

# 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 ( $T_{rmax}$ ) that maximize fitness ( $r$ ). We develop an optimality model and find that optimal body temperature ( $T_o$ ) should not be centered at  $T_{rmax}$  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  $T_{rmax}$  depresses fitness more than will a  $T_b$  displaced an equivalent amount below  $T_{rmax}$ . Our model makes several predictions. The magnitude of the optimal shift ( $T_{rmax} - T_o$ ) 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  $T_{rmax}$  (“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

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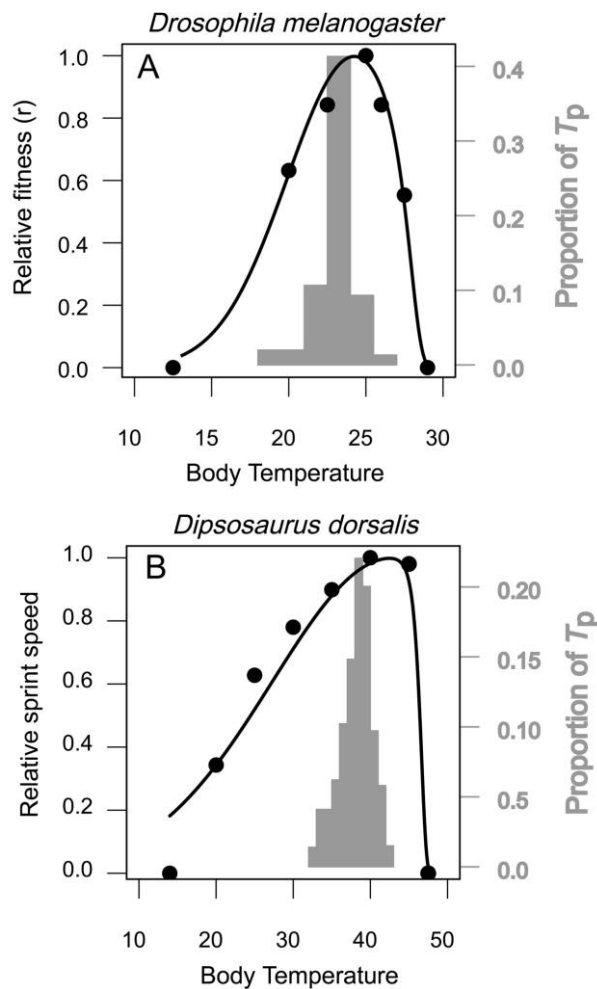
difficult to define at present for practical purposes. (Fraenkel and Gunn 1940)

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<sup>1</sup> 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

<sup>1</sup> 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  $T_p = 23.8^\circ\text{C}$  (SD =  $1.4^\circ\text{C}$ ),  $T_{r_{\max}} = 24.3^\circ\text{C}$ , 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  $T_p = 38.5^\circ\text{C}$  (SD =  $2.1^\circ\text{C}$ ),  $T_{r_{\max}} = 41.1^\circ\text{C}$ , asymmetry = 0.8).

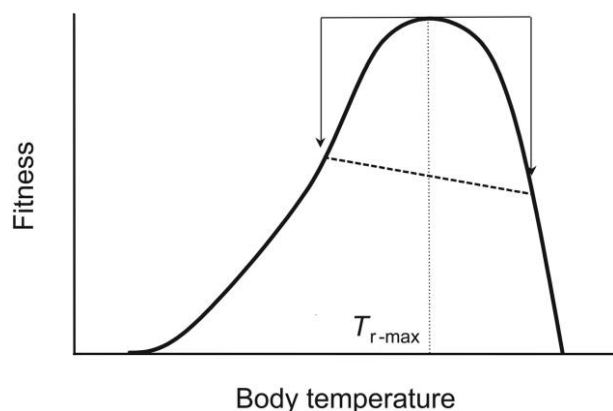
a fundamental question in behavioral physiology: which temperatures should a particular ectotherm select when given free access to a range of body temperatures? The answer might seem obvious, at least if the thermal dependence of Darwinian fitness is known for the species in question; specifically, animals should regulate at the specific temperature that maximizes fitness ( $T_{r_{\max}}$ ). For example, *Drosophila melanogaster* would be expected to select a temperature of  $\sim 24^\circ\text{C}$ , which corresponds to its  $T_{r_{\max}}$  (fig. 1A). 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  $2^\circ\text{C}$  above the fitness optimum  $T_{r_{\max}}$  will reduce fitness much more than will a body temperature  $2^\circ\text{C}$  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. 1B), 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 ( $T_{r-max}$ ) 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*

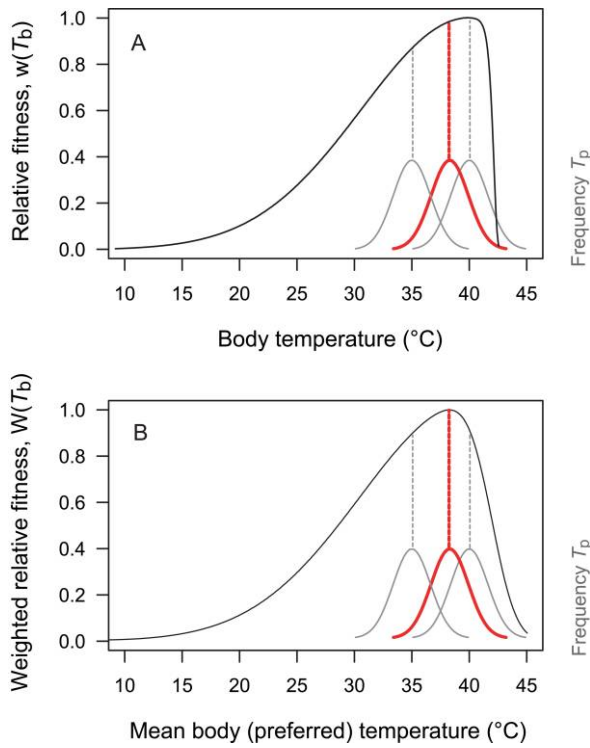
Our model is based on a model of thermoregulation developed by Huey and Slatkin (1976; see also Tracy and Christian 1983) but is simplified by excluding any costs of thermoregulation. Thus, an ectotherm’s Darwinian fitness over time depends on only two functions: (1) the frequency distribution of body 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):

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

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  $\sim 2.2^\circ\text{C}$ ). 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. 2002b; Izem and Kingsolver 2005); to describe these curves, we used a Gompertz multiplied by a Gaussian function ( $G \times G$  function; fig. 1):

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

where  $r_{\max}$  is the maximal fitness,  $\alpha$  is the rise rate controlling the steepness of the left portion of the fitness curve,  $\beta$  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  $G \times G$  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:

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

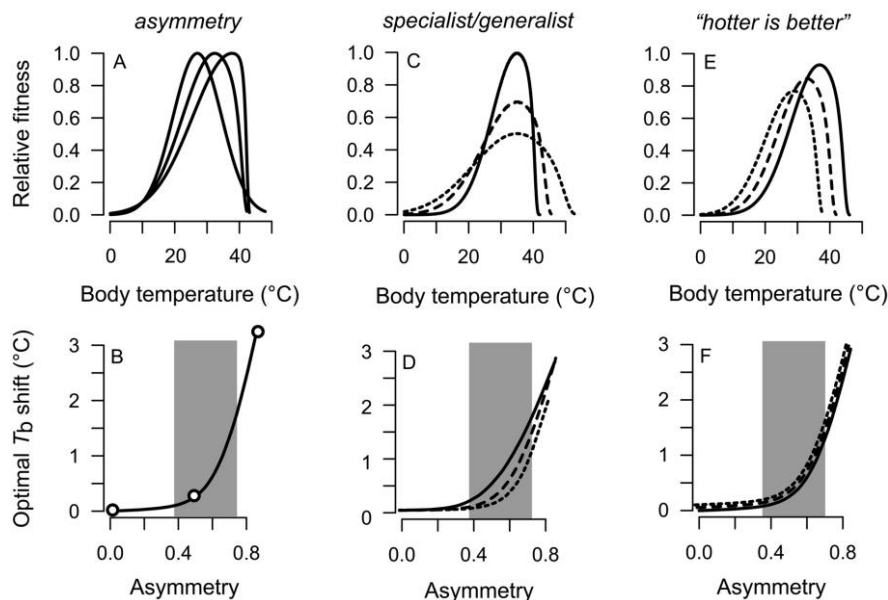
where  $T_{\max}$  and  $T_{\min}$  represent the upper and lower limiting temperatures ( $r = 0$ ). The index ranges from 0 for a perfectly symmetric curve to 1 for a right triangle.

### Simulating Optimal Thermoregulation

Because an analytical solution for equation (1) (with substituted  $G \times G$  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. 1B; tolerance range set to 35°C). When manipulating the degree of asymmetry of fitness curves (fig. 4A), we held the tolerance range constant but shifted the optimum. When manipulating the degree of generalization (fig. 4C; 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. 4E), 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. 1B). However, to simulate the effects of asymmetry (skew) of  $T_b$ , we used a  $G \times G$  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

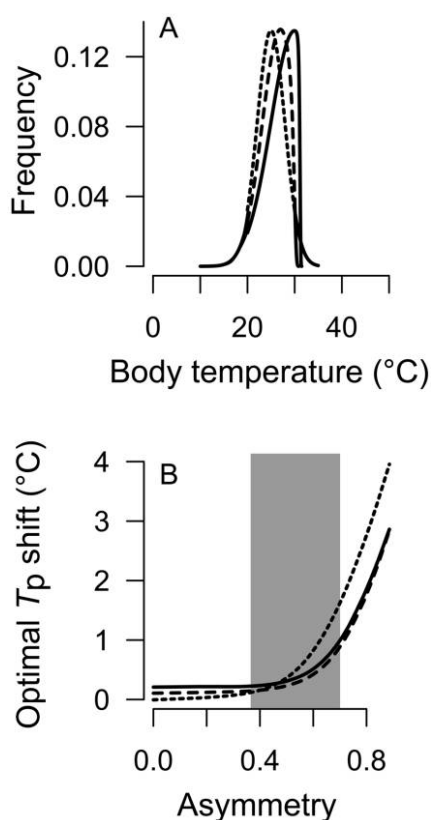
To evaluate whether the thermoregulatory behavior of ectotherms is consistent with predictions of our model, we compared the mean preferred body temperature ( $T_p$ ) of a species in a laboratory thermal gradient with the body temperature at which its fitness ( $T_{r_{max}}$ ) or sprint performance ( $T_{v_{max}}$ ) 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  $G \times G$  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  $T_{rmax}$  for  $T_b$  distributions with different asymmetries and for thermal fitness curves with different degrees of asymmetry. If thermal fitness curves are highly symmetrical (greater than  $\sim 0.5$ ), 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  $T_{vmax}$ , as well as the correlation between  $B_{85}$  and the deviation of mean  $T_p$  from  $T_{vmax}$ ; 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  $T_{vmax}$ .

## Results

### Model Predictions

**Fitness asymmetry.** To examine the effect of the degree of asymmetry of the fitness curve (fig. 4A) on the magnitude of the deviation of the optimal temperature  $T_o$  below  $T_{rmax}$  (fig. 4B), 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. 4A). As expected, the magnitude of the optimal shift ( $T_{rmax} - T_o$ ) increased with the degree of fitness-curve asymmetry (fig. 4B). 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. 4B, shaded area). At moderate to high asymmetries (fig. 4A),  $T_b$  above  $T_{rmax}$  substantially reduces fitness, thus favoring  $T_o$  well below  $T_{rmax}$ . 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. 4C. The magnitude of the optimal shift increased with the degree of specialization (fig. 4D), reflecting the relatively rapid decline in fitness at  $T_b > T_{rmax}$  for thermal specialists (fig. 4C). However, for extremely asymmetric fitness curves, optimal shifts appear to converge for different degrees of specialization (fig. 4D), as fitness curves for  $T_b > T_{rmax}$  are steep, even for thermal generalists.

**Hotter is better.** Thermodynamic considerations (Savage et al. 2004) predict that maximal fitness should be positively related to  $T_{rmax}$  (fig. 4E). This effect has no impact, however, on the optimal shift (fig. 4F). 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. 4E).

**Asymmetry of the  $T_b$  distribution.** The above simulations use a Gaussian distribution for  $T_b$ . However, because body temperature distributions are often (fig. 1B) but not always (fig. 1A) 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. 5A) in combination with different asymmetries of  $w(T_b)$  influence the optimal  $T_b$  shift. Symmetrical  $T_b$  distributions favor the largest shift in  $T_b$  (fig. 5B), 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. 5B).

## 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. 1A) 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. 2002a).

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. 1A; table 1).

More extensive data are available on the thermal pref-

erences and on thermal dependence of sprint speed of lizards (e.g., fig. 1B). 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. 2002a), 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. 2002a) and with food levels and metabolism (Brett 1971; Hainsworth 1978; Huey 1982).

Our first prediction—that  $T_p$  should be less than  $T_{r_{max}}$  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 ( $1.8^\circ\text{C}$ ; 95% confidence interval [CI] =  $1.1^\circ\text{C}$ – $2.5^\circ\text{C}$ ) 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 ( $^\circ\text{C}$ )	Source
<i>Caenorhabditis elegans</i> (nematode, CB 4856):		
$T_{r_{max}}$	~24	P. Phillips, personal communication
$T_p$	~17	P. Phillips, personal communication
<i>Artemia parthenogenetica</i> (brine shrimp):		
$T_{r_{max}}$	32.3	Jia et al. 2002
$T_p$	22.2–23.9	Zhang and Lefcort 1991
<i>Ophryotrocha labronica</i> (polychaete):		
$T_{r_{max}}$	>28	Åkesson 1976; Prevedelli and Simonini 2001
$T_p$	~20.4	Åkesson 1976
<i>Drosophila melanogaster</i> (fly):		
$T_{r_{max}}$	24.3	Siddiqui and Barlow 1972
$T_p$	23.5–25.2	Fogleman 1979
$T_p$	23.8	Sayed and Benzer 1996
<i>Tribolium castaneum</i> (beetle):		
$T_{r_{max}}$	35.3	Howe 1962
$T_{r_{max}}$	35	White 1987
$T_p$	28.2	Langer and Young 1976
<i>Pterohelaeus darlingensis</i> (beetle):		
$T_{r_{max}}$	28.2	Allsopp 1981
$T_p$	17.3	Allsopp et al. 1980
<i>Cryptolestes ferrugineus</i> (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. 6A), and the evolutionary one was 0.54 ( $P \ll .001$ ; fig. 6B).

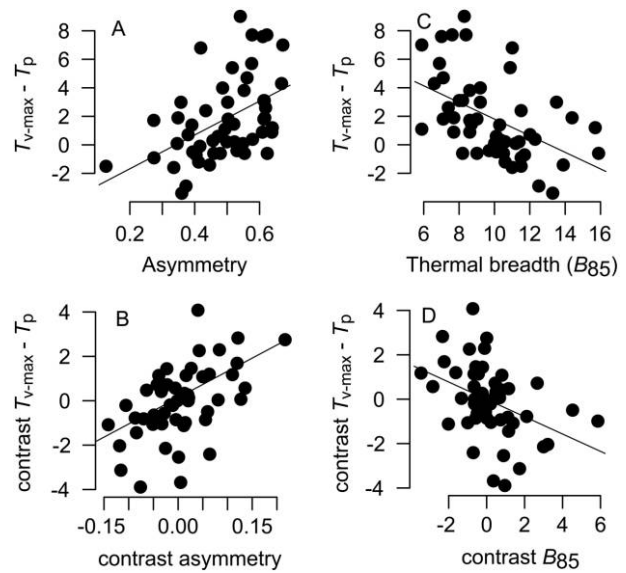
Our third prediction—that the magnitude of the difference between  $T_{v_{\max}}$  and  $T_p$  would decrease with the degree of thermal generalization (i.e., thermal breadth or  $B_{85}$ )—was also supported. The nonevolutionary correlation was  $-0.51$  ( $P < .001$ ; fig. 6C), and the evolutionary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

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.

### 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

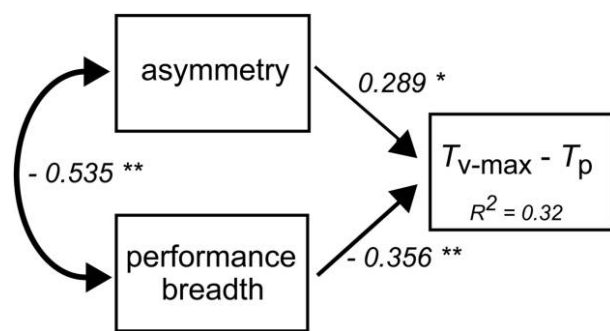


**Figure 6:** A, B, Empirical difference between  $T_{v_{\max}}$  and mean  $T_p$  increases with the asymmetry of a lizard’s performance (speed) curve (A = nonphylogenetic patterns; B = standardized independent contrasts, with regression through 0). C, D, Empirical difference between  $T_{v_{\max}}$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

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. 4B), and (3) the optimal deviation increases with the degree of thermal specialization (fig. 4D) 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. 6A, 6B) and also inversely with the degree of thermal generalization ( $B_{85}$ ; fig. 6C, 6D). These patterns hold in correlations that use raw data (fig. 6A, 6C) and in those that use standardized independent contrasts (fig. 6B, 6D). 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. 2002b) 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. 5A).

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. 2002a). 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. 2002a).

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. 2002a, 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. 5B). 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  $0.2 \pm 0.05$ . 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  $0.3^\circ \pm 0.17^\circ\text{C}$ . Asymmetry (median) was  $0.3 \pm 0.019$ , 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  $0.07 \pm 0.054$ .

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.

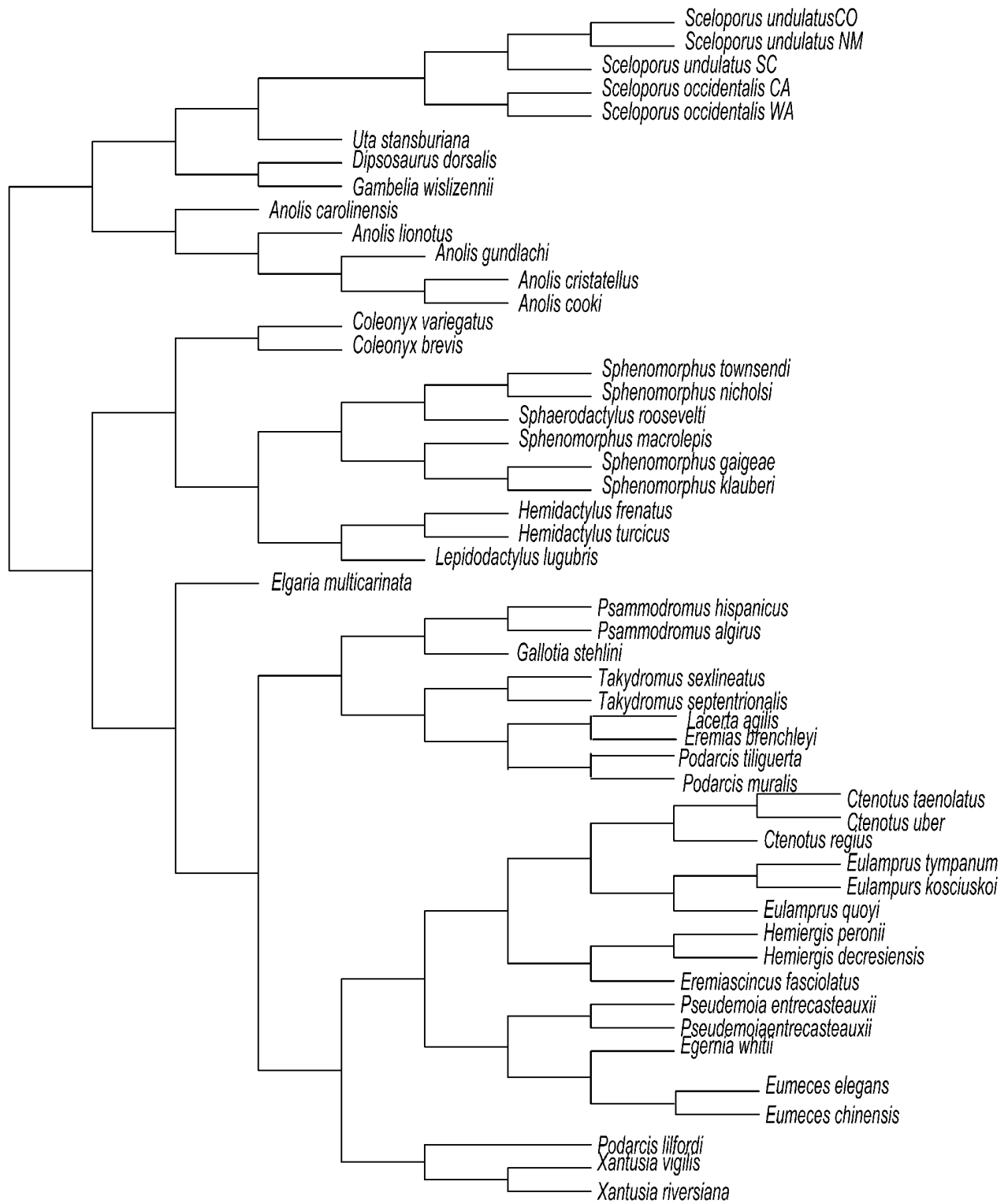


Figure A1: Phylogeny of lizards used in the comparative analysis.

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

Table A1 (Continued)

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

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