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E-Article

Why “Suboptimal” Is Optimal: Jensen’s Inequality and Ectotherm Thermal Preferences

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abstract: Body temperature (T_b) profoundly affects the fitness of ectotherms. Many ectotherms use behavior to control T_b within narrow levels. These temperatures are assumed to be optimal and therefore to match body temperatures ($T_{r_{max}}$) that maximize fitness (r). We develop an optimality model and find that optimal body temperature (T_o) should not be centered at $T_{r_{max}}$ but shifted to a lower temperature. This finding seems paradoxical but results from two considerations relating to Jensen’s inequality, which deals with how variance and skew influence integrals of nonlinear functions. First, ectotherms are not perfect thermoregulators and so experience a range of T_b. Second, temperature-fitness curves are asymmetric, such that a T_b higher than $T_{r_{max}}$ depresses fitness more than will a T_b displaced an equivalent amount below $T_{r_{max}}$. Our model makes several predictions. The magnitude of the optimal shift ($T_{r_{max}} - T_o$) should increase with the degree of asymmetry of temperature-fitness curves and with T_b variance. Deviations should be relatively large for thermal specialists but insensitive to whether fitness increases with $T_{r_{max}}$ (“hotter is better”). Asymmetric (left-skewed) T_b distributions reduce the magnitude of the optimal shift but do not eliminate it. Comparative data (insects, lizards) support key predictions. Thus, “suboptimal” is optimal.

Keywords: optimality, fitness, thermal sensitivity, thermodynamics, thermoregulation, thermal preference.

> The question naturally arises of what is the best or optimum temperature for the life of a particular species … Janisch … considers that there is an absolute optimum, but this is too difficult to define at present for practical purposes. (Fraenkel and Gunn 1940)

Body temperature has profound effects on the performance and fitness of ectotherms (fig. 1; Fry 1947; Bennett 1980; Huey and Berrigan 2001). Not surprisingly, diverse ectotherms modify their behavior (e.g., their use of sun and shade, activity time; Cowles and Bogert 1944; Heath 1965; Kingsolver and Watt 1983; Porter and Tracy 1983; Stevenson 1985) and thereby maintain body temperature (T_b) within a narrow, species-specific range, at least while active (Avery 1982; Cossins and Bowler 1987; Chown and Nicolson 2004). These thermoregulatory behaviors dominate not only spatial and temporal activity patterns of ectotherms (Roughgarden et al. 1981; Porter and Tracy 1983; Stevenson 1985; Hertz 1992) but also their performance (Hertz et al. 1983; Huey 1983; Waldschmidt and Tracy 1983; Angilletta et al. 2002*b*) and fitness (Kluger 1979; Christian and Tracy 1981; Dunham 1993).

The physiological and adaptive significance of preferred body temperatures[1] of ectotherms has been a central issue for decades. Physiological ecologists have long assumed that thermal preferences and thermal physiology are closely coadapted, such that thermal preferences coincide with temperatures that maximize Darwinian fitness (Cowles and Bogert 1944; Dawson 1975; Beitinger and Fitzpatrick 1979; Coutant 1987; Huey and Bennett 1987; Gilchrist 1995; Angilletta et al. 2006). Surprisingly, however, the assumption that thermal preferences should match temperatures optimal for fitness itself has never been examined either empirically or theoretically. Of course, many studies document that thermal preferences are generally close to body temperatures that maximize various measures of physiological performance (Angilletta et al. 2002*a*; but see Dawson 1975; Beitinger and Fitzpatrick 1979; Bennett 1980; Jobling 1981; Huey 1982; Stevenson et al. 1985; Huey and Bennett 1987).

Here we develop a simple optimality model to explore

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[1] Preferred body temperatures (T_p) of ectotherms are traditionally determined in laboratory thermal gradients (Licht et al. 1966) and are sometimes called “thermal preferenda” or “selected temperatures” (Pough and Gans 1982).

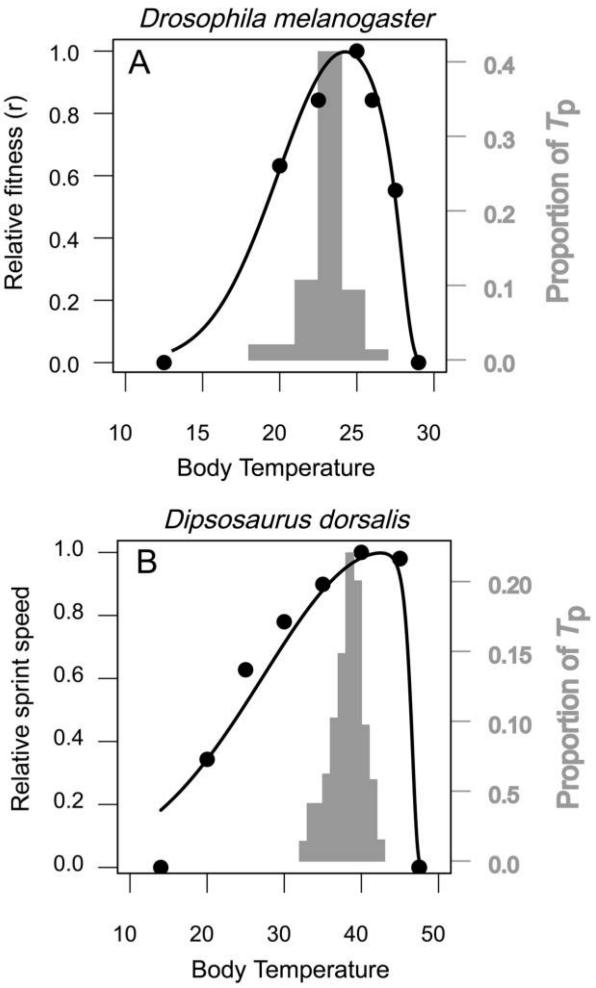

Figure 1: *A*, Thermal dependence of relative fitness (intrinsic rate of population growth *r*) versus body temperature for *Drosophila melanogaster* (data from Siddiqui and Barlow 1972), with a fitted curve. The histogram is the frequency distribution for thermal preferences T_p in the laboratory (data from Sayeed and Benzer 1996). Mean $T_p = 23.8°C$ (SD = 1.4°C), $T_{r_{\max}} = 24.3°C$, asymmetry = 0.4. *B*, Thermal dependence of sprint speed for the lizard *Dipsosaurus dorsalis* (van Berkum 1988), with a histogram showing the distribution of T_p in the laboratory (DeWitt 1967). Mean $T_p = 38.5°C$ (SD = 2.1°C, $T_{v_{\max}} = 41.1°C$, asymmetry = 0.8).

a fundamental question in behavioral physiology: which temperatures should a particular ectotherm select when given free access to a range of body temperatures? The answer might seem obvious, at least if the thermal dependence of Darwinian fitness is known for the species in question; specifically, animals should regulate at the specific temperature that maximizes fitness ($T_{r_{\max}}$). For example, *Drosophila melanogaster* would be expected to select a temperature of ~24°C, which corresponds to its $T_{r_{\max}}$ (fig. 1*A*). However, the model we develop below predicts that ectotherms will generally maximize total fitness over some time period if their T_b range is centered at a body temperature below $T_{r_{\max}}$. Surprisingly then, "suboptimal" is optimal. To our knowledge, this novel and superficially paradoxical result has been noted only once (Beuchat and Ellner 1987) in prior discussions of ectotherm thermal preferences.

Why might "suboptimal" body temperatures maximize total fitness? Two factors are involved: (1) thermal fitness curves of ectotherms are nonlinear and highly asymmetric, such that fitness drops relatively rapidly at temperatures above the optimum (figs. 1, 2; Huey and Stevenson 1979; Gilchrist 1995; Huey and Berrigan 2001; Izem and Kingsolver 2005), and (2) ectotherms are not perfect thermoregulators but experience a range of body temperatures (Huey 1974; Heinrich 1981; Feder and Lynch 1982; Pianka 1986; Hertz et al. 1993). Therefore, a body temperature 2°C above the fitness optimum $T_{r_{\max}}$ will reduce fitness much more than will a body temperature 2°C below the optimum (fig. 2). Consequently, total fitness over time might be maximized—at least in a fluctuating environment—by centering thermal preferences at a temperature below the body temperature that maximizes instantaneous fitness.

This result follows from the principle of Jensen's inequality (Smallwood 1996; Ruel and Ayers 1999), which is a mathematical property of nonlinear functions such as thermal fitness curves. Jensen's inequality states that optimal behavior cannot be correctly predicted by the average T_b alone but depends strongly on the variance and skewness in T_b (Beuchat and Ellner 1987; Ruel and Ayers 1999). An appreciation of these issues is growing in ecology (Roughgarden 1974; Smallwood 1996), physiological ecology (Beuchat and Ellner 1987; Ruel and Ayers 1999; Shine et al. 2003), and applied thermal biology (Worner 1992).

To explore these issues, we develop a deterministic model of optimal thermoregulatory behavior of ectotherms. We then use simulations to evaluate three general questions that relate to the shape and height of thermal fitness curves (Huey and Kingsolver 1989; Gilchrist 1995; Izem and Kingsolver 2005): (i) Is the mean optimal body temperature (T_o) lower than $T_{r_{\max}}$, and specifically, does the magnitude of the deviation increase with the degree of asymmetry of the thermal fitness curve? Our model predicts that ectotherms with highly asymmetric fitness curves should have T_o shifted relatively far below $T_{r_{\max}}$. (ii) Does the magnitude of the deviation of T_o below $T_{r_{\max}}$ differ for thermal generalists versus thermal specialists? Our model predicts that thermal specialists (i.e., species having narrow fitness curves; Levins 1968; Huey and Slatkin 1976; Gilchrist 1995; Izem and Kingsolver 2005) should show a relatively large deviation of T_o below $T_{r_{\max}}$ as fitness of such species shifts rapidly with temperature. For similar reasons, we predict that imprecise

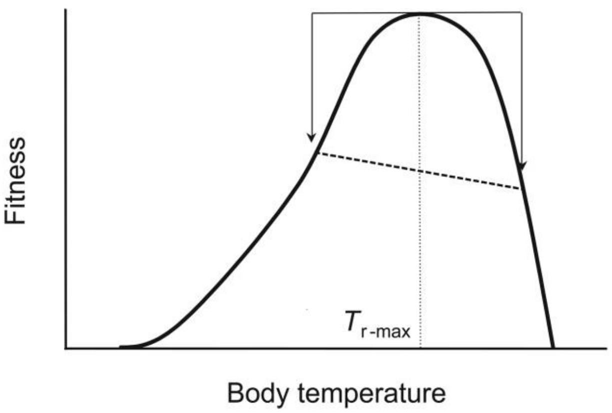

Figure 2: Thermal dependence of fitness of ectotherms is highly asymmetric (Huey and Stevenson 1979; Gilchrist 1995). Consequently, a T_b higher than $T_{r_{max}}$ reduces fitness more than a T_b the same level below the $T_{r_{max}}$.

thermoregulators (high variance in T_b) should also show relatively large shifts for a given thermal sensitivity. (iii) Is T_o influenced by thermodynamic effects on maximal fitness? A "hotter is better" model notes that metabolic processes occur faster at higher temperatures because average kinetic energy increases with temperature (Hamilton 1973; Bennett 1987; Savage et al. 2004); consequently, species with relatively high $T_{r_{max}}$ should and generally do have relatively high fitness. Thus, for several groups of ectotherms, r_{max} increases with $T_{r_{max}}$ (Savage et al. 2004; Frazier et al. 2006). However, our model predicts "hotter is better" would not affect T_o unless thermodynamics alters the shape as well as the height of the fitness curve.

We also examine the effect of asymmetrical T_b distributions (left-skewed; see fig. 1*B*), which characterize many ectotherms (DeWitt and Friedman 1979). Our model shows that highly skewed distributions should reduce but not eliminate the magnitude of the shift of T_o below $T_{r_{max}}$.

We challenge these predictions with two comparative data sets. If the thermoregulatory behavior of ectotherms is consistent with our model, then thermal preferences (T_p) of a species should be lower than temperatures ($T_{r_{max}}$) at which its rate of population growth is maximal. The requisite data (T_p and $T_{r_{max}}$) are available only for a few species of invertebrates (mainly insects). The thermal dependence of fitness has never been measured in lizards, but we can determine whether the difference between T_p and the optimal temperature for sprint performance ($T_{v_{max}}$) increases with the magnitude of asymmetry of thermal performance curves and decreases with the degree of thermal generalization. As shown below, both comparative analyses provide strong support for the model.

Methods

The General Model

Our model is based on a model of thermoregulation developed by Huey and Slatkin (1976; see also Tracy and Christian 1983) but is simplified by excluding any costs of thermoregulation. Thus, an ectotherm's Darwinian fitness over time depends on only two functions: (1) the frequency distribution of body temperatures actually experienced ($f(T_b)$) and (2) the mapping of those body temperatures onto fitness (i.e., the thermal sensitivity of fitness, $w(T_b)$; figs. 1, 2). Formally, an ectotherm's total fitness (W) is found by weighting its thermal fitness function $w(T_b)$ by the frequency of T_b ($f(T_b)$) experienced during a specified time period (see Haldane and Jayakar 1963; Huey and Slatkin 1976; Gilchrist 1995):

$$W = \int [w(T_b) \times f(T_b)]dT_b. \tag{1}$$

Thus, an ectotherm that is active at T_b near $T_{r_{max}}$ should have higher total fitness than one that is active at T_b far from $T_{r_{max}}$, all else being equal.

To determine the optimal temperature for a given $w(T_b)$, we calculated $W(T_b)$ for a variety of T_b and then determined the mean body temperature (T_o) that maximizes W, for a given thermal sensitivity $w(T_b)$ and a given shaped T_b distribution (fig. 3). We assume that the thermal environment is sufficiently heterogeneous that all T_b's within an ectotherm's tolerance zone are available, which of course is not always the case (Christian and Weavers 1996). Also, by manipulating the size and shape of fitness curves (and of T_b distributions), we evaluate the various hypotheses described in the introduction to this article.

Our model makes several assumptions. (1) The model is deterministic. (2) Animals never suffer injurious or lethal temperatures. (3) Fitness depends only on the first-order effects of temperature and is independent of prior temperature experience (Fry and Hart 1948; Wilhoft 1958), age (Brett 1970), health (Kluger 1979), reproductive status (Peterson et al. 1983; Beuchat and Ellner 1987; Schwarzkopf and Shine 1991), or feeding state (Brett 1971; Huey and Slatkin 1976; Hainsworth 1978). (4) Potential costs of thermoregulation (Huey 1974; Huey and Slatkin 1976; Withers and Campbell 1985; Blouin-Demers and Nadeau 2005; Herczeg et al. 2006) are assumed to be inconsequential. In the "Discussion," we anticipate the probable impact of relaxing some assumptions.

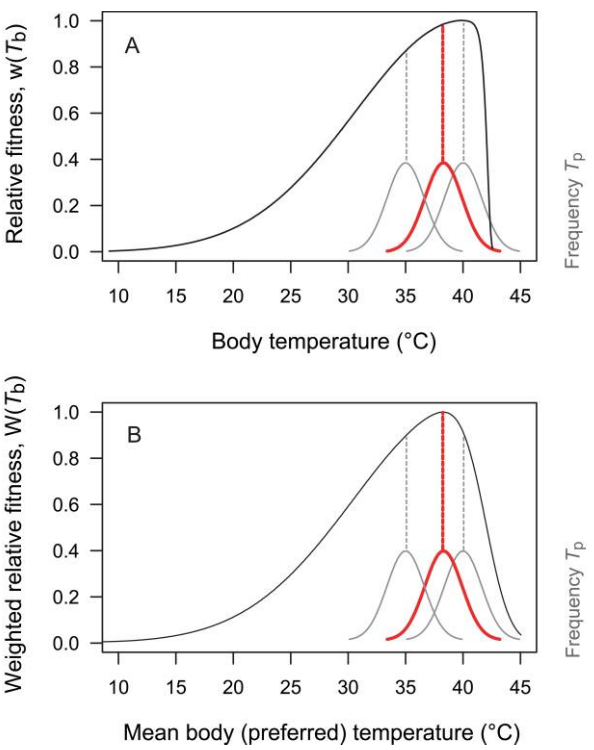

Figure 3: *A*, Relative fitness $w(T_b)$ as a function of T_b (*black line*) for a hypothetical ectotherm (optimal temperature = 40.0°C, asymmetry = 0.84) and three sample T_b distributions (*gray or red lines*: mean T_b [left to right] = 35°, 38.3°, and 40°C; variance ~2.2°C). Dashed gray or red lines connect mean T_b with the associated $w(T_b)$. *B*, Relative weighted fitness $W(T_b)$ as a function of different mean T_b's, with the three T_b distributions. Note that the T_b maximizing $W(T_b)$ (*thick red line*) is 1.7°C lower than the temperature that maximizes $f(T_b)$. The optimal T_b increases weighted fitness by 9.4%.

Modeling the Thermal Dependence of Fitness

Thermal fitness curves of ectotherms are always asymmetric (fig. 1; see also fig. 1 in Gilchrist 1995; Huey and Berrigan 2001; Angilletta et al. 2002*b*; Izem and Kingsolver 2005); to describe these curves, we used a Gaussian multiplied by a Gompertz function (G × G function; fig. 1):

$$w(T_b) = r_{\max} e^{\{-\exp[\beta(T_b - T_{r\max}) - 8] - \alpha(T_b - T_{r\max})^2\}}, \qquad (2)$$

where $r_{\max}$ is the maximal fitness, α is the rise rate controlling the steepness of the left portion of the fitness curve, β is the fall rate on the right portion, T_b is body temperature, $T_{r_{\max}}$ is the T_b at which $w(T_b)$ is maximal, and 8 is a constant that empirically improves the fit. This G × G curve is continuous, its parameters are easily modified to change the shape and position of the function, and it proved more tractable in this regard than other potential curves (e.g., Logan et al. 1976; Sharp and De Michele 1977; Gilchrist 1995). Moreover, it usually fitted empirical data reasonably well near $T_{r_{\max}}$ (fig. 1). In any case, the exact form of the model's fitness function, $w(T_b)$, will not affect qualitative predictions of the model, as long as asymmetry and convexity are maintained.

To quantify the degree of asymmetry, we developed the following index:

$$\text{asymmetry} = \frac{2T_{r_{\max}} - T_{\max} - T_{\min}}{T_{\max} - T_{\min}}, \qquad (3)$$

where $T_{\max}$ and $T_{\min}$ represent the upper and lower limiting temperatures ($r = 0$). The index ranges from 0 for a perfectly symmetric curve to 1 for a right triangle.

Simulating Optimal Thermoregulation

Because an analytical solution for equation (1) (with substituted G × G functions) does not exist, we ran numerical simulations in Matlab. To set the parameters of a basic fitness curve, $w(T_b)$, we started with parameters that gave fitness curves similar in shape to those for speed versus T_b for the lizard *Dipsosaurus dorsalis* (fig. 1*B*; tolerance range set to 35°C). When manipulating the degree of asymmetry of fitness curves (fig. 4*A*), we held the tolerance range constant but shifted the optimum. When manipulating the degree of generalization (fig. 4*C*; generalists vs. specialists), we held the area under the curve constant, as in previous models that assume a trade-off between maximal fitness and breadth (Levins 1968; Huey and Slatkin 1976; Gilchrist 1995), and manipulated the tolerance range and, thereby, breadth. When simulating "hotter is better" (fig. 4*E*), we held asymmetry and the tolerance range constant but made $r_{\max}$ directly proportional to $T_{r_{\max}}$.

Next, we set the shape of the T_b distribution. For most simulations, we used a Gaussian distribution of T_b, with a variance equivalent to that for *Dipsosaurus dorsalis* (fig. 1*B*). However, to simulate the effects of asymmetry (skew) of T_b, we used a G × G function and manipulated asymmetry (0–0.9; fig. 5).

We calculated $W(T_b)$ for a series of mean T_b values ranging from 10°C below to 10°C above $T_{r_{\max}}$, in 0.1°C steps. We then determined the mean of the T_b distribution (T_o) that yielded the highest W and computed the deviation between T_o and $T_{r_{\max}}$. A hypothetical example of the protocol is shown in figure 3. Here the T_b that maximizes $W(T_b)$ is 1.7°C below the temperature that maximizes $w(T_b)$. The shift is small but nonetheless increases $W(T_b)$ by 9.7%. (Note: we did not assign a penalty if some T_b's exceeded the upper critical temperature, where $w(T_b) \sim$

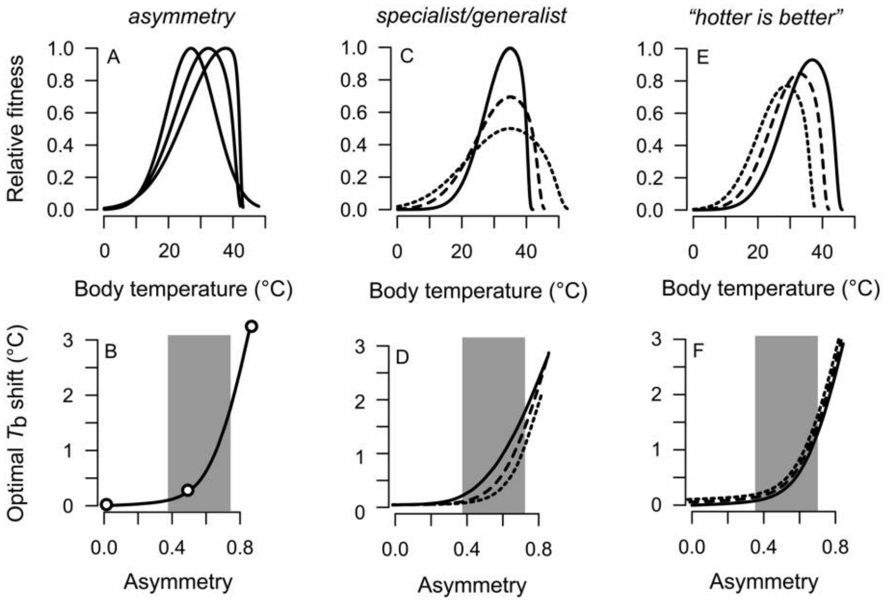

Figure 4: *A*, Fitness curves with three levels of asymmetry (left to right: 0, 0.5, 0.9). *B*, Results of a sample simulation showing that the magnitude of the optimal shift of mean T_b below $T_{r_{\max}}$ increases nonlinearly with the degree of asymmetry of the fitness curve (circles correspond to the asymmetries of fitness curves in *A*). The shaded bar shows the range of asymmetries observed for the thermal dependence of sprint speed of lizards. *C*, Fitness curves showing trade-off between generalists and specialists (three examples). Fitness breadths (temperature range over which fitness is $\geq 80\%$ of $r_{\max}$) for the three curves are 9.1°, 13.3°, and 17.6°C. *D*, The optimal shift increases with the degree of thermal specialization (*C*). *E*, Fitness curves for "hotter is better." *F*, The optimal shift is independent of "hotter is better" (*E*).

0. Had we done so, this would have favored an even larger shift in thermal preference.)

Comparative Tests

To evaluate whether the thermoregulatory behavior of ectotherms is consistent with predictions of our model, we compared the mean preferred body temperature (T_p) of a species in a laboratory thermal gradient with the body temperature at which its fitness ($T_{r_{\max}}$) or sprint performance ($T_{v_{\max}}$) is maximal. Mean T_p of diurnal lizards correlates with mean field T_b, (see fig. 5 in Huey 1982), suggesting that a lizard's thermoregulatory behavior in the field is usually governed by underlying thermal preferences, as is also suggested by neurophysiological considerations (Barber and Crawford 1977; DeWitt and Friedman 1979).

We compiled two data sets from the literature. The first set combined data on optimal temperature ($T_{r_{\max}}$) for fitness (intrinsic rate of population growth) of ectotherms (invertebrate ectotherms) and their mean thermal preferences in the laboratory; these data enabled us to test empirically whether T_p was lower than $T_{r_{\max}}$, as predicted.

The thermal dependence of fitness of lizards has never been measured, but we were able to compile published data on the thermal dependence of performance (sprint speed) and on T_p for 63 species of lizards (appendix). For asymmetry and breadth estimates, we could include only those species for which T_p, the critical thermal maximum (CT$_{\max}$), and the critical thermal minimum (CT$_{\min}$) were known ($N = 52$). To quantify speed as a continuous function of T_b, we used a cubic polynomial to fit average speed versus T_b (we used corrected speeds if given; van Berkum 1986). (Note: we substituted a cubic because the G × G function failed to converge for several species.) Then we estimated the body temperature at which speed was maximal ($T_{v_{\max}}$), the asymmetry index (eq. [3]) for each species, and the breadth of temperatures over which speed was $\geq 85\%$ of maximal speed (B_{85}), a measure of the degree of thermal generalization (Huey and Stevenson 1979).

Mean T_p's in laboratory thermal gradients (Licht et al. 1966) were culled from the literature. If multiple values were available for a given species, we selected the value with the largest sample size. Median values would have been preferable (DeWitt and Friedman 1979) but are infrequently published. Because means are lower than medians for left-skewed data, our use of means does create a small bias in favor of the first prediction, that mean T_p is below $T_{v_{\max}}$, but it should not bias the prediction that the magnitude of the shift will vary with fitness asymmetry.

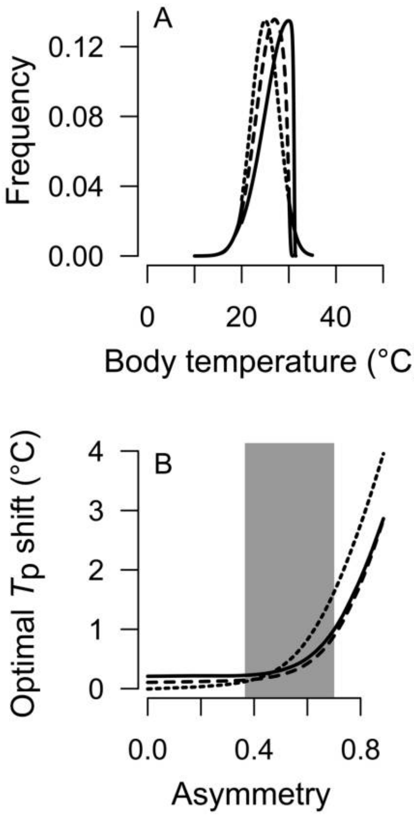

Figure 5: *A*, Body temperature distributions (T_{b}) with three levels of T_{b} asymmetry (left to right: 0, 0.5, 0.9). *B*, Magnitude of the optimal shift of T_{b} below $T_{r_{\max}}$ for T_{b} distributions with different asymmetries and for thermal fitness curves with different degrees of asymmetry. If thermal fitness curves are highly symmetric (greater than ~0.5), the magnitude of the optimal shift is greatest for symmetrical T_{b} distributions but still positive for asymmetric ones.

Because of nonindependence of species values (Felsenstein 1985), we developed a phylogenetic hypothesis for sampled species (assuming unit branch lengths; see appendix) and computed standardized independent contrasts in PDAP (Garland et al. 1993). We then estimated the evolutionary correlation between asymmetry and the deviation of mean T_{p} from $T_{v_{\max}}$, as well as the correlation between B_{85} and the deviation of mean T_{p} from $T_{v_{\max}}$; these correlations test some predictions of our model.

Asymmetry and B_{85} were inversely correlated for lizards. Thus, to evaluate the independent impact of these two traits, we ran a structural equations analysis (Bauwens et al. 1995; Kline 2005) through the origin, with separate paths from B_{85} and from asymmetry to the magnitude of the deviation of mean T_{p} from $T_{v_{\max}}$.

Results

Model Predictions

Fitness asymmetry. To examine the effect of the degree of asymmetry of the fitness curve (fig. 4*A*) on the magnitude of the deviation of the optimal temperature T_{o} below $T_{r_{\max}}$ (fig. 4*B*), we used a “generic” fitness curve and manipulated parameter values to generate a set of fitness curves ranging in asymmetry from 0 to 0.9 (fig. 4*A*). As expected, the magnitude of the optimal shift ($T_{r_{\max}} - T_{\mathrm{o}}$) increased with the degree of fitness-curve asymmetry (fig. 4*B*). The relationship is strongly nonlinear, and the optimal deviation increases steeply for very asymmetric fitness curves, especially in the observed range of asymmetries for lizard sprint speeds (fig. 4*B*, *shaded area*). At moderate to high asymmetries (fig. 4*A*), T_{b} above $T_{r_{\max}}$ substantially reduces fitness, thus favoring T_{o} well below $T_{r_{\max}}$. The optimal deviation is, of course, sensitive to the particular breadth of the fitness curves and of T_{b}, but the general pattern is robust.

Generalists versus specialists. Next, we simulated optimal deviations for thermal fitness curves having different breadths, representing a continuum of generalists and specialists, while holding the breadth of the T_{b} distribution constant. Three representative fitness curves are depicted in fig. 4*C*. The magnitude of the optimal shift increased with the degree of specialization (fig. 4*D*), reflecting the relatively rapid decline in fitness at $T_{\mathrm{b}} > T_{r_{\max}}$ for thermal specialists (fig. 4*C*). However, for extremely asymmetric fitness curves, optimal shifts appear to converge for different degrees of specialization (fig. 4*D*), as fitness curves for $T_{\mathrm{b}} > T_{r_{\max}}$ are steep, even for thermal generalists.

Hotter is better. Thermodynamic considerations (Savage et al. 2004) predict that maximal fitness should be positively related to $T_{r_{\max}}$ (fig. 4*E*). This effect has no impact, however, on the optimal shift (fig. 4*F*). This result depends on our assumption (above) that hotter-is-better influences only the height—but not the general shape—of the fitness curves (fig. 4*E*).

Asymmetry of the T*_b* *distribution.* The above simulations use a Gaussian distribution for T_{b}. However, because body temperature distributions are often (fig. 1*B*) but not always (fig. 1*A*) left-skewed, both in gradients and in the field (Barber and Crawford 1977; DeWitt and Friedman 1979), we examined how shifts in skewness of the T_{b} distribution (fig. 5*A*) in combination with different asymmetries of $w(T_{\mathrm{b}})$ influence the optimal T_{b} shift. Symmetrical T_{b} distributions favor the largest shift in T_{b} (fig. 5*B*), no doubt because high T_{b}’s are relatively frequent and thus have a major impact on total fitness. Nevertheless, asymmetrical T_{b} distributions still favor a large shift in T_{o} for moderately to highly asymmetric fitness curves (fig. 5*B*).

Comparative Tests

Our model makes several predictions that are potentially testable with empirical data. The best test would involve comparing, for multiple ectotherms, their thermal preferences and their thermal sensitivity of Darwinian fitness (e.g., fig. 1*A*) and to have both data sets gathered by the same investigators on the same stocks. The thermal dependence of fitness has been quantified for many species of invertebrate ectotherms (Huey and Berrigan 2001; Frazier et al. 2006); nevertheless, we found few species for which both thermal preferences and thermal dependence of fitness are known (table 1). In almost all cases, traits were measured by different investigators on different stocks. Moreover, estimates of T_p are somewhat sensitive to acclimation effects (Prince and Parsons 1977; Fogleman 1979), rendering any comparisons suspect. Despite these caveats, observed patterns are worth examining (Angilletta et al. 2002*a*).

Table 1 shows $T_{r_{\max}}$ and T_p for several species, most of which are insects. Consistent with our model's prediction, T_p is generally below $T_{r_{\max}}$. Possible exceptions are *Drosophila melanogaster* and *Cryptolestes ferrugineus*, for which one estimate of T_p is slightly higher than $T_{r_{\max}}$ (fig. 1*A*; table 1).

More extensive data are available on the thermal preferences and on thermal dependence of sprint speed of lizards (e.g., fig. 1*B*). Sprint speed is ecologically relevant and may influence survival (Christian and Tracy 1981; Bennett and Huey 1990; Jayne and Bennett 1990; Irschick and Garland 2001), and the thermal dependence of lizard sprint speed has been studied extensively. Note, however, that sprint speed is less sensitive to temperature (i.e., is relatively generalized) than are some other physiological traits, such as digestion (fig. 5 in Huey 1982; Angilletta et al. 2002*a*), so any impact of asymmetry will be blunted (see "Generalists versus specialists"). Consequently, a determination that patterns involving sprint speed match our predictions would be strong support for our model. Even so, we recognize that true T_o must reflect interactions with many other performance traits (Huey 1982; Angilletta et al. 2002*a*) and with food levels and metabolism (Brett 1971; Hainsworth 1978; Huey 1982).

Our first prediction—that T_p should be less than $T_{v_{\max}}$ for sprint speed—was observed in 48 of 63 species (76.2%, binomial test, $P \ll .001$). (Note: the sample size here is larger than in our comparisons with asymmetry because the latter data set required data on $CT_{\min}$, which was not available for several species.) The mean difference (1.8°C; 95% confidence interval [CI] = 1.1°C–2.5°C) was significantly greater than 0 (*t*-test, $P \ll .001$).

Table 1: Comparative data on temperature at which fitness (rate of population growth) is maximal ($T_{r_{\max}}$) and mean preferred body temperature (T_P) in laboratory thermal gradients

Species (common name) and trait	Temperature (°C)	Source
Caenorhabditis elegans (nematode, CB 4856):		
$T_{r_{\max}}$	~24	P. Phillips, personal communication
T_p	~17	P. Phillips, personal communication
Artemia parthenogenetica (brine shrimp):		
$T_{r_{\max}}$	32.3	Jia et al. 2002
T_p	22.2–23.9	Zhang and Lefcort 1991
Ophryotrocha labronica (polychaete):		
$T_{r_{\max}}$	>28	Åkesson 1976; Prevedelli and Simonini 2001
T_p	~20.4	Åkesson 1976
Drosophila melanogaster (fly):		
$T_{r_{\max}}$	24.3	Siddiqui and Barlow 1972
T_p	23.5–25.2	Fogleman 1979
T_p	23.8	Sayeed and Benzer 1996
Tribolium castaneum (beetle):		
$T_{r_{\max}}$	35.3	Howe 1962
$T_{r_{\max}}$	35	White 1987
T_p	28.2	Langer and Young 1976
Pterohelaeus darlingensis (beetle):		
$T_{r_{\max}}$	28.2	Allsopp 1981
T_p	17.3	Allsopp et al. 1980
Cryptolestes ferrugineus (beetle):		
$T_{r_{\max}}$	33.45	Smith 1965
T_p	30–36.5	Jian et al. 2002

Note: Multiple estimates of T_p or of $T_{r_{\max}}$ are available and listed for a few species.

Our second prediction—that the magnitude of the difference between $T_{v_{\max}}$ and T_{p} would increase with the degree of asymmetry of the performance curve—was also supported. The nonevolutionary correlation was 0.48 ($P < .001$; fig. 6*A*), and the evolutionary one was 0.54 ($P \ll .001$; fig. 6*B*).

Our third prediction—that the magnitude of the difference between $T_{v_{\max}}$ and T_{p} would decrease with the degree of thermal generalization (i.e., thermal breadth or B_{85})—was also supported. The nonevolutionary correlation was -0.51 ($P < .001$; fig. 6*C*), and the evolutionary one was -0.41 ($P = .003$; fig. 6*D*).

The above tests are consistent with model predictions. However, while analyzing the data, we discovered that asymmetry and breadth were negatively correlated (nonphylogenetic $= -0.53$, $P \ll .001$; phylogenetic $= -0.43$, $P = .002$). Thus, lizards with relatively asymmetric performance curves are also relatively specialized. This correlation potentially confounds our univariate comparisons above, so we ran structural equation models (fig. 7) through the origin, with and without phylogenetically independent contrasts. We report bootstrapped values. Model predictors (asymmetry, breadth) of the difference between $T_{v_{\max}}$ and T_{p} explained 32% of its variance. Standardized coefficients (maximum likelihood) were 0.289 (95% CI $= 0.094$ to 0.451) for asymmetry and -0.356 (-0.531 to -0.156) for breadth; both were significant ($P = .014$ and 0.007, respectively). Thus, patterns in the structural equation model support model predictions that the difference between $T_{v_{\max}}$ and T_{p} should increase with the degree of asymmetry but decrease with the magnitude of breadth. The nonphylogenetic model gave comparable results.

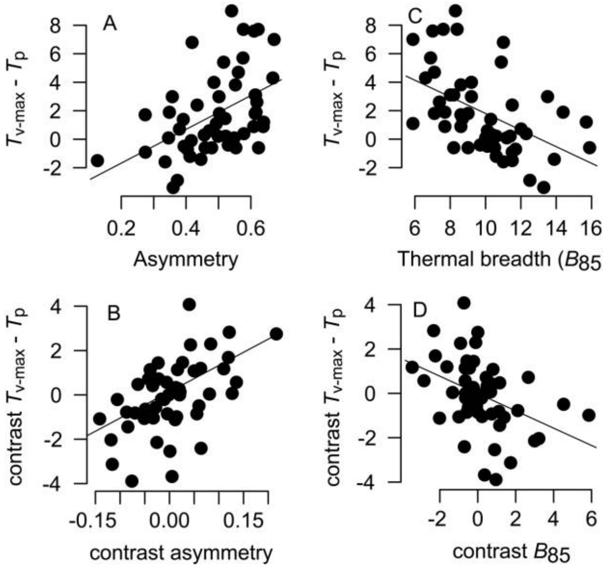

Figure 6: *A*, *B*, Empirical difference between $T_{v_{\max}}$ and mean T_{p} increases with the asymmetry of a lizard's performance (speed) curve ($A =$ nonphylogenetic patterns; $B =$ standardized independent contrasts, with regression through 0). *C*, *D*, Empirical difference between $T_{v_{\max}}$ and T_{p} decreases with a lizard's thermal performance breadth ($C =$ nonphylogenetic patterns; $D =$ standardized independent contrasts).

Discussion

A classical hypothesis in physiological ecology holds that preferred body temperatures of ectotherms should be coadapted with and match the temperatures at which Darwinian fitness is maximal (Cowles and Bogert 1944; Beitinger and Fitzpatrick 1979; Coutant 1987; Huey and Bennett 1987; Gilchrist 1995; Angilletta et al. 2006). This hypothesis has been tested only indirectly via studies that search for interspecific correlations between T_{p} and the temperatures that maximize physiological performance. In general, T_{p} are close to T_{o}, but they are often below T_{o} (see "Comparative Tests").

Here we show that the classical hypothesis is theoretically sound if and only if ectotherms are perfect thermoregulators (see also Beuchat and Ellner 1987) or if fitness curves are symmetrical about the optimum. However, because neither is true, the classical hypothesis is necessarily invalid. Our model, which explicitly incorporates variation in T_{b} as well as asymmetry of fitness curves, predicts that (1) the optimal body temperatures should be centered at a temperature below that at which fitness is maximal, (2) the optimal deviation increases with the degree of asymmetry (fig. 4*B*), and (3) the optimal deviation increases with the degree of thermal specialization (fig. 4*D*) and (4) with the variance in T_{b} (not figured). These predictions follow intuitively from the observation that temperature deviations above the $T_{r_{\max}}$ result in more of a decrement in fitness than equivalent deviations below $T_{r_{\max}}$.

Comparative data on T_{p} and fitness ($T_{r_{\max}}$) are few (table 1) but generally support the first prediction. A much larger data set is available for T_{p} and $T_{v_{\max}}$ (sprint speed) for lizards. Consistent with the model's predictions, most lizards (76.2%) do have T_{p} below $T_{v_{\max}}$. However, C. R. Tracy (personal communication) has called our attention to a possible bias in this comparison. Light intensities in laboratories are usually much lower than in nature, and low light levels can stimulate melatonin, which lowers T_{p} in some reptiles (Lutterschmidt et al. 2003). In this case, T_{p} in the laboratory might be artificially lower than true T_{p}. Similarly, if T_{p} measurements are done on fasting lizards, T_{p} might be lower (Hainsworth 1978; Huey 1982) than for lizards in nature, which normally have food in their guts (Huey et al. 2001). We cannot directly evaluate these

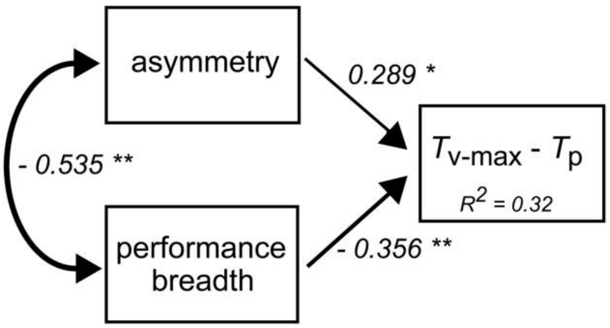

Figure 7: Structural equation model with phylogenetically independent contrasts, showing influences of asymmetry and of thermal performance breadth of lizards on difference between $T_{v_{\max}}$ and mean T_p. Numbers beside arrows are standardized coefficients (maximum likelihood) for the correlation between asymmetry and performance breadth or for the hypothesized causal relationships (*single-headed arrows*). Arrow widths are proportional to relationship strength. Asterisks indicate bootstrapped P values of <.05 (one asterisk) or <.01 (two asterisks).

possible biases in literature data. However, because T_p in our samples are not systematically lower than mean T_b in nature ($N = 32$; paired t-test, $t = -0.2425$, $P = .81$), any biases appear minor.

Lizard data support two other predictions of the model: the magnitude of the optimal deviation between $T_{v_{\max}}$ and T_p increases with the degree of asymmetry (fig. 6*A*, 6*B*) and also inversely with the degree of thermal generalization (B_{85}; fig. 6*C*, 6*D*). These patterns hold in correlations that use raw data (fig. 6*A*, 6*C*) and in those that use standardized independent contrasts (fig. 6*B*, 6*D*). However, because B_{85} and asymmetry are correlated, we ran a structural equations analysis (fig. 7), which suggests that the deviation T_p below $T_{v_{\max}}$ is sensitive both to asymmetry and especially to breadth (B_{85}).

We emphasize that thermoregulatory behavior of lizards is undoubtedly sensitive to the thermal sensitivity of many physiological traits, not just to speed. The patterns shown here for the thermal dependence of sprint speed cannot be assessed for other physiological traits (e.g., digestion; Huey 1982; Angilletta et al. 2002*b*) simply because other traits have been studied in very few species.

Relaxing Assumptions

One key assumption is that animals never experience injurious or lethal effects of extreme temperature; thus, in our model, T_b's were always within the "tolerance" limits. This assumption appears reasonable for most lizards (see table II in Huey 1982) but on occasion must be false. In any case, if animals occasionally experience extremely high body temperatures, then this should reinforce the utility of a T_o below $T_{v_{\max}}$. In effect, a low T_o would increase an animal's "safety zone" (see Heatwole 1976). This hypothesis could easily be modeled; in fact, a preliminary analysis that suggests species with highly asymmetric fitness curves (or with high variance in T_b) should maintain a wider safety zone, all else being equal. (These simulations computed T_o as the T_b at which $W(T_b)$ was highest, conditional on no T_b exceeding the upper lethal temperature.) This pattern would also hold if our model imposed a penalty (e.g., from stress) on high T_b. In any case, optimality and safety-zone models are not mutually exclusive, and both may help explain empirical patterns (fig. 5*A*).

We have also assumed that ectotherms have only a single optimal temperature. However, different physiological traits have somewhat different thermal sensitivities. For example, speed is generally less thermally sensitive than is digestion, and some traits may have slightly different thermal optima (see fig. 5 in Huey 1982; fig. 7 in Stevenson et al. 1985; fig. 8 in Angilletta et al. 2002*a*). Moreover, thermal sensitivity may shift slightly with physiological or reproductive state. Even so, what matters is the integration across traits, not individual traits. In principle, one could develop a model in which fitness is an emergent property of the integrative effects (in series or in parallel) of temperature on traits with different optimal temperatures (J. Kingsolver, personal communication). We suspect, however, that qualitative patterns predicted here should hold, given that shapes of thermal performance curves are invariably asymmetric for all performance traits (Huey 1982; Stevenson et al. 1985; Angilletta et al. 2002*a*).

Finally, we ignored costs of thermoregulation. As argued elsewhere (Huey and Slatkin 1976), the impact of costs on the degree of thermoregulation can be complex. Because costs may influence the optimal variance in T_b, a consideration of costs will undoubtedly influence predictions, likely in complex ways.

In conclusion, we have developed a simple model of temperature regulation for ectotherms. The classical expectation is that animals attempt to select body temperatures that maximize Darwinian fitness (Cowles and Bogert 1944; Huey and Bennett 1987; Angilletta et al. 2002*a*, 2006). However, our model predicts that animals should select temperatures somewhat lower than the temperature at which fitness is maximal: thus, "suboptimal" is optimal. We challenge predictions of our model with comparative tests, and those predictions are supported in evolutionary and nonevolutionary correlations. These patterns reinforce the importance to optimality models of considering the asymmetry of the fitness curve (Huey and Stevenson 1979; Gilchrist 1995) as well as the variance (Ruel and Ayers 1999) in body temperature.

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APPENDIX

Skewness of T_b *data.* The degree of asymmetry of T_b distributions has an influence on predictions of our model (fig. 5). Often T_b distributions in nature and T_p distributions in the laboratory are left-skewed (DeWitt 1967; DeWitt and Friedman 1979). If skewness is marked, this will tend to reduce the magnitude of the optimal shift (fig. 5*B*). To our knowledge, no one has thoroughly reviewed the actual skewness of T_b or T_p for diverse lizards (but see DeWitt and Friedman 1979). Consequently, we computed asymmetry (eq. [1]) for two data sets. Asymmetry was calculated from mean, maximum, and minimum T_b or T_p.

1. Van Berkum (1988) compiled T_b data for 13 species of lizards (several from multiple populations) from several families and from both tropical and temperate zone localities. Mean T_b asymmetry was 0.2 ± 0.05. Van Berkum (1988) also reported median T_b for several species and populations; median T_b was greater than mean T_b in 12 of 28 cases, and the difference averaged only 0.3° ± 0.17°C. Asymmetry (median) was 0.3 ± 0.019, slightly higher than for values using mean T_b.

2. Bennett and John-Alder (1986) reported T_p data for 13 species of skinks from Australia. The minimum and maximum T_p for each species was based on the average of individuals sampled, and we required a minimum sample size of 5. The mean asymmetry (for mean T_p) was 0.07 ± 0.054.

A comprehensive and quantitative analysis of the magnitude of skewness of lizard T_b and T_p data is needed, but the above analyses suggest that asymmetry of T_b and T_p may be relatively modest.

Sources of phylogenetic data. The phylogenetic hypothesis in figure A1 is compiled from a variety of sources: family-level relations (Vicario et al. 2003), Gekkota (Han et al. 2004), Iguanidae (Schulte et al. 1998), *Anolis* (Nicholson et al. 2005), *Sphaerodactylus* (Hass 1996), the *Sphenomorphus* group (Reeder 2003), Lacertidae (Fu 2000), and Xantusidae (Vicario et al. 2003). Branch lengths were arbitrarily set to 1. Only species with complete data are shown.

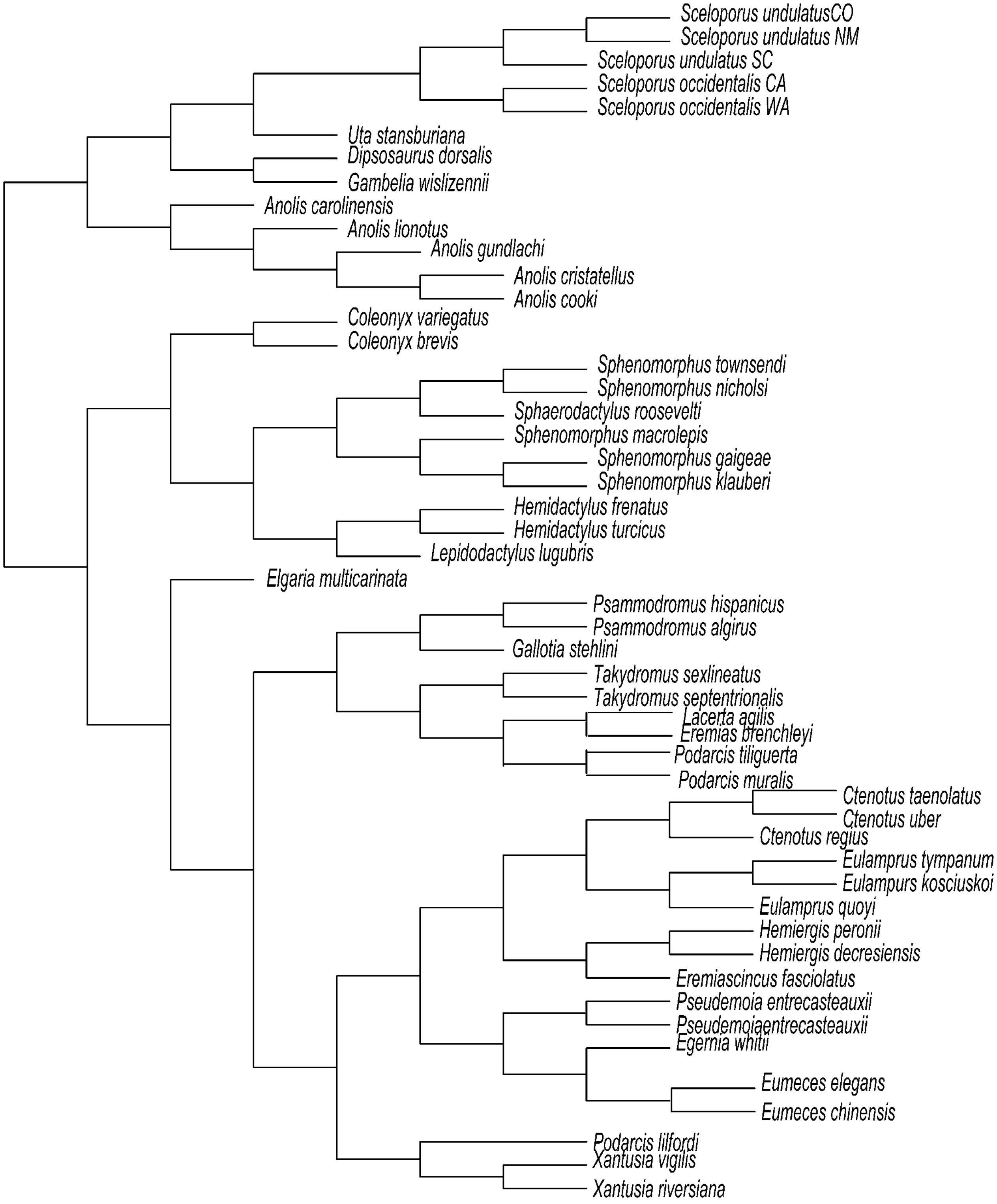

Figure A1: Phylogeny of lizards used in the comparative analysis.

Table A1: Species, $T_{v_{\max}}$, T_{p}, and sources used in the analysis of lizard sprint speed (V_{m})

Name	Taxon	$T_{v_{\max}}$ (°C)	T_{p} (°C)	V_{m} source	T_{p} source
Acanthodactylus erythrurus	Lacertidae	39.2	37.15	Bauwens et al. 1995	Bauwens et al. 1995
Anolis carolinensis	Polychrotidae	30.9	33.8	van Berkum 1988	Many
Anolis cooki	Polychrotidae	29	30.6	R. B. Huey, unpublished data	Huey and Webster 1976
Anolis cristatellus	Polychrotidae	28.7	29.4	R. B. Huey 1983	Huey and Webster 1976
Anolis gundlachi	Polychrotidae	28.9	25.1	R. B. Huey, unpublished data	Huey and Webster 1976
Anolis lionotus	Polychrotidae	28.7125	27	van Berkum 1988	Campbell 1971
Cnemidophorus murinus	Teiidae	38.4	35.9	Bennett 1980	Vitt et al. 2005
Coleonyx brevis	Gekkota	36.6	31.8	Huey et al. 1989	Dial 1978
Coleonyx variegatus	Gekkota	35.9	28.6	Huey et al. 1989	Brattstrom 1965
Ctenotus regius	Scincidae	31.6	35.6	Huey and Bennett 1987	Bennett and John-Alder 1986
Ctenotus taeniolatus	Scincidae	35.9	35.3	Huey and Bennett 1987	Bennett and John-Alder 1986
Ctenotus uber	Scincidae	35.6	35.3	Huey and Bennett 1987	Bennett and John-Alder 1986
Dipsosaurus dorsalis	Iguanidae	41.1	38.5	van Berkum 1988	DeWitt 1967
Egernia whitii	Scincidae	33.7	34.1	Huey and Bennett 1987	Bennett and John-Alder 1986
Eremiascincus fasciolatus	Scincidae	33.4	24.4	Huey and Bennett 1987	Bennett and John-Alder 1986
Eremias brenchleyi	Lacertidae	33	33.7	Xu et al. 2001	Xu et al. 2001
Eumeces chinensis	Scincidae	32.7	33.5	Ji et al. 1995	Ji et al. 1995
Eumeces elegans	Scincidae	32.9	28.6	Du et al. 2000	Du et al. 2000
Gallotia simonyi	Lacertidae	38	36.8	Cejudo and Márquez 2001	Márquez et al. 1997
Gallotia stehlini	Lacertidae	37.7	30	Cejudo and Márquez 2001	Márquez et al. 1997
Gambelia wislizennii	Crotaphytidae	37.4	35.4	Crowley and Pietruszka 1983	
Gerrhonotus multicarinatus	Anguidae	33	33.6	Bennett 1980	Bennett 1980
Hemidactylus frenatus	Gekkota	34.8	31.8	Huey et al. 1989	Huey et al. 1989
Hemidactylus turcicus	Gekkota	36.5	29.1	Huey et al. 1989	Angilletta et al. 1999
Hemiergis decresciensis	Scincidae	32.4	24.8	Huey and Bennett 1987	Bennett and John-Alder 1986
Hemiergis peroni	Scincidae	30.3	23.5	Huey and Bennett 1987	Bennett and John-Alder 1986
Lacerta agilis	Lacertidae	37	34.7	Bauwens et al. 1995	Bauwens et al. 1995
Lacerta monticola	Lacertidae	35.1	33.7	Bauwens et al. 1995	Bauwens et al. 1995
Lacerta schreiberi	Lacertidae	37.9	35.3	Bauwens et al. 1995	Bauwens et al. 1995
Lacerta vivipara	Lacertidae	33.9	32.1	van Damme et al. 1991	van Damme et al. 1986
Leiolopisma "entre A"	Scincidae	31.9	32.5	Huey and Bennett 1987	Bennett and John-Alder 1986
Leiolopisma "entre B"	Scincidae	32.7	32.5	Huey and Bennett 1987	Bennett and John-Alder 1986
Lepidodactylus lugubris	Gekkota	33.7	29.2	Huey et al. 1989	Huey et al. 1989
Platysaurus intermedius	Cordylidae	33.1	31.2	Lailvaux et al. 2003	Lailvaux et al. 200
Podarcis bocagei	Lacertidae	35.3	35.15	Bauwens et al. 1995	Bauwens et al. 1995
Podarcis hispanica atrata	Lacertidae	36.7	34.5	Bauwens et al. 1995	Bauwens et al. 1995
Podarcis hispanica hispanica	Lacertidae	36.2	34.4	Bauwens et al. 1995	Bauwens et al. 1995
Podarcis lilfordi	Lacertidae	37.6	35	Bauwens et al. 1995	Bauwens et al. 1995
Podarcis muralis	Lacertidae	36	34.15	Bauwens et al. 1995	Bauwens et al. 1995
Podarcis tiliguerta	Lacertidae	36.6	35.5	van Damme et al. 1989	van Damme et al. 1989
Psammodromus algirus	Lacertidae	35.8	35.4	Bauwens et al. 1995	Bauwens et al. 1995
Psammodromus hispanicus	Lacertidae	36	35.1	Bauwens et al. 1995	Bauwens et al. 1995
Sceloporus graciosus	Phrynosomatidae	31.9	35.4	van Berkum 1988	Licht 1965
Sceloporus occidentalis (California)	Phrynosomatidae	33.2	34.6	van Berkum 1988	Bennett 1980

Table A1 (*Continued*)

Name	Taxon	$T_{v_{\max}}$ (°C)	T_p (°C)	V_m source	T_p source
S. occidentalis (Washington)	Phrynosomatidae	31.7	34.6	van Berkum 1988	Bennett 1980
Sceloporus undulatus (Colorado)	Phrynosomatidae	36.1	35.2	Crowley 1985	Crowley 1987
S. undulatus (New Mexico)	Phrynosomatidae	36.1	35.2	Crowley 1985	Crowley 1987
S. undulatus (South Carolina)	Phrynosomatidae	35.1	33	Angilletta et al. 2002*a*	Angilletta 2001
Sphaerodactylus gaigeae	Gekkota	31.6	27.6	Alvarez 1992	Alvarez 1992
Sphaerodactylus klauberi	Gekkota	30.8	25.1	Alvarez 1992	Alvarez 1992
Sphaerodactylus macrolepis	Gekkota	30.6	27.6	Alvarez 1992	Alvarez 1992
Sphaerodactylus nicholsi	Gekkota	32.6	30.2	Alvarez 1992	Alvarez 1992
Sphaerodactylus roosevelti	Gekkota	29.3	30.2	Alvarez 1992	Alvarez 1992
Sphaerodactylus townsendi	Gekkota	28.7	30.2	Alvarez 1992	Alvarez 1992
Sphenomorphus kosciuscoi	Scincidae	32.9	29.8	Huey and Bennett 1987	Bennett and John-Alder 1986
Sphenomorphus quoyi	Scincidae	30.2	28.8	Huey and Bennett 1987	Bennett and John-Alder 1986
Sphenomorphus tympanum	Scincidae	32.7	29.6	Huey and Bennett 1987	Bennett and John-Alder 1986
Takydromus septentrionalis	Lacertidae	31.7	30	Xiang et al. 1996	Xiang et al. 1996
Takydromus sexlineatus	Lacertidae	32.4	31.5	Zhang and Ji 2004	Zhang and Ji 2004
Uma inornata	Phrynosomatidae	38.9	37	Bennett 1980	Brattstrom 1965
Uta stansburiana	Phrynosomatidae	35.6	35.5	Waldschmidt and Tracy 1983	Sartorius et al. 2002
Xantusia riversiana	Xantusiidae	28.4	28.3	Mautz et al. 1992	Mautz et al. 1992
Xantusia vigilis	Xantusiidae	31.1	31.6	Kaufmann and Bennett 1989	Kaufmann and Bennett 1989

Literature Cited in Appendix

Alvarez, H. J. 1992. Thermal characteristics of *Sphaerodactylus* species in Puerto Rico and their implications for the distribution of species in Puerto Rico. PhD thesis, University of Puerto Rico, San Juan.

Angilletta, M. J., Jr. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). Ecology 82:3044–3056.

Angilletta, M. J., Jr., L. G. Montgomery, and Y. L. Werner. 1999. Temperature preference in geckos: diel variation in juveniles and adults. Herpetologica 55:212–222.

Bennett, A. F., and H. B. John-Alder. 1986. Thermal relations of some Australian skinks (Sauria: Scincidae). Copeia 1986:57–64.

Campbell, H. W. 1971. Observations on the thermal activity of some tropical lizards of the genus *Anolis* (Iguanidae). Caribbean Journal of Science 11:17–20.

Cejudo, D., and R. Márquez. 2001. Spring performance in the lizards *Gallotia simonyi* and *Gallotia stehlini* (Lacertidae): implications for species management. Herpetologica 57:87–98.

Crowley, S. R. 1985. Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology. Oecologia (Berlin) 66:219–225.

———. 1987. The effect of desiccation upon the preferred body temperature and activity level of the lizard *Sceloporus undulatus*. Copeia 1987:25–32.

Crowley, S. R., and R. D. Pietruszka. 1983. Aggressiveness and vocalization in the leopard lizard (*Gambelia wislizennii*): the influence of temperature. Animal Behaviour 81:1055–1060.

Dial, B. E. 1978. The thermal ecology of two sympatric nocturnal *Coleonyx* (Lacertilia: Gekkonidae). Herpetologica 34:194–201.

Du, W.-G., S.-J. Yan, and X. Ji. 2000. Selected body temperature, thermal tolerance and thermal dependence of food assimilation and locomotor performance in adult blue-tailed skinks, *Eumeces elegans*. Journal of Thermal Biology 25:197–202.

Fu, J. 2000. Toward the phylogeny of the family Lacertidae—why 4708 base pairs of mtDNA sequences cannot draw the picture. Biological Journal of the Linnean Society 71:203–217.

Han, D., K. Zhou, and A. M. Bauer. 2004. Phylogenetic relationships among gekkotan lizards inferred from C-mos nuclear DNA sequences and a new classification of the Gekkota. Biological Journal of the Linnean Society 83:353–368.

Hass, C. A. 1996. Relationships among West Indian geckos of the genus *Sphaerodactylus*: a preliminary analysis of mitochondrial 16S ribosomal RNA sequences. Pages 175–194 *in* R. Powell and R. W.

Henderson, eds. Contributions to West Indian herpetology: a tribute to Albert Schwartz. Society for the Study of Amphibians and Reptiles, Ithaca, NY.

Huey, R. B., and T. P. Webster. 1976. Thermal biology of *Anolis* lizards in a complex fauna: the *cristatellus* group on Puerto Rico. Ecology 57:985–994.

Huey, R. B., P. H. Niewiarowski, J. Kaufmann, and J. C. Herron. 1989. Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? Physiological Zoology 62:488–504.

Ji, X., X. Zheng, Y. Xu, and R. Sun. 1995. Some aspects of the thermal biology of the skink (*Eumeces chinensis*). Acta Zoologica Sinica 41: 268–274.

Kaufmann, J. S., and A. F. Bennett. 1989. The effect of temperature and thermal acclimation on locomotor performance in *Xantusia vigilis*, the desert night lizard. Physiological Zoology 62:1047–1058.

Lailvaux, S. P., G. J. Alexander, and M. J. Whiting. 2003. Sex-based differences and similarities in locomotor performance, thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. Physiological and Biochemical Zoology 76:511–521.

Licht, P. E. 1965. The relation between preferred body temperatures and testicular heat sensitivity in lizards. Copeia 1965:428–436.

Márquez, R., D. Cejudo, and V. Pérez-Mellado. 1997. Selected body temperatures of four lacertid lizards from the Canary Islands. Herpetological Journal 7:122–124.

Mautz, W. J., C. B. Daniels, and A. F. Bennett. 1992. Thermal dependence of locomotion and aggression in a xantusiid lizard. Herpetological Natural History 48:271–279.

Nicholson, K. E., R. E. Glor, J. J. Kolbe, A. Larson, S. B. Hedges, and J. B. Losos. 2005. Mainland colonization by island lizards. Journal of Biogeography 32:929–938.

Reeder, T. W. 2003. A phylogeny of the Australian *Sphenomorphus* group (Scincidae: Squamata) and the phylogenetic placement of the crocodile skinks (*Tribolonotus*): Bayesian approaches to assessing congruence and obtaining confidence in maximum likelihood inferred relationships. Molecular Phylogenetics and Evolution 27:384–397.

Sartorius, S. S., J. P. S. do Amaral, R. D. Durtsche, C. M. Deen, and W. I. Lutterschmidt. 2002. Thermoregulatory accuracy, precision, and effectiveness in two sand-dwelling lizards under mild environmental conditions. Canadian Journal of Zoology 80:1966–1976.

Schulte, J. A., Jr., J. R. Macey, A. Larson, and T. J. Papenfuss. 1998. Molecular tests of phylogenetic taxonomies: a general procedure and example using four subfamiles of the lizard family Iguanidae. Molecular Phylogenetics and Evolution 10:367–376.

van Damme, R., D. Bauwens, and R. F. Verheyen. 1986. Selected body temperatures in the lizard *Lacerta vivipara*: variation within and between populations. Journal of Thermal Biology 11:219–222.

van Damme, R., D. Bauwens, A. M. Castilla, and R. F. Verheyen. 1989. Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. Oecologia (Berlin) 80:516–524.

van Damme, R., D. Bauwens, and R. F. Verheyen. 1991. The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. Functional Ecology 5:507–517.

Vicario, S., A. Caccone, and J. Gautier. 2003. Xantusiid "night" lizards: a puzzling phylogenetic problem revisited using likelihood-based Bayesian methods on mtDNA sequences. Molecular Phylogenetics and Evolution 26:243–261.

Vitt, L. J., J. P. Caldwell, S. S. Sartorius, W. E. Cooper Jr., T. A. Baird, and V. Pérez-Mellado. 2005. Pushing the edge: extended activity as an alternative to risky body temperatures in a herbivorous teiid lizard (*Cnemidophorus murinus*: Squamata). Functional Ecology 19:152–158.

Xiang, J., D. Weiguo, and S. Pingyue. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis*. Journal of Thermal Biology 21:155–161.

Xu, X.-F., Q. Zhao, and X. Ji. 2001. Selected body temperature, thermal tolerance and influence of temperature on food assimilation and locomotor performance in lacertid lizards, *Eremias brenchleyi*. Zoological Research 22:443–448.

Zhang, Y.-P., and X. Ji. 2004. The thermal dependence of food assimilation and locomotor performance in southern grass lizards, *Takydromus sexlineatus* (Lacertidae). Journal of Thermal Biology 29:45–53.

Literature Cited

Åkesson, B. 1976. Temperature and life cycle in *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). Ophelia 15:37–47.

Allsopp, P. G. 1981. Development, longevity and fecundity of the false wireworms *Pterohelaeus darlingensis* and *Pterohelaeus alternatus* (Coleoptera, Tenebrionidae). 1. Effect of constant temperature. Australian Journal of Zoology 29:605–629.

Allsopp, P. G., G. D. Adams, and D. G. Butler. 1980. Response of larvae of *Pterohelaeus darlingensis* Carter (Coleoptera: Tenebrionidae) to moisture, temperature and gravity. Journal of the Australian Entomological Society 19:281–285.

Angilletta, M. J., Jr., P. H. Niewiarowski, and C. A. Navas. 2002*a*. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology 27:249–268.

Angilletta, M. J., Jr., T. Hill, and M. A. Robson. 2002*b*. Is physiological performance optimized by thermoregulatory behavior? a case study of the eastern fence lizard, *Sceloporus undulatus*. Journal of Thermal Biology 27:199–204.

Angilletta, M. J., Jr., A. F. Bennett, H. Guderley, C. A. Navas, F. Seebacher, and R. S. Wilson. 2006. Coadaptation: a unifying principle in evolutionary thermal biology. Physiological and Biochemical Zoology 79:282–294.

Avery, R. A. 1982. Field studies of body temperatures and thermoregulation. Pages 93–166 *in* C. Gans and F. H. Pough, eds. Biology of the Reptilia. Vol. 12. Physiology C. Academic Press, London.

Barber, B. J., and E. C. Crawford. 1977. A stochastic dual-limit hypothesis for behavioral thermoregulation in lizards. Physiological Zoology 50:53–60.

Bauwens, D., T. Garland Jr., A. M. Castilla, and R. Van Damme. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. Evolution 49:848–863.

Beitinger, T. L., and L. C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature in fish. American Zoologist 19:319–329.

Bennett, A. F. 1980. The thermal dependence of lizard behaviour. Animal Behaviour 26:455–462.

———. 1987. Evolution of the control of body temperature: is warmer better? Pages 421–431 *in* P. Dejours, C. R. Taylor, and E. R. Weibel, eds. Comparative physiology: life in water and on land. Liviana, Padova, Italy.

Bennett, A. F., and R. B. Huey. 1990. Studying the evolution of physiological performance. Pages 251–284 *in* D. J. Futuyma and J. Antonovics, eds. Oxford Surveys in Evolutionary Biology. Vol. 7. Oxford University Press, Oxford.

Beuchat, C. A., and S. Ellner. 1987. A quantitative test of life history theory: thermoregulation by a viviparous lizard. Ecological Monographs 57:45–60.

Blouin-Demers, G., and P. Nadeau. 2005. The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behavior. Ecology 86:560–566.

Brattstrom, B. H. 1965. Body temperature of reptiles. American Midland Naturalist 73:376–422.

Brett, J. R. 1970. Temperature, fishes. Pages 515–560 *in* O. Kinne, ed. Marine ecology. Vol. 1. Wiley, New York.

———. 1971. Energetic responses of salmon to temperatures: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist 11: 99–113.

Chown, S. L., and S. W. Nicolson. 2004. Insect physiological ecology: mechanisms and patterns. Oxford University Press, Oxford.

Christian, K. A., and C. R. Tracy. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. Oecologia (Berlin) 49:218–223.

Christian, K. A., and B. W. Weavers. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecological Monographs 66:139–157.

Cossins, A. R., and K. Bowler. 1987. Temperature biology of animals. Chapman & Hall, New York.

Coutant, C. 1987. Thermal preference: when does an asset become a liability? Environmental Biology of Fishes 18:161–172.

Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bulletin of the American Museum of Natural History 83:261–296.

Dawson, W. R. 1975. On the physiological significance of the preferred body temperatures of reptiles. Pages 443–473 *in* D. M. Gates and R. Schmerl, eds. Perspectives of biophysical ecology. Springer, New York.

DeWitt, C. B. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. Physiological Zoology 40:49–66.

DeWitt, C. B., and R. M. Friedman. 1979. Significance of skewness in ectotherm thermoregulation. American Zoologist 19:195–209.

Dunham, A. E. 1993. Population responses to environmental change: physiologically structured models, operative environments, and population dynamics. Pages 95–119 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, eds. Biotic interactions and global change. Sinauer, Sunderland, MA.

Feder, M. E., and J. F. Lynch. 1982. Effects of latitude, season, elevation, and microhabitat on field body temperatures of Neotropical and temperate zone salamanders. Ecology 63:1657–1664.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Fogleman, J. C. 1979. Oviposition site preference for substrate temperature in *Drosophila melanogaster*. Behavior Genetics 9:407–412.

Fraenkel, G. S., and D. L. Gunn. 1940. The orientation of animals: kineses, taxes and compass reactions. Oxford University Press, Oxford.

Frazier, M. R., R. B. Huey, and D. Berrigan. 2006. Thermodynamics constrains the evolution of insect population growth rates: "warmer is better." American Naturalist 168:512–520.

Fry, F. E. J. 1947. Effects of the environment on animal activity. University of Toronto Studies in Biology 55:1–62.

Fry, F. E. J., and J. S. Hart. 1948. Cruising speed of goldfish in relation to water temperature. Journal of the Fisheries Research Board of Canada 7:169–175.

Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265–292.

Gilchrist, G. W. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. American Naturalist 146:252–270.

Hainsworth, F. R. 1978. Feeding: models of costs and benefits in energy regulation. American Zoologist 18:701–714.

Haldane, J. B. S., and S. D. Jayakar. 1963. Polymorphism due to selection of varying direction. Journal of Genetics 58:237–242.

Hamilton, W. J., III. 1973. Life's color code. McGraw-Hill, New York.

Heath, J. E. 1965. Temperature regulation and diurnal activity in horned lizards. University of California Publications in Zoology 64:97–136.

Heatwole, H. 1976. Reptile ecology. University of Queensland Press, St. Lucia.

Heinrich, B. 1981. Insect thermoregulation. Wiley, New York.

Herczeg, G., A. Gonda, J. Saarikivi, and J. Merilä. 2006. Experimental support for the cost-benefit model of lizard thermoregulation. Behavioral Ecology and Sociobiology 60:405–414.

Hertz, P. E. 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. Ecology 73:1405–1417.

Hertz, P. E., R. B. Huey, and E. Nevo. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. Evolution 37: 1075–1084.

Hertz, P. E., R. B. Huey, and R. D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. American Naturalist 142:796–818.

Howe, R. W. 1962. The effects of temperature and humidity on the oviposition rate of *Tribolium castaneum* (Hbst.) (Coleoptera, Tenebrionidae). Bulletin of Entomological Research 53:301–310.

Huey, R. B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. Science 184:1001–1003.

———. 1982. Temperature, physiology, and the ecology of reptiles. Pages 25–91 *in* C. Gans and F. H. Pough, eds. Biology of the Reptilia. Vol. 12. Physiology C. Academic Press, London.

———. 1983. Natural variation in body temperature and physiological performance in a lizard. Pages 484–490 *in* A. G. J. Rhodin and K. Miyata, eds. Advances in herpetology and evolutionary biology: essays in honor of Ernest E. Williams. Museum of Comparative Zoology, Cambridge, MA.

Huey, R. B., and A. F. Bennett. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. Evolution 41:1098–1115.

Huey, R. B., and D. Berrigan. 2001. Temperature, demography, and ectotherm fitness. American Naturalist 158:204–210.

Huey, R. B., and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology & Evolution 4:131–135.

Huey, R. B., and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. Quarterly Review of Biology 51:363–384.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. American Zoologist 19:357–366.

Huey, R. B., E. R. Pianka, and L. J. Vitt. 2001. How often do lizards run on empty? Ecology 82:1–7.

Irschick, D. J., and T. Garland Jr. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. Annual Review of Ecology and Systematics 32:367–396.

Izem, R., and J. G. Kingsolver. 2005. Variation in continuous reaction norms: quantifying directions of biological interest. American Naturalist 166:277–289.

Jayne, B. C., and A. F. Bennett. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. Evolution 44:1204–1229.

Jia, Q. X., N. Xu, J. Zhu, M. Q. Xu, and H. Cao. 2002. Effects of temperature on the development and population growth of brine shrimp (*Artemia parthenogenetica gahai*). Acta Zoologica Sinica 48:175–182.

Jian, F., D. S. Jayas, N. D. G. White, and W. E. Muir. 2002. Temperature and geotaxis preference by *Cryptolestes ferrugineus* (Coleoptera: Laemophloeidae) adults in response to 5°C/m temperature gradients at optimum and hot temperatures in stored wheat and their mortality at high temperature. Environmental Entomology 31:816–826.

Jobling, M. 1981. Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. Journal of Fish Biology 19:439–455.

Kingsolver, J. G., and W. B. Watt. 1983. Thermoregulatory strategies of *Colias* butterflies: thermal stress and the limits to adaptation in temporally varying environments. American Naturalist 121:32–55.

Kline, R. B. 2005. Principles and practice of structural equation modeling. Guilford, New York.

Kluger, M. J. 1979. Fever, its biology, evolution, and function. Princeton University Press, Princeton, NJ.

Langer, G. S., and A. M. Young. 1976. Habitat selection in two species of flour beetles (*Tribolium*) on a temperature gradient. American Midland Naturalist 95:131–143.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, NJ.

Licht, P. E., W. R. Dawson, V. H. Shoemaker, and A. R. Main. 1966. Observations on the thermal relations of Western Australian lizards. Copeia 1966:97–110.

Logan, J. A., D. J. Wollkind, S. C. Hoyt, and L. K. Tanigoshi. 1976. An analytical model for description of temperature dependent rate phenomena in arthropods. Environmental Entomology 5:1133–1140.

Lutterschmidt, D. I., W. I. Lutterschmidt, and V. H. Hutchison. 2003. Melatonin and thermoregulation in ectothermic vertebrates: a review. Canadian Journal of Zoology 81:1–13.

Peterson, C. R., A. R. Gibson, and M. E. Dorcas. 1983. Snake thermal ecology: the causes and consequences of body-temperature variation. Pages 241–314 *in* R. A. Siegel and J. T. Collins, eds. Snakes, ecology and behavior. McGraw-Hill, New York.

Pianka, E. R. 1986. Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton University Press, Princeton, NJ.

Porter, W. P., and C. R. Tracy. 1983. Biophysical analyses of energetics, time-space utilization, and distributional limits. Pages 55–83 *in* R. B. Huey, E. R. Pianka, and T. W. Schoener, eds. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, MA.

Pough, G. H., and C. Gans. 1982. The vocabulary of reptilian thermoregulation. Pages 17–23 *in* C. Gans and F. H. Pough, eds. Biology of the Reptilia. Vol. 12. Physiology C. Academic Press, London.

Prevedelli, D., and R. Simonini. 2001. Effect of temperature on demography of *Ophryotrocha labronica* (Polychaeta: Dorvilleidae). Vie Milieu 51:173–180.

Prince, G. J., and P. A. Parsons. 1977. Adaptive behavior of *Drosophila* adults in relation to temperature and humidity. Australian Journal of Zoology 25:285–290.

Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. Theoretical Population Biology 5:163–186.

Roughgarden, J., W. P. Porter, and D. Heckel. 1981. Resource partitioning of space and its relationship to body temperatures in *Anolis* lizard populations. Oecologia (Berlin) 50:256–264.

Ruel, J. J., and M. P. Ayers. 1999. Jensen's inequality predicts effects of environmental variation. Trends in Ecology & Evolution 14: 361–366.

Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. American Naturalist 163:429–441.

Sayeed, O., and B. Benzer. 1996. Behavioral genetics of thermosensation. Proceedings of the National Academy of Sciences of the USA 93:6079–6084.

Schwarzkopf, L., and R. Shine. 1991. Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: why do gravid females bask more? Oecologia (Berlin) 88:562–569.

Sharp, P. J. H., and D. W. De Michele. 1977. Reaction kinetics of poikilotherm development. Journal of Theoretical Biology 64:649–670.

Shine, R., M. Elphick, and E. G. Barrott. 2003. Sunny side up: lethally high, not low, temperatures may prevent oviparous reptiles from reproducing at high elevations. Biological Journal of the Linnean Society 78:325–334.

Siddiqui, W. H., and C. A. Barlow. 1972. Population growth of *Drosophila melanogaster* (Diptera: Drosophilidae) at constant and alternating temperatures. Annals of the Entomological Society of America 65:993–1001.

Smallwood, P. D. 1996. An introduction to risk sensitivity: the use of Jensen's inequality to clarify evolutionary arguments of adaptation and constraint. American Zoologist 36:392–317.

Smith, L. B. 1965. The intrinsic rate of natural increase of *Cryptolestes ferrugineus* (Stephens) (Coleoptera, Cucujidae). Journal of Stored Product Research 1:35–49.

Stevenson, R. D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. American Naturalist 126:362–386.

Stevenson, R. D., C. R. Peterson, and J. S. Tsuji. 1985. The thermal dependence of locomotion, tongue flicking, digestion and oxygen consumption in the wandering garter snake. Physiological Zoology 58:46–57.

Tracy, C. R., and K. A. Christian. 1983. Ecological relations among space, time and thermal niche axes. Ecology 67:609–615.

van Berkum, F. H. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. Evolution 40:594–604.

———. 1988. Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. American Naturalist 132:327–343.

Waldschmidt, S., and C. R. Tracy. 1983. Interactions between a lizard and its thermal environment: implications for sprint performance and space utilization in the lizard *Uta stansburiana*. Ecology 64: 476–484.

White, G. C. 1987. Effects of temperature and humidity on the rust-red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) in wheat grain. Australian Journal of Zoology 35:43–59.

Wilhoft, D. C. 1958. The effect of temperature on thyroid histology and survival in the lizard, *Sceloporus occidentalis*. Copeia 1958: 265–276.

Withers, P. C., and J. D. Campbell. 1985. Effect of environmental cost on thermoregulation in the desert iguana. Physiological Zoology 58:329–339.

Worner, S. P. 1992. Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. Environmental Entomology 21:689–699.

Zhang, L., and H. Lefcort. 1991. The effects of ploidy level on the thermal distributions of brine shrimp *Artemia parthenogenetica* and its ecological implications. Heredity 66:445–452.

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