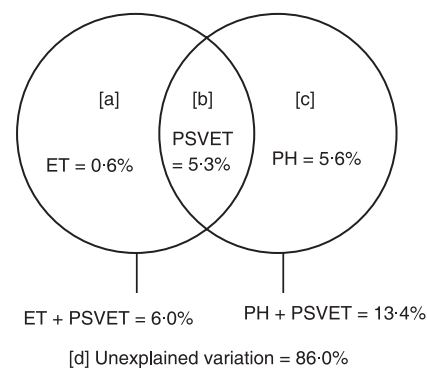


Fig. 3. Partitioning of the variation in thermal windows among ecological traits (ET, parts [a + b] of the Venn diagram), phylogeny (PH, parts [b + c]) and phylogenetically structured variation of ecological traits (PSVET, the intersection [b]). The rectangle represents 100% of the variation, of which [d] is the unexplained part. Values do not add up exactly because of rounding errors.

possible interactions appeared insignificant ($F = 1.673$; $df = 11, 54$; $P = 0.105$). In the former model, the effect of body mass and its interactions with zones and food specializations were insignificant (deletion test: $F = 1.239$; $df = 4, 62$; $P = 0.305$), and that of geographical zone only marginally significant ($F = 3.123$; $df = 1, 63$; $P = 0.082$), suggesting that the thermal windows of species originating from the tropics are 2.2°C narrower (standard error $SE = 1.767$, $df = 62$) than those of subtropical or temperate species. Herbivores feeding on living plants and 'seed eaters' did not differ significantly in thermal windows (deletion test on factor level reduction: $F = 1.585$; $df = 1, 64$; $P = 0.213$); however, those of predators and parasitoids (deletion test: $F = 4.067$; $df = 1, 64$; $P = 0.048$) are significantly 1.5°C narrower ($SE = 0.744$, $df = 64$) than those of grazers, sap feeders and 'seed eaters'.

However, the net effect of ecological traits (part [a] in Fig. 3) appeared insignificant ($F = 1.457$; $df = 1, 64$; $P = 0.232$), containing only a negligible portion of the variation ($r^2 = 0.6\%$; part [a] in Fig. 3); this suggests that any effect of ecological traits have to be attributed to a joint influence of phylogenetic and ecological traits (part [b] in Fig. 3 which cannot be statistically tested). That is, though there is a small but significant contribution of ecological traits to the variation

in thermal windows, explaining 6.0% of variance (part [a + b] in Fig. 3), this has to be attributed to phylogenetically structured variation of ecological traits. That is, the thermal windows are independent of ecological traits.

When ascertaining phylogenetically related fractions of variation in thermal windows that included the embedded parts of phylogenetically structured variation in ecological traits (fractions [b + c] in Fig. 3), only the first principal coordinate (PC) appeared significant and was retained in the model ($F = 9.863$; $df = 1, 64$; $P = 0.002$). Its eigenvalue represented 36.9% of the total variance of the patristic distance matrix and explained 13.4% of the variation in thermal windows (fractions [b + c] in Fig. 3). Because the order of the PCs roughly describes decreasing phylogenetic scales, this means that only differences at the largest phylogenetic scales were important; this is further supported by the fact that only the second PC still appeared marginally significant ($t = 1.786$; $df = 64$; $P = 0.079$). The sum of the eigenvalues of the first two PCs represented 68.3% of the total variance of the patristic distance matrix. The difference between the average thermal window among the highest phylogenetic clades, the Hemipteroid complex vs. Endopterygota, was highly significant (t -test: $t = 2.865$; $df = 64$; $P = 0.006$), with the average range 2.4 °C wider for the Hemipteroids (insect orders Psocoptera, Thysanoptera and Hemiptera) than for the Endopterygota (Neuroptera, Coleoptera, Diptera, Hymenoptera and Lepidoptera). That is, the widths of thermal windows are non-randomly distributed between these two taxonomic groups of insects.

The part of the variation strictly due to phylogeny (fraction [c] in Fig. 3) explained the largest percentage of variance (8.0%; $F = 6.950$; $df = 1, 64$; $P = 0.010$) and together with the phylogenetically structured variation of ecological traits (fraction [b] in Fig. 3) contributed 13.4% to the variation in width of thermal windows (fractions [b] and [c] in Fig. 3). Because in total the fractions of variation simultaneously related to both ecological traits and phylogeny (fractions [a + b + c] in Fig. 3) account for 14% of the variation ($F = 5.698$; $df = 2, 63$; $P = 0.005$), the overwhelming amount of variation in thermal windows was clearly attributed to phylogeny. However, despite these phylogenetic effects, most of the variation (86.0%; part [d] in Fig. 3) remains unexplained.

THE RELATIONSHIP BETWEEN THE MINIMUM AND MAXIMUM DEVELOPMENTAL TEMPERATURES

The relationship between $t_{d\min}$ and $t_{d\max}$ for the individual species was highly significant (least square regression LS: $t_{d\max} = 24.78 + 0.50t_{d\min}$; $F = 32.45$; $df = 1, 64$; $P < 0.001$) and explained 33.6% of the variance ($r^2 = 0.336$); very similar results were obtained for phylogenetically independent contrasts (LS: $t_{d\max} = 0.54t_{d\min}$; $F = 14.24$; $df = 1, 34$; $P < 0.001$; $r^2 = 0.29$). The slope of the major axis (MA) for individual species suggested an increase in $t_{d\max}$ of 1.3 °C ($t_{d\max} = -28.0 + 1.27t_{d\min}$) for each one degree centigrade increase in $t_{d\min}$, and the 95% confidence interval (CI) of this slope (CI = 0.90–1.85) broadly overlapped the significant MA slope for phylogenetically

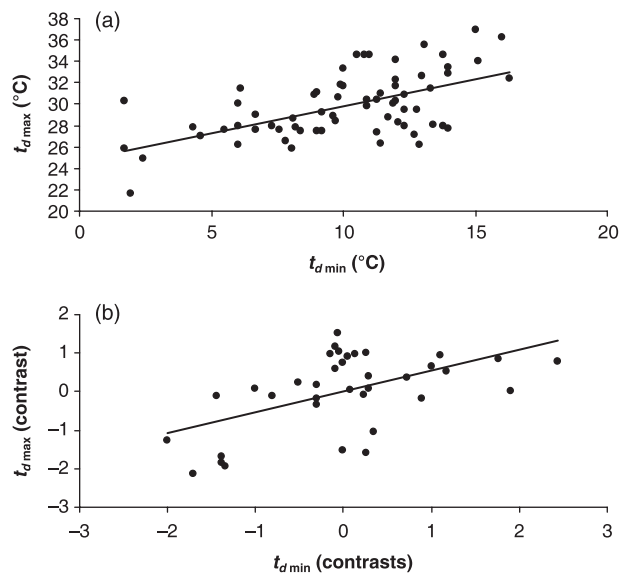


Fig. 4. The relationship between the temperatures at which the developmental rates are at the minimum ($t_{d\min}$) and maximum ($t_{d\max}$) for individual species (a) and that of the phylogenetically independent contrasts (b). Statistics for the slopes of least square regressions (LS: equation, F , df) are given in the text.

independent contrasts ($b = 1.00$; $CI = 0.56$ – 1.78) (Fig. 4). This means that there is a strong relationship between $t_{d\min}$ and $t_{d\max}$ among species, and this relationship is independent of the phylogeny of the species.

Discussion

This analysis of empirical results on thermal requirements showed that the thermal window between $t_{d\min}$ and $t_{d\max}$ is similar among insect species. This is in accord with Charnov & Gillooly's (2003) theoretical prediction. A similar prediction can be derived from a linear approximation of the slope of the derivative of the Sharpe-Schoolfield developmental rate model at the middle of the temperature range (Schoolfield, Sharpe & Magnuson 1981). Both models predict thermal windows of about 20 °C, with ranges narrower than 10 or wider than 25 °C requiring a rather extreme combination of physiological parameters. This accords with our empirical results for insects (Fig. 2), and strengthens the theoretical premise that this phenomenon is physiologically rather than ecologically based. In addition, there are indications that ectothermic animals other than insects have thermal windows of similar widths (Blöchl *et al.* 1997; Moore 1942, 1949), and that the thermal window for plant development is also about 20 °C (Bonhomme 2000). Thus, it is likely that this is a general feature of all ectothermic organisms.

Biochemists at the end of the 19th century developed temperature-coefficient equations, based on thermodynamic reasoning for simple inorganic systems, to account for the effect of temperature on the rate of biological processes (Arrhenius 1889; van't Hoff 1894). It was also appreciated that these relationships do not apply to the entire temperature range, but only narrow segments, depending on the species of animal,

or in particular the enzyme(s) that control development. As the temperature rises, the enzymes begin to denature, with the effect that the accelerating effect of temperature on the speed of development may be counteracted by the inactivating effect on the limiting enzyme(s) (Chick & Martin 1910). It is possible limiting enzymes are similarly affected by temperatures at the lower end of the ecologically relevant range. These physiological constraints could delimit the widths of thermal windows in ectotherms in general.

The analysis of empirical results on thermal requirements for insects further showed that species that have a low $t_{d\min}$ have a low $t_{d\max}$ and *vice versa*, as predicted by Charnov and Gillooly (2003). Recently, it was suggested that the trade off between $t_{d\min}$ and the D° required for development has a basis in the thermal adaptation of enzymes (van Straalen 1994; van der Have & de Jong 1996; van der Have 2002; Trudgill *et al.* 2005), and that the same reasoning as for northern vs. southern species (Bodenheimer 1927) can be applied to the difference in performance throughout the year of closely related early spring and/or autumn vs. summer species of aphids in the temperate zone (Dixon & Hopkins, unpublished). In addition, there are indications that the $t_{d\min}$ of C3 plants is lower than that for C4 plants, which accords with their respective predominantly temperate and tropical distributions (Bonhomme 2000). Thus, it is likely that, as with the widths of thermal windows, the trade-off between $t_{d\min}$ and $t_{d\max}$ is a general and physiologically based feature of all ectothermic organisms.

Fitness is often viewed in terms of potential rate of population increase. If development rate and population rate of increase are correlated, as they are in related insect species (Dixon 1998, 2000), then it would appear to be generally advantageous for tropical species and those temperate species that develop in summer to have a lower $t_{d\min}$, as this would enable these species to develop even faster at the high temperatures. However, this assumes there are no constraints to developing even faster at the temperatures prevailing in the tropics and high summer in temperate regions. Theory and this study indicate that the constraint is that each species can only develop over a narrow range of temperatures. That is, fitness is constrained by physiology, with the optimization of fitness in a variable thermal environment the central issue. Or put another way fitness is maximized by optimizing thermal reaction norms (Angilletta *et al.* 2003). Viewed in this way seasonal development and distribution are very similar in that they both involve adaptation to development over a particular temperature range. Northern species and those temperate species that start developing early in a year, have to be able to tolerate relatively low temperatures, those temperate species that develop in summer and tropical species, relatively high temperatures. That is, although the rate of population increase is constrained by thermodynamics (Frazier *et al.*, 2006) cold adapted species perform better than warm adapted species over more of the temperature range experienced in cold environments and *vice versa* in warm environments.

This study indicates that the widths of thermal windows are non-randomly distributed within the highest taxonomic

groups of insect, slightly affected by phylogenetically structured variation of ecological traits, but not by ecological traits. The marginally significant effect of climatic zones, suggesting narrower windows for tropical compared with more cold-tolerant species, could be attributed to temperate species being exposed to a wider temperature range if development proceeds through spring and summer, whereas tropical species might develop in narrower temperature ranges. However, the indication that insects tend to be thermal specialists in the tropics and thermal generalists in temperate regions needs to be verified using a larger data set, preferably measured in terms of rates of development. The same holds for the narrower windows of predators and parasitoids compared with grazers, sap feeders and species feeding on dry seeds and dead plants and animals. This is because the overwhelming portion of variance in this relationship must be attributed to phylogenetically structured variation, which cannot be tested statistically.

The broader windows of the species in the Hemipteroid complex (orders Psocoptera, Thysanoptera and Hemiptera) compared with the Endopterygota (Neuroptera, Coleoptera, Diptera, Hymenoptera and Lepidoptera) may be attributed to differences in their postembryonic development. The Hemipteroids lack a true pupal stage and their larvae live in the same environment as the adults. On the other hand, in the Endopterygota larvae and adults often live in completely different environments, and the species undergo a complete histolysis of larval tissues during pupation. These innovations may have enabled the evolution of narrower thermal windows, which may have contributed to their greater ecological radiation. That is, as argued by Angilletta *et al.* (2003) a unified theory that includes all classes of trade-offs is more likely to provide a better understanding of the mechanisms that drive the evolution of thermal reaction norms. However, the ecological significance of these differences in the width of their thermal windows, if confirmed, needs to be determined.

That most of the variation in the range of thermal windows remained unexplained, and the relationship between $t_{d\max}$ and $t_{d\min}$, though highly significant accounts for only 34% of the variance, may in part be due to the quality of the original data. There has been a tendency to monitor the development of insects at a fixed interval, usually a day, irrespective of the temperature. This can lead to errors in the estimates of the duration of development, especially at higher temperatures (van Rijn, Mollema & Steenhuis-Broers 1995; Jarošík, Honek & Dixon 2002). In addition, mortality during development at each of the temperatures is very rarely recorded. This can lead to errors in the estimates of the duration of development especially at low temperatures, at which the individuals with the fastest development complete their development early while the rest succumb to adverse conditions (Jarošík, Honek & Dixon 2002). Another factor that could have affected the results is food quality, which will be extremely difficult to standardize for insects and especially for ectotherms in general.

Theory and this analysis of empirical data indicate that each species of insect can only develop over a limited range of temperatures and is independent of species traits. That is, the evidence favours constrained rather than variable thermal

windows, which suggests that most if not all insects are thermal specialists. In addition, the relationship between the temperatures at which the minimum and maximum developmental rates are recorded co-vary, independent of species phylogeny. This may help identify the biochemical adaptations underlying the thermal sensitivity of ectotherms. This could be an important step in achieving a better understanding of how communities work and integrating physiology and ecology at the community scale. In addition, this concept might help when predicting the effect of climate change on the distribution and abundance (e.g. Harrington & Stork 1995; Yamamura & Kiritani 1998; Dixon 2003; Kiritani 2006), and spread of invasive insects (e.g. Simberloff, Parker & Windle 2005; Baker *et al.* 2005; Hatherly *et al.* 2005).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of the species and their populations included in the analysis, with their ecological traits and estimated values of $t_{d\min}$ and $t_{d\max}$.

Appendix S2. Analytical solution for the maximum temperature $t_{d\max}$ and numerical solution for the minimum temperature $t_{d\min}$.

Appendix S3. Summaries of Lactin *et al.*'s (1995) model parameters for the species and their populations included in the analysis.

Appendix S4. Summaries of Brière *et al.*'s (1999) model parameters of the species and their populations included in the analysis.

Appendix S5. Partitioning of the variance in thermal windows.

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