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The Temperature-Size Rule in Ectotherms: May a General Explanation Exist after All?

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ABSTRACT: The majority of ectotherms mature at a larger size at lower rearing temperatures. Although this temperature-size rule is well established, a general explanation for this phenomenon has remained elusive. In this article, we address the problem by exploring the proximate and ultimate reasons for why a temperate grasshopper, *Chorthippus brunneus*, is an exception to the temperature-size rule. Using a complete set of life-history data to parameterize an established life-history model, we show that it is optimal for this species to mature at a larger size at higher temperatures. We also show that plasticity in adult size is determined by the relative difference between the minimum temperature thresholds for growth and development rates. The mechanism relates to aspects of the biophysical model of van der Have and de Jong. Ectotherms that obey the temperature-size rule are identified as having a higher temperature threshold for development rate than for growth rate; exceptions are identified as having a lower temperature threshold for development rate than for growth rate. The latter scenario may arise broadly in two ways. These are discussed in reference to the thermal biology of temperate grasshoppers and ectotherms in general.

Keywords: Bergmann's rule, Orthoptera, plasticity, reaction norm, temperature threshold.

Age and size at maturity are arguably the most important life-history traits (Stearns and Koella 1986); the vast range in adult size among organisms, from the smallest of bacteria to the largest of mammals, is testament to such an assertion and has long posed biologists with a multitude

of questions to answer in relation to the constraints and selection pressures that could lead to such diversity (Roff 1992; Stearns 1992). Body size, in turn, is also recognized to affect every aspect of an organism's biology, from its anatomy and physiology to its life history, behavior, and ecology (Naganuma and Roughgarden 1990). The theoretical basis underlying age and size at maturity is well established (Roff 2001), but its application to certain biological rules has failed to satisfactorily explain patterns of responses among organisms, particularly in respect to temperature (Atkinson 1994; Angilletta and Dunham 2003).

In 1847, Bergmann first proposed a general rule for organism size with temperature based on intraspecific comparisons of size among endotherms; he noted that organism size tended to increase with latitude (Mayr 1956). Bergmann surmised that a smaller surface area to volume ratio, associated with a larger mass, might have evolved to reduce heat loss in colder environments. Similar reasoning was applied to Allen's rule, which stated that organisms tend to have shorter extremities in colder climates (Reiss 1989). However, these biological rules were also found to apply to ectotherms, which do not internally regulate their internal body temperature. Approximately 80% of the ectotherms reviewed by Ray (1960) obeyed Bergmann's rule. Moreover, the response of ectotherms to latitude was found, at least in part, to be a phenotypic response to rearing temperature. Subsequently, the adaptationist hypothesis that a larger body must convey a significant fitness advantage in colder environments was questioned and, as a result, largely dismissed (Geist 1987).

In the wake of a growing number of apparent exceptions to these biological rules, Atkinson (1994) reassessed the available empirical evidence to ascertain whether there was any genuine support for a general relationship between phenotypic body size and temperature. Atkinson's (1994) review of ectotherms, which included examples of animals, plants, protists, and a bacterium, concluded that in 83.5% of cases, colder rearing temperatures led to an increase in organism size, supporting Ray's (1960) earlier finding that ectotherms do conform to a temperature-size rule. Sup-

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port for the temperature-size rule has reignited much interest in the topic and again raised the question of why organisms in general should mature at a larger size in colder environments (Atkinson 1994, 1995; Sibly and Atkinson 1994; van der Have and de Jong 1996; van Voorhies 1996; Atkinson and Sibly 1997; Ashton et al. 2000; Ashton 2001, 2002a, 2002b; Bernardo and Reagan-Wallin 2002; Day and Rowe 2002; Angilletta and Dunham 2003; Arnett and Gotelli 2003; Ashton and Feldman 2003; de Queiroz and Ashton 2004; Litzgus et al. 2004).

Some authors have expressed doubt as to whether such biological rules actually exist (Mousseau 1997; Bernardo and Reagan-Wallin 2002); however, recent reviews on a range of taxonomic groups, including both endotherms and ectotherms, suggest that there is empirical evidence to support them (Ashton et al. 2000; Ashton 2001, 2002a, 2002b; Angilletta and Dunham 2003; Ashton and Feldman 2003). A general reason for why an organism should mature at a larger size in a colder environment, however, has remained elusive. It is not clear whether the response is an adaptation or simply a product of physiological constraints. Angilletta and Dunham (2003) suggest that a simple general explanation for such rules may not exist and that efforts might be best directed toward finding explanations for organisms that share the same physiology and behavior.

In this article, we investigate age and size at maturity in a univoltine species of temperate grasshopper, *Chorthippus brunneus*, as a function of temperature. Like many other grasshoppers, *C. brunneus* is an exception to the temperature-size rule (Masaki 1978; Atkinson 1994; Mousseau 1997; Willott and Hassall 1998; Telfer and Hassall 1999). Using an already established model of grasshopper life history (Grant et al. 1993) and a substantive data set on a suite of life-history traits over a 15°C temperature range, we first demonstrate that it is optimal for this species to mature at a larger size at higher rearing temperatures. Second, we use the model to investigate the mechanistic reasons that underlie observed plasticity in adult size resulting from a change in temperature. We show that adult size relates to the relative position of the minimum temperature thresholds for growth and development rates. These thresholds relate to the differential activation energy constants in van der Have and de Jong's (1996) biophysical model that determine the slopes of the quasi-linear relationships of growth and development rates over an ecologically relevant temperature range (Jarošík et al. 2004). However, we show that it is the relative positions of the different temperature thresholds of these rates, and not the gradients of their slopes per se, that determine whether an ectotherm will obey or be an exception to the temperature-size rule.

Methodology

Study Species

The field grasshopper *Chorthippus brunneus* (Orthoptera: Acrididae) is a temperate species typical of open, dry, and sunny habitats (Ragge 1965). It is a common species that has an extensive distribution that stretches across much of Europe and temperate Asia (Marshall and Haes 1988; Kleukers et al. 1997). *Chorthippus brunneus* has a univoltine life cycle with an obligate egg diapause. The eggs start to hatch in May, and nymphs pass through four instars to adult eclosion, though some females may pass through five nymphal instars by inserting an additional IIa instar between the second and third stages (Hassall and Grayson 1987). The first adults appear in June and can be found until as late as October until the onset of the first frosts. Mature adult females oviposit in the soil. Clutches of up to 14 eggs are laid continually every few days until death.

Like other grasshoppers (Acrididae), *C. brunneus* is a high-temperature specialist and needs to elevate its internal body temperature by basking in radiant heat if it is to successfully complete its life cycle at temperate latitudes (Uvarov 1966, 1977; Begon 1983; Willott 1997; Willott and Hassall 1998). In the field, *C. brunneus* can elevate its internal body temperature to 40°C (Willott 1997). In the absence of radiant heat, *C. brunneus* is found to be unable to successfully reach the final adult stage at an ambient rearing temperature of 20°C (Willott and Hassall 1998).

There is a clear relationship of increasing body size along a cline in climate continentality from wetter and cooler oceanic areas in the northwest of the British Isles to the drier and warmer more continental areas of the south and east (Telfer and Hassall 1999). To incorporate genetic differences in adult size evident within this species' range, laboratory F2 generation egg stocks from two populations were used in the following experiment, one derived from Inch in County Kerry, Ireland (52.150°N, 9.980°W), which has a very oceanic climate, and the other from Braunsbedra in Saxony-Anhalt, Germany (51.300°N, 11.900°E), which has a very continental climate. Data on traits from these two ecotypes were pooled together for this modeling exercise. Approximately 20 mature females plus males were originally collected from each founding site. Individuals were immediately transported back to the laboratory and were reared in aluminum glass-fronted cages (32.5 cm × 32.5 cm × 41.0 cm). The cages were lit internally with 40-W tungsten bulbs, and a nylon bolting mesh (Northern Mesh and Technical Fabrics) cylinder was provided as a basking surface. The grass feed consisted of a three-species mix of *Festuca ovina* L., *Agrostis capillaris* L., and *Poa pratensis* L. grown for 6 weeks under constant greenhouse conditions on Levington multipurpose compost and was provided ad lib. Small Perspex pots con-

taining sterilized sand were provided for oviposition. These were checked daily for egg pods. Collected egg pods were transferred to sterilized Perspex pots with snap-shut lids containing moist (10% water by volume) sterilized sand, and the egg pods were buried upright just below the surface. The transferred eggs were stored at room temperature for 3 weeks before being transferred to cold storage (4°C), where they were kept for a minimum of 2 months to break diapause (Kelly-Stebbins and Hewitt 1972). When required, egg pods were removed from cold storage and transferred to an incubator set on a 30°/20°C 14:10 h day/night cycle to complete postdiapause development (Kelly-Stebbins and Hewitt 1972; Willott and Hassall 1998). Rearing conditions for the F1 generation were as above.

Experimental Design

On hatching, individuals were sexed and weighed to the nearest 0.01 mg. Male-female pairs from different egg pods were assigned to different cylindrical cages. The cages consisted of a cylinder (90 mm diameter × 300 mm height) of 1 mm nylon bolting mesh fitted around a pot (88 mm diameter × 88 mm depth) of sown grass (see above) and enclosed at the top with a tightly fitting petri dish lid. Once a female had reached adult eclosion, a small Perspex pot containing sterilized sand was provided for oviposition. The sand was checked daily for the first egg pod and every 2 days thereafter for subsequent egg pods.

The cylindrical cages were kept in four Fisons 140G2 growth cabinets (Fisons, Ipswich), which varied <1°C from their set temperature. The growth cabinets were set to a 14D:10L photoperiod with a nighttime temperature of 15°C (Willott and Hassall 1998). Each Fisons growth cabinet was lit internally from above by four 40-W fluorescent bulbs fitted behind clear Perspex. The lids of the cylindrical cages were situated approximately 30 cm below this light source. Because there is minimal radiant heat available, internal body temperatures of grasshoppers approximate that of the cabinet's set ambient temperature. The two ecotypes were reared at the following 14-h daytime rearing temperatures: 25°, 30°, 35°, and 40°C. Squirrel data loggers (Grant Instruments, Cambridge) were also used to monitor the internal temperature of each cabinet during the experiment. Cylindrical containers were rotated regularly to reduce the effects of small variations in environmental temperature within the cabinets.

Data Collection

The following life-history trait data were collected at each of the four rearing temperature regimes for females (male traits were not recorded): growth rate (eq. [1], adapted

from Sibly and Calow 1985), development rate (the inverse of time [days] from hatching to adult eclosion), mass at various times during nymphal development (mg), mass at adult eclosion (mg), juvenile mortality rate (proportion day⁻¹), maturation rate (time from final eclosion to first laid egg pod; day⁻¹), oviposition rate (egg pods day⁻¹), and dry egg mass (mg; eggs were heated at 70°C for 24 h in a drying oven) of third-laid clutch (the third-laid clutch was chosen for analysis because the number of eggs in the first-laid clutch tends to be atypically small; Willott and Hassall 1998):

$$\text{growth rate} = \frac{(\text{adult mass}) - (\text{hatching mass})}{\text{development time}}. \quad (1)$$

Modeling

Fitness was calculated using the Grant et al. (1993) model of grasshopper life history (eq. [2]), which is adapted from the earlier model by Sibly and Monk (1987). Fitness (F) in the model is equal to the number of copies of a gene in adults laying their first eggs in season 2 divided by the equivalent number in season 1:

$$F = \frac{0.5n \exp(-\mu_1 t_1 - M) \{1 - \exp[-(S - t_1)\mu_2]\}}{1 - \exp(-\mu_2 t_2)}, \quad (2)$$

where 0.5 is the genetic contribution of an adult to its offspring in a sexual species; n is the number of eggs per clutch; μ_1 and μ_2 are juvenile and adult mortality rates, respectively; t_1 is time from hatching to first oviposition; t_2 is the time interval between clutches; S is season length; and M is the overwinter egg mortality. The term $\exp(-M)$ describes the probability of surviving winter, $\exp(-\mu_1 t_1)$ describes the probability of surviving from hatching to the first oviposition, and $\exp(-\mu_2 t_2)$ describes the probability of surviving between clutches. Fitness is equal to $0.5n \exp(-M - \mu_1 t_1) + 0.5n \exp(-M - \mu_1 t_1) \exp(-\mu_2 t_2) + 0.5n \exp(-M - \mu_1 t_1) \exp(-2\mu_2 t_2) + \dots + 0.5n \exp(-M - \mu_1 t_1) \exp[-(m-1)\mu_2 t_2]$, where m is equal to the maximum number of clutches. Because $(m-1)t_2$, the time from the first oviposition to the last, is equal to $(S - t_1)$, the term $\exp[-(m-1)\mu_2 t_2]$ is simplified to $\exp[-(S - t_1)\mu_2]$ (noting that the correct term $\exp[-(S - t_1)\mu_2]$ replaces the typographical error of $\exp[-(S - t_1)t_2]$ in the published article by Grant et al. [1993]). Fitness is written in a condensed form (eq. [2]) using the formula for the sum of a geometric series (Caus-ton 1983; Sibly and Monk 1987).

Values for overwinter egg mortality, juvenile mortality rate, adult mortality rate, and season length in the following analyses were taken from a review of field measure-

ments (Sibly and Monk 1987). Field estimates of these parameter values were used in the model because season length is not a limiting factor in the laboratory, and laboratory estimates of mortality rates do not include extrinsic causes of mortality. It was necessary to use laboratory estimates for the temperature dependence of the other life-history traits (table 1).

Adult size was modeled using a growth trajectory of square-root-transformed mass of individuals (recorded from hatching to adult eclosion over the temperature range 25°–40°C) plotted against the sum of effective temperatures (SET; Jarošík et al. 2004). SET for growth rate (SET_G) is calculated as the total amount of time (t) in hours that the rearing temperature (T) was greater than the minimum temperature threshold for growth rate (TT_G): SET_G = $t(T - TT_G)$. Total time t to adult eclosion, however, is assumed to be dependent on a constant SET for development rate: SET_D = $t(T - TT_D)$, where TT_D is the minimum temperature threshold for development rate. This is a reasonable assumption because ectotherms are expected to show developmental isothermy, an approximately linear relationship describing development rate over an ecologically relevant temperature range (van Straalen 1983; Gilbert and Raworth 1996; Jarošík et al. 2002). Note that the relationship between SET_D and the linear slope of development rate against temperature (S_D) is constant (SET_D = $1/S_D$; Jarošík et al. 2004). Estimates of the minimum temperature thresholds for growth and development rates were calculated by extrapolating the linear responses of these rates against temperature to the X-axis (table 1; van Straalen 1983; Gilbert and Raworth 1996). Time to adult eclosion in the model is equal to the sum of juvenile development time from hatching to adult eclosion (which was allowed to vary in the modeling of optimal age and size at adult eclosion) plus maturation time, the time from adult eclosion to first oviposition. The latter was derived directly as a function of temperature (table 1) because it was not found to be dependent on adult size.

Clutch size was indirectly calculated as a function of adult size. Total dry egg mass of the third-laid clutch (y) was calculated as a sigmoidal function of adult mass at eclosion (x) using the Hill model curve (eq. [3]). The curve

was fitted using the computer graphics package SigmaPlot 2001. Constant a determines the asymptotic height of the curve, b determines the steepness of the slope, and c is the inflexion point of the curve (where $x = a/2$). Because individual egg mass was unrelated to adult mass ($P > .05$), clutch size was calculated as total clutch egg mass divided by the mean dry mass of a single egg (1.36 mg; Walters 2003):

$$y = \frac{ax^b}{c^b + x^b}. \quad (3)$$

Reanalysis of Published Data

Life-history data on four sympatric species of temperate grasshopper (Willott and Hassall 1998), including the study species *C. brunneus*, were reanalyzed in respect to relative plasticity. The authors reared all four of these species at 25°, 30°, and 35°C under conditions similar to those conducted here. Only trait values recorded at 30° and 35°C are used in the following analyses because *Stenobothrus lineatus* and *Myrmeleotettix maculatus* could not be successfully reared at the lowest rearing temperature. Plasticity in adult size (calculated as trait value at 35°C divided by trait value at 30°C) was regressed against the estimated difference in the minimum temperature thresholds for growth and development rate. A two-way ANOVA without replication was used to test for the effects of sex and species (entered as fixed factors) on plasticity in adult size. An ANCOVA was conducted to predict plasticity in adult size as a function of plasticity in growth rate (covariate), sex, and species (fixed factors). Analyses were conducted using SPSS, version 11.5.

Results

Life-History Traits and Temperature

Growth rate, development rate, adult size, maturation rate, oviposition rate, and juvenile mortality rate of female *Chorthippus brunneus* were all significantly positively lin-

Table 1: Regression analyses of life-history traits of female *Chorthippus brunneus* as a function of temperature

Trait	Equation	R ²	df	F value	P
Growth rate	$y = .026660x - .4945$.86	150	889.1	<.001
Development rate	$y = .002054x - .02761$.86	164	983.0	<.001
Adult mass at eclosion	$y = 4.378x - 17.4$.48	149	136.2	<.001
Maturation rate	$y = .009962x - .1936$.57	133	173.8	<.001
Oviposition rate	$y = .018320x - .2584$.42	87	62.1	<.001
Juvenile mortality rate	$y = .01029x - .1296$.98	3	112.1	<.01

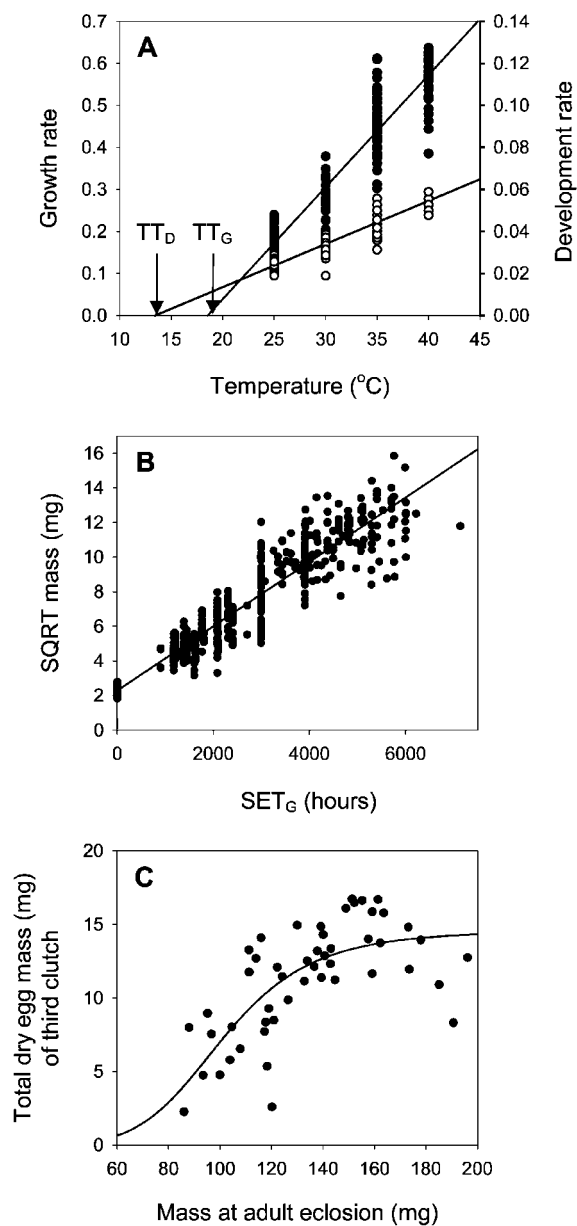


Figure 1: A, Calculation of minimum temperature thresholds for growth rate (TT_G ; filled circles) and development rate (TT_D ; open circles). B, Growth trajectory calculated as the square root of mass as a function of degree hours above TT_G . C, Clutch egg mass as a function of female adult size (Hill sigmoidal model parameters: $a = 15.17 \pm 1.42$, $t = 10.73$, $P < .001$; $b = 5.12 \pm 1.17$, $t = 4.36$, $P < .001$; $c = 103.6 \pm 5.42$, $t = 19.12$, $P < .001$).

early related to temperature (table 1). The minimum temperature thresholds for growth rate and development rate were calculated to be $18.55^\circ \pm 1.28^\circ\text{C}$ and $13.44^\circ \pm 1.26^\circ\text{C}$, respectively (fig. 1A). Square-root-transformed mass of individuals was significantly linearly related to the

cumulative number of degree hours above TT_G ($y = 0.001859x + 2.285$; $R^2 = 0.92$, $F = 8,385.9$, $df = 693$, $P < .001$; fig. 1B). Total egg mass of the third-laid clutch was modeled as a sigmoid function of mass at adult eclosion ($R^2 = 0.69$, $F = 68.7$, $df = 61$, $P < .001$; fig. 1C).

Predictions of Optimal Age and Size at Final Eclosion

It is predicted that as temperature increases, *C. brunneus* females should eclose at a larger adult mass; that is, the optimal life-history strategy of this insect is to follow the converse of the temperature-size rule (fig. 2). Optimal fitness peaks agree well with the observed range of values for development time (fig. 2A) and adult size (fig. 2B) for intermediate juvenile mortality rates. The potential benefit of a larger size at higher temperatures is partially offset by an increase in intrinsic juvenile mortality rate with

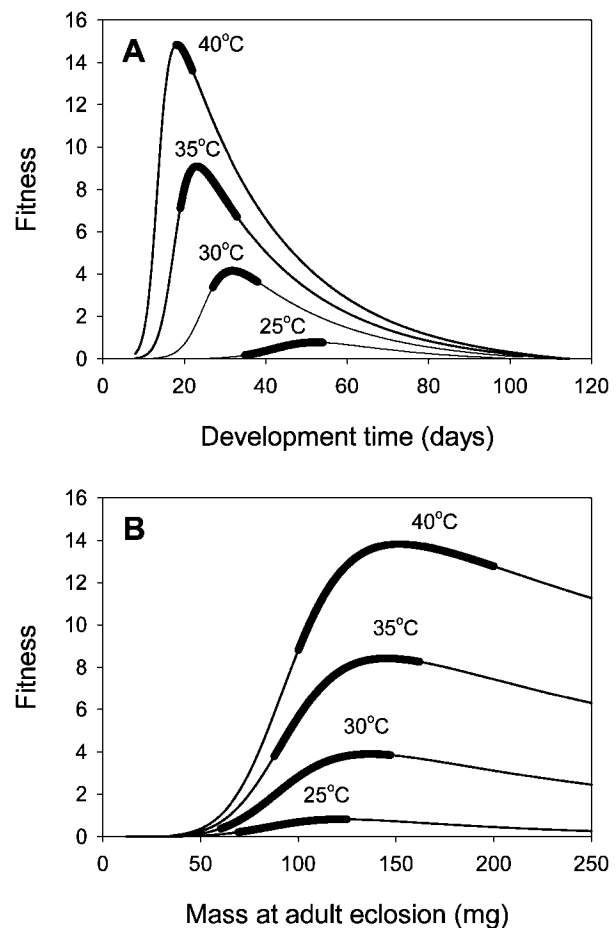


Figure 2: Predicted fitness clines for (A) development time and (B) mass at adult eclosion under four different rearing temperature regimes. Thick portions of lines indicate range of observed values. Model parameters held constant: $\mu_1 = 0.04$, $\mu_2 = 0.05$, $M = 0.25$, and $S = 120$.

temperature (1.4% over the temperature range 25°–40°C; table 1); however, it is not sufficient to override the potential benefits of a larger clutch size (fig. 3). A larger adult mass is still favored at higher temperatures even if a steep cline in juvenile mortality rate from 1% to 6% is assumed to occur across the temperature range from 25° to 40°C (fig. 3B). Optimality predictions are relatively insensitive to changes in adult mortality rate over the range of values recorded in the field (3%–13%; Sibly and Monk 1987). Changes to season length (70–120 days) have little impact on predictions at temperatures >28°C (results not shown).

Predictions of the model agree well with observations at higher temperatures to which this species actively raises its internal body temperature in the field (Willott 1997) but less so at lower temperatures. To optimize size at maturity across the temperature range, assuming an intermediate rate of juvenile mortality (4% day⁻¹; fig. 3B), TT_D should equal 16.8°C, notably higher than that observed (fig. 1A). This is assuming that the whole thermal reaction norm for development rate is exposed to selection. If selection were largely restricted to the part of the thermal reaction norm reflective of typical thermal conditions experienced in the field, selection for a change in S_D in response to mean thermal conditions might exert relatively little pressure on TT_D . The result is that the selected constant SET_D (van Straalen 1983; Gilbert and Raworth 1996; Jarošík et al. 2004) could lead to suboptimal adult sizes at temperatures outside this normal temperature range. This is demonstrated in the following modeling exercise (fig. 4). Here we model changes in adult size determined by different values of SET_D that are predicted to optimize age at maturity at different mean rearing temperatures, assuming a fixed value of TT_D (here assumed to be the observed value, 13.44°C). When SET_D is assumed to have been selected in respect to higher rearing temperatures, lower temperatures lead to adult sizes much smaller (fig. 4B) than that predicted to be optimal (fig. 3B). Conversely, when SET_D is assumed to be selected in respect to a lower set of rearing temperatures, higher temperatures lead to adult sizes much larger (fig. 3B) than that predicted to be optimal (fig. 4B).

Minimum Temperature Thresholds for Growth and Development

For *C. brunneus*, similar predicted responses of adult size to temperature produced by a constant SET_D , whether assumed to be derived as a result of selection across a wide temperature range (fig. 3B) or over a narrow temperature range (fig. 4B), make it difficult to distinguish the true adaptive significance of observed plasticity in size. The reason why adult size is predicted to positively increase with temperature despite assuming a fixed TT_D relates to

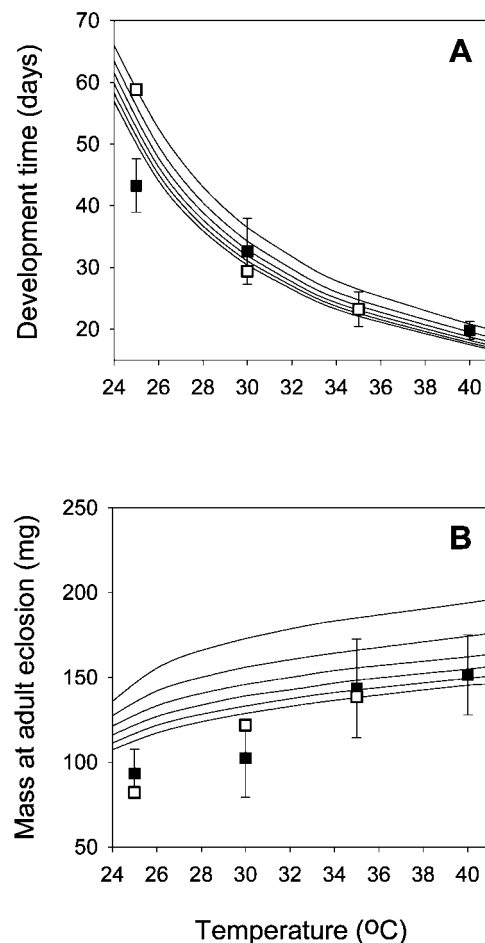


Figure 3: Predictions of optimal (A) development time and (B) mass at adult eclosion as a function of temperature. Lines indicate optimality curves under various juvenile mortality rate scenarios (lines from top to bottom: $\mu_1 = 0.01$ – 0.06 , in 0.01 increments). Squares represent observed means; bars represent ± 1 SD (closed squares = experimental results; open squares = values taken from Willott and Hassall 1998). Model parameters held constant: $TT_G = 18.55^\circ\text{C}$, $\mu_2 = 0.05$, $M = 0.25$, and $S = 120$.

the relative positions of TT_G and TT_D . In the following modeling exercise, we demonstrate how adult size could vary nonadaptively at temperatures at which development rate is exposed to minimal selection pressure by manipulating TT_G relative to TT_D .

Because manipulation of TT_G leads to a change in growth rate that could otherwise be solely attributed to a change in the slope of growth rate (S_G), TT_G (fig. 5Ai) and S_G (fig. 5Aii) are manipulated separately. Life-history theory predicts that, all else being equal, an increase in growth rate will lead to a larger optimal size at maturity (Stearns 1992). Larger optimal adult sizes predicted as a result of either a decrease in TT_G (fig. 5Bi) or an increase in S_G (fig.

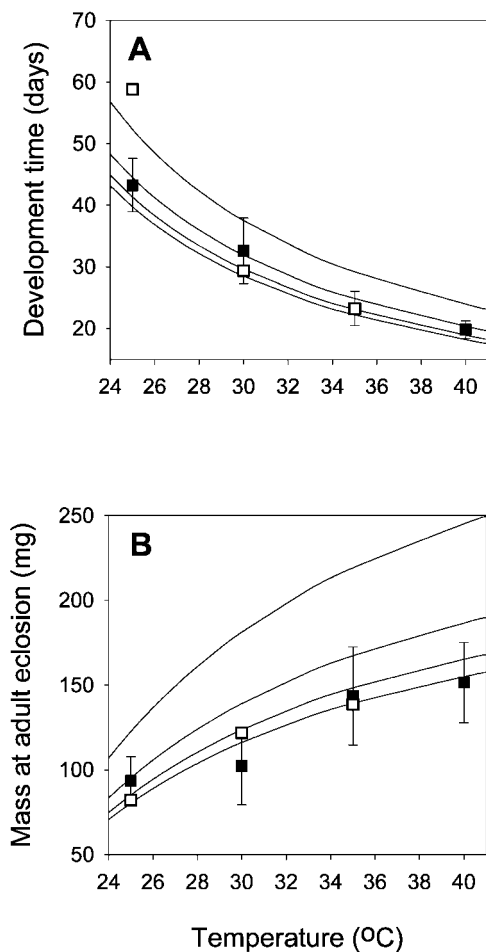


Figure 4: Predicted (A) development times and (B) masses at adult eclosion in response to temperature when a constant value of a sum of effective temperatures for development rate (SET_D) is selected in respect to a fixed minimum temperature threshold for development rate (TT_D). Lines indicate responses to constant values of SET_D that optimize fitness under four alternative thermal scenarios (lines from top to bottom: 25°, 30°, 35°, and 40°C). Symbols are same as figure 3. Model parameters held constant: $TT_G = 18.55^\circ\text{C}$, $TT_D = 13.44^\circ\text{C}$, $\mu_1 = 0.04$, $\mu_2 = 0.05$, $M = 0.25$, and $S = 120$.

5Bii) are found to similarly increase with temperature. In both cases, to optimize adult size across the whole temperature range, it is necessary that TT_G be lower than TT_D . As TT_G is manipulated, a shift in TT_D is required (for growth rates, see fig. 5Ai, a–e: $TT_D = 16.83^\circ$, 14.35° , 10.13° , 5.26° , and 0.09°C , respectively), while a change in S_G only does not necessitate any change in TT_D . In an alternative scenario, we assume that selection on development rate is largely restricted to a narrow temperature range; here we arbitrarily choose the temperature 38°C . Because selection at a single temperature may not necessitate a change in TT_D , TT_D is assumed to be fixed at the

observed value of 13.44°C . Under this scenario, manipulation of TT_G relative to a fixed TT_D can lead to markedly different responses of adult size to temperature being dependent on the relative positions of TT_G and TT_D (fig. 5Ci). Conversely, a change in S_G has little discernible effect on the response of adult size to temperature (fig. 5Cii). The differential effects on adult size determined by gradients versus temperature thresholds that are used to define the slopes of growth rate and development rate can be summarized mathematically.

Let the mass (square root transformed) of an individual be expressed as linear function of time:

$$\text{mass} = m_0 + Gt, \quad (4)$$

where m_0 is mass on hatching, G is growth rate (mass increase per unit time), and t is time since hatching (adapted from van der Have and de Jong 1996). Because G (square-root-transformed mass/ t) is dependent on temperature (fig. 1A), mass can alternatively be expressed as a linear function of SET_G (as in fig. 1B), which is equal to $t(T - TT_G)$:

$$\text{mass} = m_0 + S_G t(T - TT_G), \quad (5)$$

where S_G is equal to the slope of G against temperature. While mass increases as a function of SET_G , time t to adult eclosion is dependent on the constant sum of effective temperatures for development rate (SET_D), which is equal to $t(T - TT_D)$. Because SET_D is constant, time to adult eclosion varies as the following function of temperature:

$$t = \frac{SET_D}{T - TT_D}. \quad (6)$$

Substituting the equality for t (eq. [6]) into equation (5) and simplifying using the equality $1/S_D = SET_D$, where S_D is equal to the slope of development rate ($1/t$) against temperature (Jarošík et al. 2004), we find that age and size at maturity can be expressed as the following function of temperature:

$$\text{adult mass} = m_0 + \frac{S_G}{S_D} \left(\frac{T - TT_G}{T - TT_D} \right). \quad (7)$$

It can be seen from equation (7) that a relatively larger adult size will occur at all temperatures if there is an increase in S_G and/or a decrease in S_D . A change in either one of these terms does not, however, affect the response of adult size to temperature, which is encapsulated in the term $[(T - TT_G)/(T - TT_D)]$. Adult mass will decrease with temperature in ectotherms where $TT_D > TT_G$, will increase

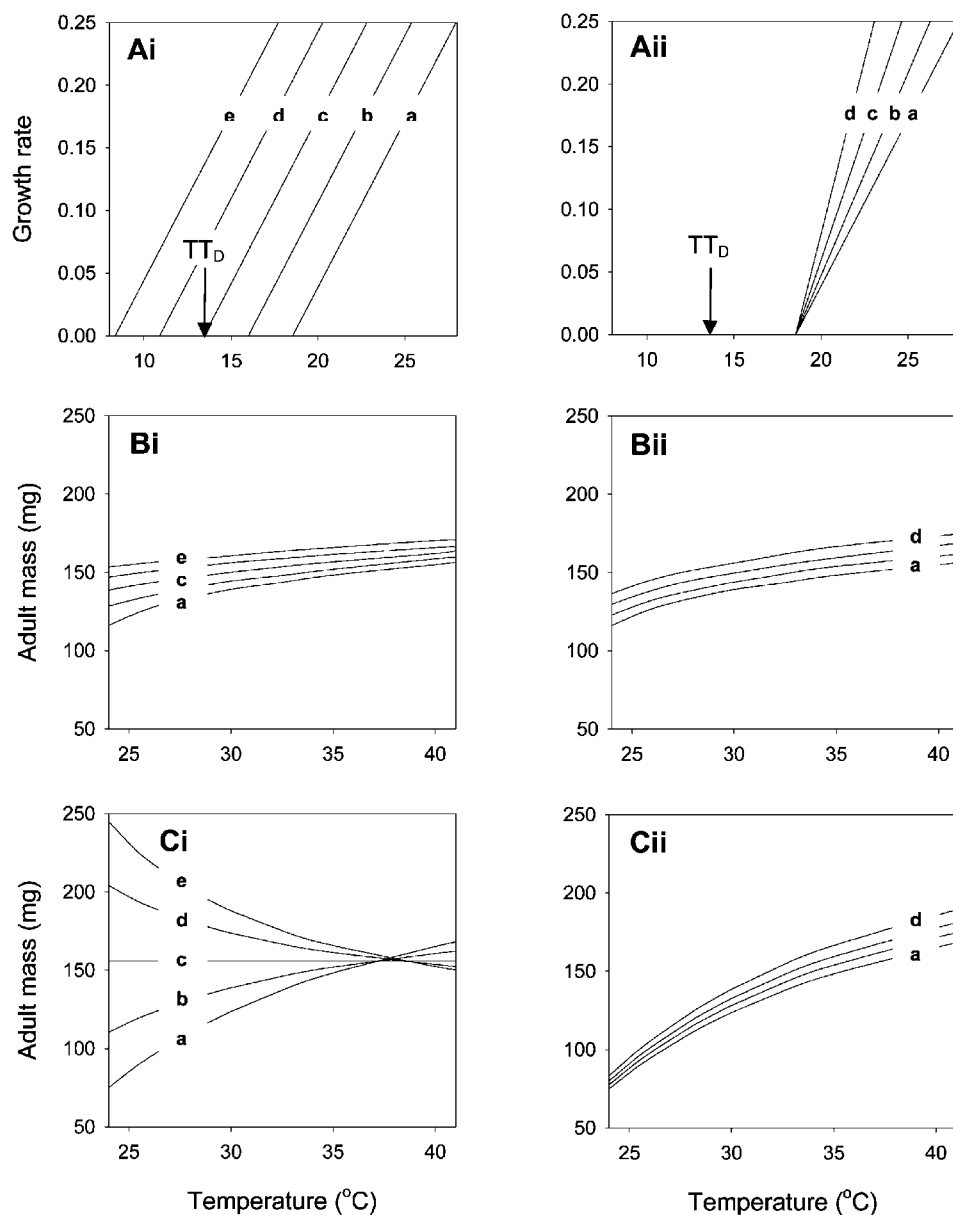


Figure 5: A, Potential consequences for mass at adult eclosion when (i) temperature thresholds for growth rate (TT_G ; a–e: 18.34°, 15.99°, 13.44°, 10.89°, and 8.35°C) and (ii) slope of growth rate (S_G ; a–d: 0.00186, 0.00226, 0.00286, and 0.00366) are independently manipulated relative to observed temperature threshold for development rate (TT_D). Lines represent linear approximations of actual growth rates; line a represents the observed growth rate in each case. B, Predicted response of adult mass to temperature in response to a change in (i) TT_G and (ii) S_G when a constant sum of effective temperatures of development rate (SET_D) is assumed to be determined by selection for optimal body size over a wide temperature range (SET_D may be determined by changes to both TT_D and slope of development rate [S_D]). C, Predicted response of adult mass to temperature in response to a change in (i) TT_G and (ii) S_G when a constant SET_D is assumed to be determined by selection for optimal body size in respect to mean thermal conditions, here arbitrarily assumed to be 38°C (SET_D is assumed to be determined solely by a change in S_D ; TT_D is held constant at 13.44°C). Model parameters held constant: $\mu_1 = 0.04$, $\mu_2 = 0.05$, $M = 0.25$, and $S = 120$.

with temperature in ectotherms where $TT_G > TT_D$, and will remain unchanged in ectotherms where $TT_G = TT_D$. The extent to which mass responds to temperature is dependent on the absolute difference between TT_G and TT_D . At

high temperatures, mass converges on $(m_0 + S_G/S_D)$. The effects of the relative positions of TT_G and TT_D on growth trajectories to final adult eclosion are illustrated in figure 6.

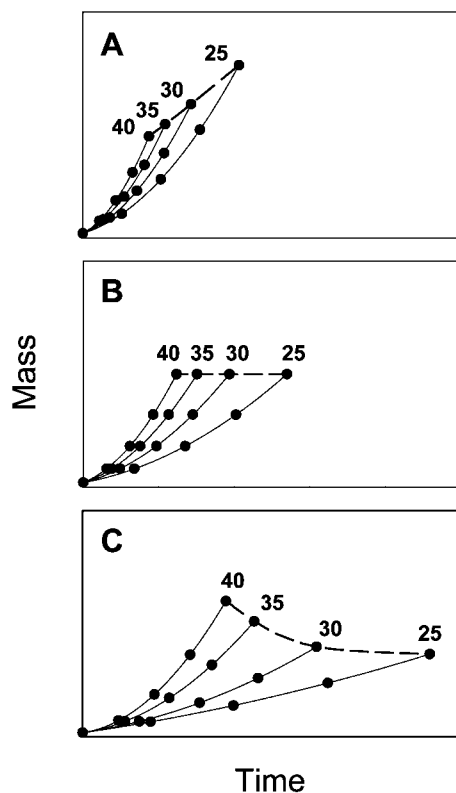


Figure 6: Predicted growth trajectories (solid lines), timing of molts (circles), and mass at adult eclosion (dashed lines) under different rearing temperatures ($^{\circ}\text{C}$). Three scenarios are shown: A, $TT_G < TT_D$; B, $TT_G = TT_D$; and C, $TT_G > TT_D$ (scenarios equivalent to lines e, c, and a, respectively, in fig. 5C).

The prediction that the level of plasticity in adult size shown with temperature is related to the relative difference between TT_G and TT_D was tested using published life-history data on four sympatric species of temperate grasshoppers. As predicted, relative plasticity in adult size was found to be significantly related to the difference between the minimum temperature thresholds for growth rate and development rate ($R^2 = 0.70$, $F = 14.30$, $df = 7$, $P = .009$; fig. 7A). The results of a two-way ANOVA without replication suggest that there was a significant difference between the sexes ($F = 12.80$, $df = 1, 3$, $P = .037$) and a possible species effect ($F = 6.89$, $df = 3, 3$, $P = .074$) in relation to the level of plasticity in adult size with temperature. Adult size plasticity was also found to be significantly related to plasticity in growth rate ($F = 166.06$, $df = 1, 2$, $P = .006$; fig. 7B). The ANCOVA also suggests there are strong sex ($F = 644.77$, $df = 1, 2$, $P = .002$) and species ($F = 83.77$, $df = 3, 2$, $P = .012$) effects.

Discussion

There is currently no clear consensus as to why more than 80% of ectotherms should conform to the temperature-size rule (Angilletta and Dunham 2003). Because virtually all physiological processes are temperature dependent, the intuitive expectation would be for most ectotherms to mature at a larger rather than a smaller adult size at higher temperatures because an increase in temperature can be considered equivalent to a potential increase in season length (Roff 1980). Our modeling results, based on empirical data, support this prediction.

Mousseau (1997) argues that the enigmatic nature of the temperature-size rule relates not to why organisms would find themselves exceptions to it but to why they

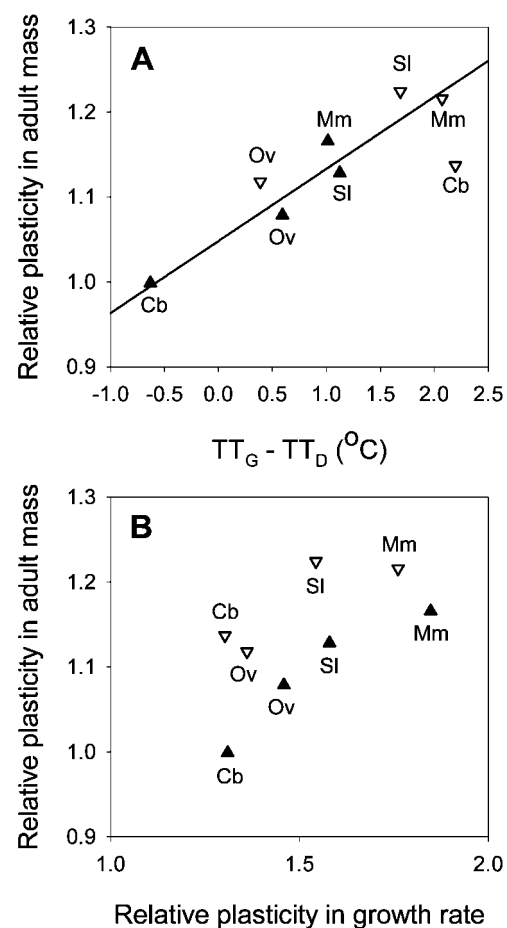


Figure 7: A, Relative plasticity in adult size plotted as a function of the absolute difference between the minimum temperature thresholds for growth and development rate. B, Relationship between relative plasticity in adult size and relative plasticity in growth rate. Data reanalyzed from Willott and Hassall (1998). Species: Cb = *Chorthippus brunneus*; Mm = *Myrmeleotettix maculatus*; Ov = *Omocestus viridulus*; SI = *Stenobothrus lineatus*. Filled triangles = males; open triangles = females.

should conform to it at all. To understand this puzzling response to temperature, it is essential to first understand the proximate mechanisms that determine adult size in ectotherms. Van der Have and de Jong (1996) proposed a proximate mechanism based on enzyme kinetics to show how adult size in ectotherms is dependent on the relative difference between the enthalpy of activation for growth rate ($\Delta H_{A,g}^\ddagger$) and the enthalpy of activation for development rate ($\Delta H_{A,d}^\ddagger$). The term “enthalpy of activation” (ΔH_A^\ddagger), in the Sharpe-Schoolfield equation on which their biophysical model is based, determines the relative slope of the quasi-linear relationship between rate and temperature over the ecologically relevant temperature range. Van der Have and de Jong (1996) demonstrated that if $\Delta H_{A,d}^\ddagger - \Delta H_{A,g}^\ddagger > 0$, the slope of adult size with temperature is negative; that is, the ectotherm should obey the temperature-size rule. Furthermore, the larger the difference between $\Delta H_{A,d}^\ddagger$ and $\Delta H_{A,g}^\ddagger$, the steeper the slope of adult size with temperature. This proximate mechanism has been shown to accurately predict changes in adult size in response to temperature for two temperate and two tropical species of *Drosophila*, all of which conform to the temperature-size rule (Gibert and de Jong 2001).

The quasi-linear region of the relationship between a rate and temperature described by the Sharpe-Schoolfield equation can be closely approximated by fitting a linear relationship (e.g., fig. 8) through values empirically determined within the range of ecologically relevant temperatures (van Straalen 1983; Gilbert and Raworth 1996, 2000; Jarošík et al. 2004). By doing so, the slope of a rate can be described simply as a function of its gradient and intercept in respect to the X-axis (minimum temperature threshold). Manipulating these two terms independently in our degree-time model reveals that plasticity in adult size with temperature is solely dependent on the relative difference between TT_G and TT_D and is not affected by changes to the gradients of these slopes (S_G and S_D , respectively). We show that if $TT_D - TT_G > 0$, an ectotherm should obey the temperature-size rule; if $TT_D - TT_G < 0$, as is the case for *Chorthippus brunneus*, an ectotherm should be an exception to the temperature-size rule. These results together with those of Gibert and de Jong (2001) suggest that this proximate mechanism has the potential to provide a unifying mechanism to describe the response of adult size to temperature in all ectotherms.

Why should TT_G differ from TT_D ? Moreover, why should more than 80% of ectotherms mature at a smaller size in warmer environments ($TT_G < TT_D$), particularly when it would appear to be a nonadaptive strategy, at least at lower temperatures? Van der Have and de Jong (1996) provide a tentative biological explanation. They assume that the processes associated with cell growth and cell differentiation are primarily associated with protein synthesis

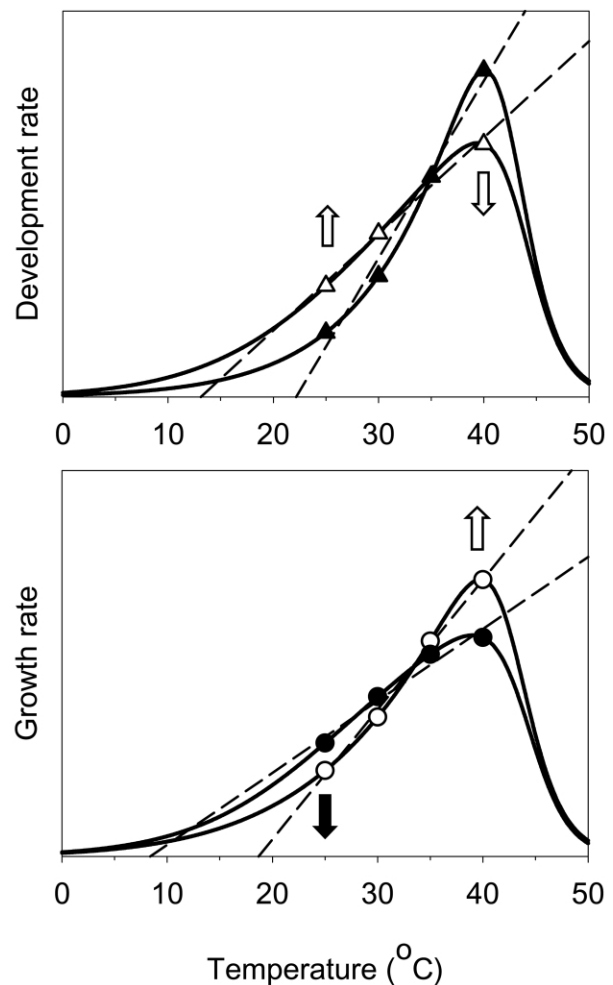


Figure 8: Two alternative theoretical scenarios depicting how a value of $TT_G - TT_D > 0$ might evolve. Solid lines represent empirical rates predicted by the Sharpe-Schoolfield equation; dashed lines represent linear approximations of the quasi-linear region of this relationship over the ecologically relevant temperature range that are used to determine minimum temperature thresholds. *Top*, lower TT_D may evolve as a consequence of selection for optimal adult size across a range of temperatures (adaptive plasticity). Here greater selection pressure for a lower TT_D is depicted for individuals within a univoltine population (open triangles) relative to a multivoltine population (filled triangles). *Bottom*, higher TT_G may evolve as a consequence of selection for greater thermal specialization in growth rate. Here greater selection pressure for a higher TT_G is depicted for individuals within a stenothermal population (open circles) relative to a eurythermal population (filled circles). Open arrows indicate direction of selective pressure; filled arrow indicates effects of genetic constraints on rate.

and DNA replication, respectively. They suggest that the DNA polymerases associated with DNA replication are less dependent on diffusion processes than the larger ribosomal subunits involved in protein synthesis. Because diffusion processes are generally independent of temperature (Q_{10}

close to 1; Hochachka 1991), diffusion is expected to be more rate limiting for protein synthesis than for DNA replication, which will more closely reflect the enzymatic speed of the polymerases (Q_{10} nearer to 2). As a result, the slope coefficient for development rate is expected to be relatively higher than that for growth rate, thereby leading to a higher TT_D .

In van der Have and de Jong's (1996) biophysical model, growth and differentiation are determined by functionally different mechanisms. The enzymes associated with these processes are also assumed to have a heritable basis and are therefore subject to independent selection (though the extent to which TT_G and TT_D can be potentially uncoupled is likely to be subject to genetic constraints; Gilbert and Raworth 1996). If this intracellular explanation is correct, it provides a null hypothesis against which adaptive explanations can be tested (Roff 1992; van der Have and de Jong 1996). Thus, for those species that are exceptions to the temperature-size rule, that is, those where $TT_G - TT_D > 0$, we can ask what factors might have selected for either a relatively lower TT_D or a relatively higher TT_G .

We have shown that when a phenotypic increase in adult size with temperature is adaptive, selection favors a lower TT_D (figs. 3, 5B); specifically, the object of selection is a value of $TT_G - TT_D > 0$. To achieve this, selection must act across the whole thermal reaction norm of development rate (fig. 8, *top*). To do so, it is necessary that temperature be positively related to potential season length (de Jong 1995; Gotthard and Nylin 1995; Nylin and Gotthard 1998). This poses a problem for multivoltine populations because an individual will not be able to distinguish whether, for example, warm conditions that it may currently be experiencing are indicative of a potentially longer season length (sum of effective temperatures) or simply a reflection of the time of year when it has emerged. Furthermore, because of the stochastic nature of pressure fronts, thermal conditions experienced early in development are likely to differ from those experienced at a later stage. Nonetheless, temperature may be used to fine-tune a response if used in conjunction with a reliable cue such as photoperiod. If temperature cannot be used as a reliable cue of potential season length, then selection must favor a development time (SET_D) that optimizes adult size in respect to mean thermal conditions experienced among generations (e.g., fig. 4). In such cases, SET_D , not the value of $TT_G - TT_D$, will be the object of selection. Depending on the response of S_D to such selection pressure, a change in SET_D may or may not lead to a change in TT_D .

The extent to which adult size may potentially be subject to selection will depend on the voltinism of a population. Individuals within univoltine populations stand to benefit the most by maturing at larger size with temperature because fitness will be directly related to the potential fe-

cundity of females. Selection pressure on individuals within multivoltine populations is expected to be relatively weaker because the potential benefit of a given increase in season length will be shared between successive generations. If entering a dormancy stage such as diapause is facultative, maximizing fitness is likely to be more easily achieved by increasing the potential number of generations that can be completed within a given season. Consequently, selection pressure for a positive value of $TT_G - TT_D$ might be expected to be greater in univoltine species such as *C. brunneus* than in multivoltine ectotherms such as *Drosophila*.

An alternative, but not mutually exclusive, adaptive explanation for why $TT_G - TT_D > 0$ relates to independent selection pressure on TT_G . One way in which a higher TT_G could occur is if there is selection for greater thermal specialization or stenothermy in growth rate (Huey and Hertz 1984; Gilchrist 1995). Stenothermal species have narrower response curves and exhibit higher plasticity over a given range of temperatures relative to eurythermal species, which are characterized as having wider response curves and lower plasticity (fig. 8, *bottom*). Stenothermal species thus have steeper thermal reaction norms and hence higher temperature thresholds relative to thermal generalists for a given thermal optimum. At temperatures close to the thermal optima for growth rate, stenotherms are expected to have relatively greater fitness than eurytherms because they can attain a larger, potentially more fecund adult size within a given amount of time.

Chorthippus brunneus is typical of the Acrididae in that it can be regarded as a stenotherm or a high-temperature specialist (Begon 1983; Willott and Hassall 1998). The Acrididae are essentially an insect group of tropical origin (Uvarov 1966, 1977) and have evolved to optimize performance at high internal body temperatures in the region of 35°–40°C (Uvarov 1966, 1977 and references therein; Willott 1997; Willott and Hassall 1998; Walters 2003). Although some species, such as *C. brunneus*, are distributed as far north as Scotland and Scandinavia (Kleukers et al. 1997), thermal optima among the Acrididae, from the tropical locusts to temperate *Chorthippus* spp., appear to have varied little. The reason why grasshoppers have managed to maintain such high thermal optima appears to relate to their extremely efficient thermoregulatory behavior (May 1985). By basking in radiant heat, even relatively small species of grasshoppers can elevate their internal body temperatures by more than 10°C above ambient air temperatures (Richards and Waloff 1954; Uvarov 1977; Anderson et al. 1979; Willott 1997). Such behaviors allow even temperate species such as *C. brunneus* to maintain, at least for part of their lifetime, an internal body temperature in the region of 35°–40°C (Willott 1997). Because the activity of enzymes tends to be restricted to

a narrow temperature range, the maintenance of a high thermal optimum is likely to constrain TT_G to relatively high temperatures (Huey and Hertz 1984; Gilchrist 1995).

The prediction that selection of stenothermal growth strategies leads to greater plasticity in adult size was tested by conducting a comparative analysis on four sympatric species of temperate grasshoppers. The two species considered to be the most thermally specialist in respect to adult size (*Myrmeleotettix maculatus* and *Stenobothrus lineatus*) had, as predicted, the greatest level of growth rate plasticity. They also had the greatest absolute differences in their minimum temperature thresholds for growth and development rates compared with the two more eurythermal species, *C. brunneus* and *Omocestus viridulus* (Willott and Hassall 1998; fig. 7A). Because the response of adult size to temperature is determined only by the relative difference in the minimum temperature thresholds for growth and development rates and not by the gradients of the slopes of these two traits (fig. 5), it would seem likely that selection for greater plasticity in growth rate among these species is at least partly responsible for greater plasticity in adult size with temperature.

To what extent might selection for greater thermal specialization in growth rate provide an adaptive explanation for other exceptions to the temperature-size rule? Grasshoppers appear to have evolved greater thermal specialization as a consequence of their effective use of radiant heat to regulate their internal body temperatures. Other exceptions to the temperature-size rule might therefore share similar traits relating to thermoregulatory behavior. For an ectotherm to take full advantage of radiant heat, it must be terrestrial and large enough in order to substantially raise its internal body temperature above ambient air temperatures (Willmer and Unwin 1981). These conditions are consistent with the findings that among the reptiles, turtles are, in general, found to conform to Bergmann's rule, while, in general, snakes and lizards are found to be exceptions to it (Ashton and Feldman 2003). We do not claim that this adaptive explanation applies to all of the exceptions to the temperature-size rule (Atkinson 1994). Some of these organisms, however, have evolved life-history strategies that have reduced their exposure to variable thermal conditions and hence might have developed a greater degree of thermal specialization.

Whatever the adaptive explanations for the relative positions of the minimum temperature thresholds for growth and development rates, all ectotherms should, in theory, conform to an underlying mechanism based on their enzyme kinetics. For a general explanation of the temperature-size rule to be truly general, it must include the causal mechanisms that explain why most organisms should obey the temperature-size rule, as well as why some organisms are exceptions to it (Dunham and Beaupre 1998; Angilletta

and Dunham 2003). We believe that the mechanistic explanation originally proposed by van der Have and de Jong (1996) meets this condition. In identifying the role of temperature thresholds, we show that adaptive explanations for ectotherm responses may be sought in relation to independent selection pressures acting on growth and development rates.

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