Thermodynamic Effects on the Evolution of Performance Curves

Dee A. Asbury and Michael J. Angilletta Jr.*

Department of Biology, Indiana State University, Terre Haute, Indiana 47809

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Abstract: Models of thermal adaptation assume that warm-adapted and cold-adapted organisms can achieve the same fitness, yet recent comparative studies suggest that warm-adapted organisms outperform cold-adapted ones. We explored how this thermodynamic effect on performance might influence selective pressures on thermal physiology. In the absence of a thermodynamic effect, natural selection favors a thermal optimum for performance that closely matches the mean (or modal) body temperature. When warm-adapted organisms outperform cold-adapted organisms, natural selection can favor a thermal optimum that exceeds the mean body temperature. The optimal mismatch between the thermal optimum and the mean temperature increases as does the variation in body temperature within generations. This result holds regardless of whether performance affects fitness through fecundity or survivorship. The selective pressures generated by a thermodynamic effect might explain the substantial mismatch between thermoregulatory behavior and thermal physiology that has been observed in some species.

Keywords: heterogeneity, performance, temperature, thermodynamics.

Introduction

Since the seminal work of Levins (1968), biologists have used the concept of a performance curve to model the effects of environmental heterogeneity on fitness. Most models focus on two aspects of these curves: the environment that permits maximal performance (environmental optimum of performance) and the range of conditions over which performance can occur (environmental breadth of performance). Both spatial and temporal variations in environmental conditions influence the evolution of a performance curve (Lynch and Gabriel 1987; Gabriel 1988; Gilchrist 1995, 2000). Predictable environmental cues select for genotypes that can developmentally alter their performance curves in the face of environmental heterogeneity (Gabriel and Lynch 1992; Gabriel 1999, 2005). Prompted by the ecological impacts of human population growth, some biologists have extended the basic models to evaluate the evolution of performance curves in environments that change directionally over time (Huey and Kingsolver 1993; Lynch and Lande 1993; Burger and Lynch 1995). Most recently, other biologists have investigated the coevolution of performance curves among interacting species (de Mazancourt et al. 2008; Johansson 2008). These models make a common prediction about the outcome of natural selection: the environmental mode of performance should closely match the most frequent state of the environment. This prediction stems from the assumption that adaptation enables organisms to perform equally well at any environmental optimum.

In contrast to current models, adaptation does not always confer the same capacity for performance in all selective environments. In particular, thermodynamics has been hypothesized to constrain adaptation to thermal variation (Angilletta et al. 2010b). Because temperature affects the mean kinetic energy of molecules, biochemical reactions proceed more quickly at higher temperatures (Mortimer 2000; Hochachka and Somero 2002). On the basis of this thermodynamic effect, some researchers have argued that adaptation to warm environments should confer greater performance than adaptation to cold environments, leading to the notion that “hotter is better” (Bennett 1987; Huey and Kingsolver 1989; Kingsolver and Huey 2008). In support of this hypothesis, maximal rates of population growth for warm-adapted genotypes generally exceed those for cold-adapted genotypes (Eppley 1972; Frazier et al. 2006; Knies et al. 2009). Both comparative and experimental studies of other performances also suggest that hotter is usually better (reviewed in Angilletta 2009; Angilletta et al. 2010b). Although the magnitude of this thermodynamic effect varies considerably among traits and taxa, the metabolic theory of ecology postulates a precise relationship between body temperature and maximal performance (Savage et al. 2004).

To explore the influence of thermodynamics on adaptation, we introduced a thermodynamic effect into a model of optimal performance curves. We modeled this ther-
modynamic effect according to the Boltzmann factor, which describes how reaction kinetics vary with temperature (Gillooly et al. 2001). As with previous models, we imposed a trade-off between specialization and generalization (Angilletta et al. 2003). Because many performance curves appear asymmetric (Huey and Stevenson 1979; Angilletta et al. 2002; Angilletta 2009), we permitted the shape of the performance curve to evolve along with the thermal optimum and thermal breadth. Our model suggests that thermodynamic constraints can favor the evolution of a thermal optimum that exceeds the mean body temperature. This mechanism could partially explain the frequent mismatch between thermoregulatory behavior and thermal physiology in ectotherms (see Martin and Huey 2008).

The Model

We developed a model to examine the optimal performance curve in an environment that varies seasonally and stochastically. The thermal sensitivity of performance \(Z\) was described by a nonlinear function:

\[
Z(T) = \frac{e \times [\Gamma(\frac{T - \alpha}{b})^{\gamma + (1 - \gamma - \gamma')}]^2}{\Gamma(\gamma'/\beta)[\Gamma(1 - \gamma'/\beta)]} \times e^{e^{2\pi T}},
\]

where \(T\) equals the body temperature in Kelvin, \(k\) equals the Boltzmann constant, and \(E\) equals the energy of activation (0.6 eV; Gillooly et al. 2001). The variables \(\alpha\), \(\beta\), and \(\gamma\) determine the mode, breadth, and skewness of the performance curve, respectively (fig. 1A–1C). The parameter \(b\) sets the maximal breadth, and the parameter \(c\) scales the value of performance. The second term, based on the metabolic theory of ecology (Brown et al. 2004), represents a hypothetical thermodynamic effect on mean performance (Savage et al. 2004; Frazier et al. 2006). In the absence of this thermodynamic effect, the integral of the performance curve would equal \(bc\) despite changes in \(\alpha\), \(\beta\), and \(\gamma\); this constraint would force a trade-off between specialization and generalization (Angilletta et al. 2003). However, the thermodynamic effect enables greater mean performance when the maximal performance occurs at higher temperatures. Because empirical performance curves usually appear asymmetrical, our function provides a more realistic representation of these curves than does the Gaussian function used by other researchers (see Lynch and Gabriel 1987).

We modeled both seasonal and stochastic variations in body temperature. Seasonal variation was modeled according to a sinusoidal function, such that daily mean temperatures \((T)\) were calculated as

\[
T = \delta \left[ \sin \left( \frac{d \times \pi}{s} - \frac{1}{2} \right) \right] + 293.15,
\]

where \(s\) equals the length of the active season in days, \(d\) equals the day of the season, and \(\delta\) equals the seasonal range of daily mean temperatures (fig. 1D–1F). Stochastic variation within days was modeled using a Gaussian function \((F)\):

\[
F = \begin{cases} 
\frac{1}{\sigma \sqrt{2\pi}} \exp \left[ -\frac{(T - \bar{T})^2}{2\sigma^2} \right] & \text{if } F(T) > 1 \times 10^{-3}, \\
0 & \text{otherwise},
\end{cases}
\]

where \(\sigma\) determines the magnitude of daily variation (fig. 1G–1I). This discontinuous function maintained the Gaussian distribution used in previous work while constraining the range of body temperatures; this constraint became critical when we modeled the effect of performance on survivorship (see below). Following Gilchrist (1995), we assumed an organism with a short life span (5 days) relative to the length of the active season (180 days). Because the mean temperature varies among days, both seasonal and stochastic changes contribute to thermal variation within generations, whereas only seasonal change contributes to thermal variation among generations. We considered nine patterns of thermal heterogeneity, based on combinations of \(\sigma\) and \(\delta\) \((\sigma = \{0.5, 3.5, 6.5\} \text{ and } \delta = \{0, 10, 20\})\). These assumptions about generation time and body temperature captured a range of thermal variations within and among generations (fig. 1). In principle, the model applies to ectotherms or endotherms, as long as one chooses appropriate values of \(\sigma\) and \(\delta\) (see Angilletta et al. 2010a).

We modeled the fitness of phenotypes \((w)\) as the product of survivorship and fecundity:

\[
w = R \times \prod_{j=1}^{L} \prod_{T_{min}}^{T_{max}} S(T(g, j), T),
\]

where \(R\) equals the fecundity at maturation, \(S\) equals survivorship, \(g\) equals the generation, \(j\) equals the age of the organism in the current generation, \(L\) equals the life span, and \(T_{min}\) and \(T_{max}\) equal the minimal and maximal body temperatures experienced during the current day. This function provides a valid estimate of fitness for a semelparous organism in a stable population (Kozłowski et al. 2004). Using our fitness function, we modeled fitness landscapes for two scenarios. In the first scenario, we assumed that performance contributed directly to fecundity without affecting survivorship \((S = 1\) for all values of \(T)\), such that fitness simply equaled the fecundity at maturation.
Figure 1: A, Parameter $\alpha$ determines the position of the performance curve along the thermal axis. All else being equal, increasing $\alpha$ by 1 will increase the thermal optimum by 1°C. Because of the thermodynamic effect (eq. [1]), increasing the value of $\alpha$ also increases the maximal performance. B, Parameter $\beta$ determines the breadth of the performance curve. An increase in $\beta$ causes a proportional increase in the performance breadth and a proportional decrease in the maximal performance. Because of the thermodynamic effect, increasing the value of $\beta$ also increases the thermal optimum. C, Parameter $\gamma$ determines the skew of the performance curve. Values of $\gamma < 0.5$ cause a positive skew, and values $>0.5$ cause a negative skew. Because of the thermodynamic effect, increasing the value of $\gamma$ also increases the maximal performance. D–F, Parameter $\delta$ determines the variation in body temperature experienced among days. These plots show seasonal variations in body temperature for the values of $\delta$ used to generate fitness landscapes. G–I, Parameter $\sigma$ determines the variation in body temperature experienced within days. These plots show distributions of body temperatures for the values of $\sigma$ used to generate fitness landscapes.

As per Gilchrist (1995), we assumed that fecundity scaled proportionally to the sum of performance throughout life:

$$w = R = m \times \sum_{j=1}^{L} \sum_{T_{b}=T_{\text{min}}}^{T_{\text{max}}} F(T(d(g, j)), T_{b}) \times Z(T_{b}), \quad (5)$$

where $F$ equals the frequency of a given $T_{b}$ and $m$ converts units of performance into the number of offspring. In biological terms, one can envision performance as a measure of energy assimilation, egg maturation, or some other process that limits fecundity.

In the second scenario, we assumed that fecundity and survivorship depend on body temperature. We modeled the thermal sensitivity of survivorship as a step function, because probabilities of survival generally remain high and constant over a range of temperatures and drop sharply outside this range (van der Have 2002; Angilletta 2009). Thus, fitness for this scenario was calculated as

$$w = \left[ m \times \sum_{j=1}^{L} \sum_{T_{b}=T_{\text{min}}}^{T_{\text{max}}} F(T(d(g, j)), T_{b}) \times Z(T_{b}) \right] \times \left[ \prod_{j=1}^{L} \prod_{T_{b}=T_{\text{min}}}^{T_{\text{max}}} F(T(d(g, j)), T_{b}) \times S(Z(T_{b})) \right], \quad (6)$$
by two Gaussian functions with different modes. To create these bimodal distributions, we followed Kelvin.

For either scenario, the long-term mean fitness of a phenotype was calculated as

\[ S = \begin{cases} 1 & \text{if } Z(T_b) > 1 \times 10^{-12}, \\ 0 & \text{otherwise.} \end{cases} \quad (7) \]

Equation (7) ensures that the evolution of a narrow breadth of performance also reduces the range of temperatures tolerated by the organism. In biological terms, this relationship could stem from a positive genetic correlation between the thermal sensitivities of fecundity and survivorship.

Because distributions of body temperatures for real organisms usually differ from Gaussian distributions, we also constructed fitness landscapes for several bimodal distributions. To create these bimodal distributions, we followed Gilchrist (1995), who summed the frequencies generated by two Gaussian functions with different modes:

\[ F = \frac{1}{\sigma \sqrt{2\pi}} \exp \left( -\frac{(T_b - T_L)^2}{2\sigma^2} \right) + \frac{1}{\sigma \sqrt{2\pi}} \exp \left( -\frac{(T_b - T_U)^2}{2\sigma^2} \right) \quad (9) \]

If \( F(T_b) > 1 \times 10^{-12} \), and \( F = 0 \) otherwise, where \( T_L \) and \( T_U \) define the lower and upper modes of the distribution, respectively, for a given magnitude of thermal variation (\( \sigma \)). We chose values of \( T_L \) and \( T_U \) such that the modes of the distribution were 20°C and 30°C for each value of \( \sigma \).

Results and Discussion

A thermodynamic effect qualitatively alters the optimal performance curve in a heterogeneous environment. In the absence of a thermodynamic effect, natural selection favors a thermal optimum that equals or slightly exceeds the mean body temperature (Gilchrist 1995). When body temperature varies little within generations, the performance breadth should scale proportionally to the variation in body temperature among generations. Given a thermodynamic effect, variation in body temperature within generations favors a greater mismatch between the mean temperature and the thermal optimum (fig. 2). This phenotype imposes some loss of performance at the mean body temperature but confers a substantial increase in performance at higher body temperatures. Importantly, an organism realizes this benefit only when its body temperature varies throughout its life. Thus, the optimal mismatch between the thermal optimum and the mean temperature increases with increasing thermal heterogeneity. A thermodynamic effect has no impact on the optimal performance curve when body temperature remains constant.

A thermodynamic effect imposes a similar selective pressure when performance affects survivorship as well as fecundity (fig. 3). When performance determines fecundity only, fitness depends on the sum of performance over time. In this scenario, a genotype can fail to perform for extended periods, as long as favorable temperatures occur at some point in each generation. When performance determines survivorship (as in eq. [7]), an individual must perform at all times to achieve any fitness. Therefore, greater variation in body temperature within generations favors a wider performance breadth (fig. 3), as described by Lynch and Gabriel (1987). Close inspection of the fitness landscapes in figures 2 and 3 also reveals that stronger stabilizing selection of the thermal optimum occurs when performance determines survivorship (e.g., the steepness of the fitness landscape along the Y-axis of fig. 3 exceeds that of fig. 2C). Nevertheless, variation within generations still favors a thermal optimum that exceeds the mean body temperature (fig. 4A, 4C). Thus, the qualitative impact of a thermodynamic effect does not depend on the mechanism by which performance affects fitness.

Changing the distribution of body temperatures from unimodal to bimodal did not alter the basic predictions of our model (fig. 5). In the absence of a thermodynamic effect, natural selection would drive the thermal optimum of performance toward either the lower or the upper mode of body temperature (Gilchrist 1995). But when hotter is better, selection favors a thermal optimum that equals or exceeds the upper mode (fig. 4B, 4D). When body temperature varies little within generations, the thermal optimum should lie close to the upper mode. Increasing the thermal heterogeneity within generations leads to selection for a thermal optimum that exceeds the upper mode. This result does not depend on whether performance contributes to fitness via fecundity or survivorship; however, the optimal performance breadth depends strongly on the relationship between performance and fitness (cf. fig. 4B, 4D).

Several factors could quantitatively alter our predictions about the optimal mismatch between the mean temperature and the thermal optimum. First, the actual ther-
Figure 2: Fitness landscapes for nine patterns of thermal heterogeneity when the performance of an organism determines its fecundity. To reduce the landscape to three dimensions, we plotted results only for $\gamma = 0.5$. Values of parameters were as follows: $b = 80$, $c = 1$, $L = 5$, $N = 36$. Contour lines depict the relative fitness, ranging from 0 to 1 (interval = 0.1). When body temperature varies within generations, a thermodynamic effect on performance favors a thermal optimum that exceeds the mean body temperature (see fig. 4A). As in Gilchrist’s model, thermal specialists are favored whenever the thermal variation within generations equals or exceeds the thermal variation among generations.

A thermodynamic effect on performance likely differs from the one modeled here. We used the Boltzmann factor to model a thermodynamic effect, but estimated thermodynamic effects vary considerably among traits and taxa (Angilletta et al. 2010b); for example, the thermodynamic effect on the population growth rate of insects exceeded the effect described by the Boltzmann factor (Frazier et al. 2006). A change in either the form or the magnitude of the thermodynamic effect would alter the fitness landscapes described by our model. Second, reversible acclimation of the performance curve would effectively reduce the impact of thermal heterogeneity on performance (see Gabriel 2005). Although we did not model this phenomenon, our intuition suggests that the mismatch between the mean
Figure 3: Fitness landscapes for nine patterns of thermal heterogeneity when the performance of an organism determines its fecundity and survivorship. To reduce the landscape to three dimensions, we plotted results only for $\gamma = 0.5$. Values of parameters were as follows: $b = 80$, $c = 1$, $L = 5$, $N = 36$. Contour lines depict the relative fitness, ranging from 0 to 1 (interval = 0.1). In this case, generalists are favored whenever temperature varies greatly within generations. Nevertheless, variation within generations still favors a thermal optimum that exceeds the mean body temperature (see fig. 4C).

Temperature and the thermal optimum should depend on the time lag for acclimation. For an organism with no lag, the thermal optimum should instantaneously track the body temperature. As the time lag increases, the optimal mismatch should approach that of an organism without the ability to acclimate. Finally, a closer match between the mean temperature and the thermal optimum could result from complex relationships between performance and fitness. In our model, we considered a relatively simple fitness function, in which the timing of performance had no consequence for fitness. However, real organisms probably need to perform at certain levels during specific periods. Such a requirement would translate to a more complex fitness function than those considered to date. By
The conclusion also holds for both Gaussian (left) and bimodal (right) distributions of body temperatures. Each plot shows optimal performance curves for three levels of thermal heterogeneity within generations ($\sigma = \{0.5, 3.5, 6.5\}$). In all cases, we assumed that distributions of body temperatures remained constant among generations (i.e., $\delta = 0$). Dotted vertical lines denote mean or modal body temperatures.

refining our assumptions about the magnitude of the thermodynamic effect, the capacity for thermal acclimation, and the relationship between performance and fitness, we can better resolve the generality of the selective pressures described by our model.

By varying the shape of the performance curve, we compared the fitnesses of symmetric and asymmetric curves. When performance affects fecundity only, a strongly skewed curve confers the greatest fitness in all environments (see fig. 4A, 4B). Yet thermal heterogeneity selects for weaker skews (and wider breadths) when performance affects survivorship (see fig. 4C, 4D). These results have important implications for the interpretation of previous theoretical and empirical work. Most evolutionary models assume a symmetric curve, because the functions that describe such curves possess convenient mathematical properties (Lynch and Gabriel 1987; Gabriel 1988, 2005; Gabriel and Lynch 1992; Kopp and Gavrilets 2006). For example, the Gaussian function has two variables that independently determine the mode and breadth of the curve. By contrast, we used a function with multiple parameters that interact to determine the mode and breadth of the curve (eq. [1]). Although both approaches yield qualitatively similar predictions about certain aspects of thermal physiology, our approach led to novel predictions about the selective pressures on the shape of a performance curve. These predictions accord well with empirical observations. Asymmetric functions nicely describe the thermal sensitivities of assimilation, growth, development, and locomotion in many ectotherms (Huey and Stevenson 1979; Angilletta et al. 2002; Angilletta 2009). Asymmetric functions even describe the thermal sensitivities of common estimates of fitness, such as $r$ and $R_0$ (Huey and Berrigan 2001). Nevertheless, symmetric functions better describe thermal sensitivities of survivorship (e.g., see Angilletta et al. 2008). In light of our model, the symmetry of performance curves for survivorship and the asymmetry of other performance curves might reflect evolutionary adaptations rather than physical constraints.

Our model potentially explains some known discrepancies between the thermoregulatory behaviors and the thermal physiologies of ectotherms. Martin and Huey
Figure 5: A–C, Bimodal distributions of body temperatures approach the shape of a Gaussian distribution as the magnitude of thermal variation increases within generations. Values of $\sigma$ were 0.5, 3.5, and 6.5 for low, medium, and high variation, respectively. For all three distributions, the intermodal distance equals 10°C. D–F, Fitness landscapes corresponding to the distributions of body temperatures depicted in A–C, respectively, when the performance of an organism determines its fecundity. To reduce the landscape to three dimensions, we plotted results only for $\gamma = 0.5$. Values of parameters were as follows: $b = 80, c = 1, L = 5, N = 36, \delta = 0$. Contour lines depict the relative fitness, ranging from 0 to 1 (interval = 0.1). When body temperature varies little within generations, natural selection favors a thermal optimum that matches the higher modal body temperature (see fig. 4B). When body temperature varies greatly within generations, a thermodynamic effect on performance favors a thermal optimum that exceeds the higher modal body temperature (see fig. 4B). G–I, Fitness landscapes corresponding to the distributions of body temperatures depicted in A–C, respectively, when the performance of an organism determines its fecundity and survivorship. Values of parameters were the same as those used for D–F. When body temperature varies little within generations, natural selection favors a thermal optimum near the higher modal body temperature (see fig. 4D). As the variation in body temperature increases within generations, natural selection favors an increase in the thermal optimum and the performance breadth (see fig. 4D); these changes in the optimal performance curve result from an increase in the optimal value of $\beta$ as variation in body temperature increases within generations (fig. 1B illustrates this effect of $\beta$ on the performance curve).

(2008) showed that the optimal temperature for sprinting usually exceeds the preferred body temperature. They attributed this mismatch to a selective pressure imposed by imperfect thermoregulation. Their argument goes as follows. Most performance curves possess an asymmetric shape, such that relatively high temperatures impair performance more than relatively low temperatures do. If an animal regulates its temperature imprecisely, periods of
high temperature impose a severe cost. This cost would be minimized if genotypes expressed a thermal optimum that exceeded the mean body temperature. This particular thermal physiology provides a safety margin in the event of overheating; in fact, unusually high temperatures would enhance rather than impair performance when the thermal optimum exceeds the mean body temperature. According to their model, a greater degree of asymmetry in the performance curve favors a greater shift in the thermal optimum. In support of their model, Martin and Huey showed that the mismatch between thermoregulatory behavior and thermal physiology was significantly correlated with the degree of asymmetry among species of reptiles. Nevertheless, the preferred temperature and the thermal optimum differed by as much as 8°C, while their model predicts a discrepancy of only 1°C–2°C. Large mismatches between thermoregulatory behavior and thermal physiology might be explained partly by the selective pressures imposed by thermodynamics.

Interestingly, Martin and Huey (2008) concluded that a thermodynamic effect has no influence on the optimal mismatch between thermoregulatory behavior and thermal physiology. This counterintuitive result occurred because these researchers optimized the distribution of body temperatures for a fixed performance curve, whereas we optimized the performance curve for a fixed distribution of body temperatures. In Martin and Huey’s model, selection favors a relatively low mean body temperature, which increases performance at high body temperatures while decreasing performance at the mean body temperature. In our model, selection favors an increase in the thermal optimum to enhance performance at high body temperatures without necessarily impairing performance at the mean body temperature. In fact, the two models describe independent selective pressures associated with variation in body temperature: selection imposed by the negative skew of a performance curve and selection imposed by a thermodynamic effect on the mean performance.

The selective pressures described by our model might account for a very important macrophysiological pattern. By analyzing global patterns of thermal physiology for several groups of animals, Deutsch et al. (2008) discovered an interesting contrast between temperate and tropical ectotherms. Temperate ectotherms perform best at body temperatures that greatly exceed the mean air temperatures of their environments. By contrast, tropical ectotherms perform best at body temperatures that lie close to their mean environmental temperatures. Deutsch et al. (2008) defined two metrics to quantify the relative impacts of warming on these species. The first metric, termed the safety margin, equals the difference between the thermal optimum for performance (or fitness) and the mean environmental temperature. The second metric, termed the warming tolerance, equals the difference between the critical thermal maximum and the mean environmental temperature. Both the safety margin and the warming tolerance tend to increase with increasing latitude (Deutsch et al. 2008). Therefore, climate change could pose a greater threat to tropical ectotherms, which possess narrow safety margins and warming tolerances (Tewksbury et al. 2008). Importantly, this macrophysiological pattern accords with a prediction of our model: the safety margin and warming tolerance should correspond to the variation in body temperature within generations (see fig. 4). Given that temperate ectotherms likely experience more variation in body temperature than do tropical ectotherms (Ghalambor et al. 2006), we should expect temperate species to enjoy wider safety margins and warming tolerances. This connection between our evolutionary model and a macrophysiological pattern underscores the value of theoretical development by evolutionary physiologists. Ultimately, a sound theory of physiological evolution would help biologists to address pressing ecological issues, such as the potential loss of biodiversity during climate change (Chown and Gaston 2008; Gaston et al. 2009; Chown et al. 2010).

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Literature Cited


