



Invited review

The evolution of thermal physiology in ectotherms

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Abstract

During the last quarter of a century, the evolution of the thermal sensitivity of performance in ectotherms has become a major focus of research programs in evolutionary physiology. Graphical and mathematical models describe how the relationship between body temperature and performance, termed the performance function, should evolve in response to the thermal environment. Interspecific comparisons of the thermal sensitivity of locomotor performance have revealed that the performance function is evolutionarily labile in some taxa but is more conservative in others. A lack of heritable variation or weak selection on performance may explain the conservation of thermal physiology in certain groups, but evolutionary trade-offs do not appear to have been important constraints. Other aspects of thermal physiology, such as the thermal sensitivity of growth rate, have evolved rapidly in ectotherms. Despite the apparent lability of thermal physiology in some taxa, there is limited evidence that thermoregulatory behavior and thermal physiology are coadapted. Future studies should broaden taxonomic and phenotypic foci, while paying close attention to the assumptions of current theories. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Body temperature; Coadaptation; Performance breadth; Thermal optimum; Thermal sensitivity; Thermoregulation

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1. Introduction

Body temperature (T_b) is perhaps the most important ecophysiological variable affecting the performance of ectotherms. Virtually all aspects of the behavior and physiology of ectotherms are sensitive to T_b (Huey and Stevenson, 1979; Huey, 1982), including **locomotion** (e.g., McConnell and Richards, 1955; Bennett, 1980; Hirano and Rome, 1984; Weinstein, 1998; Ojanguren and Brana, 2000), **immune function** (e.g., Mondal and Rai, 2001), **sensory input** (e.g., Stevenson et al., 1985; Werner, 1976), **foraging ability** (e.g., Greenwald, 1974; Ayers and Shine, 1997; Carrière and Boivin, 1997), **courtship** (e.g., Navas and Bevier, 2001), and **rates of feeding and growth** (e.g., Warren and Davis, 1967; Dutton et al., 1975; Kingsolver and Woods, 1997). During acute exposure to a broad range of temperatures, the relationship between T_b and a specific type of performance is described by an asymmetric function, in which performance is maximized at an intermediate temperature (Fig. 1). Several characteristics of performance functions aid biologists in understanding the relationship between the thermal environment and organismal performance. First, the **thermal optimum** (T_o) is the T_b at which performance is maximal. Second, the **performance breadth** is the range of T_b 's over which

performance is greater than or equal to an arbitrary level of performance, usually expressed as a percent of the maximal level. For example, the 80% performance breadth (B_{80}) is the range of T_b 's over which performance is greater than or equal to 80% of the maximum. Finally, the **critical thermal limits** are the minimum (CT_{Min}) and maximum (CT_{Max}) body temperatures that permit performance (see Lutterschmidt and Hutchison, 1997, for a review of the concept of a critical thermal limit and its application).

Since T_b has such a profound effect on performance, it is not surprising that ectotherms manage to respond to heterogeneity of the thermal environment in several ways. Hertz (1981) characterized these responses by the time-scale over which they enable organisms to cope with variation in environmental temperature. At the most rapid extreme, an individual may use behavior, physiology, or both to regulate its T_b within a narrower range than the range of environmental temperatures (Cowles and Bogert, 1944; see reviews by Casey, 1981; Avery, 1982; and Hutchison and Dupré, 1992). Not only is the rapidity of thermoregulation advantageous, its effects are readily reversible. Thus, thermoregulation is an effective means of dealing with spatial and temporal heterogeneity in the thermal environment. However, some variation in T_b is unavoidable because the capacity for thermoregulation is linked to the availability of solar radiation, which varies temporally and spatially. Precise thermoregulation may be difficult or even impossible at certain times of day or in some environments, or may be disadvantageous in certain ecological contexts (Huey and Slatkin, 1976). The increased risk of mortality, greater energy expenditure, or missed opportunities associated with thermoregulation may make alteration of the performance function a more effective strategy.

Adaptive shifts in the performance function can result from biological processes that occur over longer time scales. Within the lifetime of an individual, the performance function can be altered through acclimation to environmental temperature. Acclimation of thermal physiology involves expression of allozymes, modifications of cell membranes, or alterations to the intracellular environment that may or may not be reversible (Somero et al., 1996). It should be noted that the potential for thermoregulation can also be altered by phenotypic changes that occur via acclimation (e.g., increased vascularization, altered structure of the epidermis or cuticle). Finally, on the scale of multiple generations, performance functions may evolve in response to the thermal environment. Therefore, natural

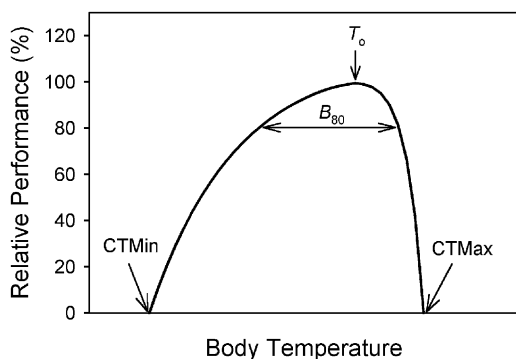


Fig. 1. A common form of the relationship between body temperature and performance in ectotherms (based on Huey and Stevenson, 1979). The thermal optimum (T_o) is the body temperature that maximizes performance and the performance breadth is the range of body temperatures that permits performance that is equal to or greater than a specified level. For example, the 80% performance breadth (B_{80}) is the range of body temperatures over which performance is $\geq 80\%$ of maximum. The critical thermal minimum (CT_{Min}) and critical thermal maximum are the minimum and maximum body temperatures, respectively, at which performance is possible.

selection may alter key parameters of performance functions (T_o , B_{80} , CT_{Min} and CT_{Max}) and the capacity for these parameters to be modified by acclimation (Kingsolver and Huey, 1998).

The extent to which performance functions can evolve by natural selection has been debated since Hertz et al. (1983) discussed two alternative views of the evolution of thermal physiology: the conservative view and the labile view. The conservative view maintains that thermal physiology does not evolve readily, and implies that altering the performance function provides only a minor benefit, incurs a major cost, or is otherwise constrained (*sensu* Burt, 2001). Initially, this view was supported by findings that the thermal sensitivity of performance was similar among closely related taxa despite ecological divergence (e.g., Hertz et al., 1983; Crowley, 1985). More recently, the labile view has garnered support from observations that the thermal sensitivity of physiological performance can vary greatly within and among species (see review by Huey and Kingsolver, 1989). A long term change in performance can occur through acclimation or evolution, but available data suggest that the capacity for thermal acclimation of performance is limited (Bennett, 1990). If the labile view is correct, there is the potential for natural selection to result in the rapid evolution of performance functions.

The labile and conservative views are actually two ends of a continuum of evolutionary patterns (Hertz et al., 1983). Since the evolution of thermal physiology is governed by complex genetic and environmental factors, performance functions will no doubt be more labile in some taxa than it will be in other taxa. Regardless of the taxon in question, the thermal sensitivity of some performances will evolve more readily than that of others. Rather than seek general support for one view over the other, we recommend that thermal biologists try to determine the factors that have influenced the evolution of thermal physiology in specific cases. That is, thermal biologists should carefully consider the assumptions of existing theories and ask whether their predictions are better supported by empirical studies when the assumptions are valid. Other disciplines of evolutionary biology have profited from this approach (e.g., optimal foraging; see Stephens and Krebs, 1986), and its application to the study of thermal physiology is long overdue.

In this paper, we shall review the growing body of comparative and experimental work on the evolution of thermal physiology in ectotherms, and explore mechanistic bases for the rates at which performance functions evolve. First, we shall synthesize existing theories, examining the assumptions of these theories and the major predictions that follow from these assumptions. Then, we shall use data from several paradigms to illustrate the ways, in which the thermal physiology of

ectotherms responds to natural selection, including the coadaptation of thermal physiology and thermoregulatory behavior. In doing so, we wish to emphasize that there has been no concerted effort to validate the assumptions of the theory in the taxa studied by empiricists. We hope that this discussion will encourage researchers to make greater efforts to validate the assumptions of a model prior to testing its predictions for the evolution of thermal physiology in ectotherms.

2. Assumptions and predictions of theory

Biologists have relied heavily on verbal arguments and graphical models to generate predictions about the evolution of thermal physiology (e.g., see Huey and Stevenson, 1979; Huey and Bennett, 1987). If one assumes that (1) there is heritable variation in the performance functions of individuals, and (2) there is a positive relationship between performance and fitness, then natural selection should favor individuals that perform better at T_b 's typically experienced during the performance in question (Figs. 2A and B). This argument leads to two testable predictions about the

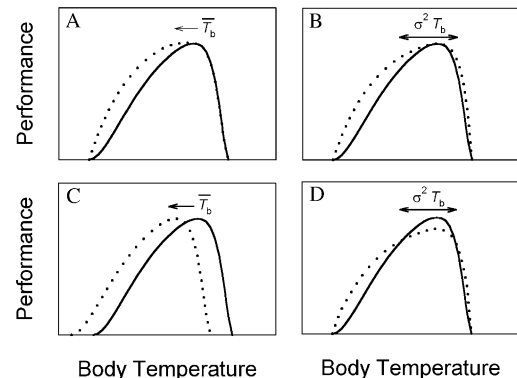


Fig. 2. Hypothetical responses of performance functions to variation in the thermal environment (adapted from Huey and Kingsolver, 1993; *The American Naturalist*, © 1993 by The University of Chicago). A shift in the mean body temperature should result in the evolution of enhanced performance at the new mean body temperature (A). An increase in the variance in body temperature should produce a corresponding increase in performance breadth (B). If genetic correlations between performance at high and low temperatures are present, the same shifts in body temperature will have different effects on the evolution of the performance function. A shift in the mean body temperature might result in increased performance at the new mean body temperature and decreased performance at the old one (C). Similarly, an increase in the performance breadth might be accompanied by a decrease in absolute performance at some body temperatures (D).

evolution of the thermal sensitivity of physiological performance. First, the T_o for a given performance should correspond to the average T_b of individuals when that performance occurs naturally (Hertz et al., 1983). Second, the performance breadth (e.g., B_{80}) should be correlated with some measure of the variation in T_b (van Berkum, 1986). These predictions are derived by considering the effects of the mean T_b and variation in T_b on the fitness of individuals, mediated through performance. When the two assumptions are valid, one would expect to find support for these predictions.

Graphical models contain implicit assumptions about the existence of evolutionary trade-offs acting on thermal physiology. Evolutionary trade-offs arise from negative genetic correlations between performance at different temperature or between different performances at a given temperature (Huey and Kingsolver, 1993). Such trade-offs can have a dramatic influence on the lability of the performance function (Figs. 2C and D). If there is no trade-off between performance at high and low temperatures, one might observe the evolution of enhanced performance at all temperatures (Levins, 1968), eventually leading to the thermal insensitivity of performance. If there is a strong negative genetic correlation between performance at high and low temperatures, selection for greater performance at a high temperature would result in lesser performance at a low temperature (or vice versa). Additionally, selection for a wider performance breadth could result in decreased absolute performance at some temperatures (Levins, 1968). Huey and Hertz (1984) recognized the importance of evolutionary trade-offs when they coined the phrase “a jack-of-all-temperatures but master of none”. The existence of evolutionary trade-offs would make it difficult for evolution to produce a genotype that exhibits enhanced performance at all temperatures.

Huey and Kingsolver (1993) provided a quantitative model of the evolution of thermal physiology that reaffirmed existing predictions and generated additional ones. They assumed that the relationship between environmental temperature and performance was described by a normal distribution, and that an individual's fitness was directly proportional to its performance (note that they implicitly assumed that T_b is equivalent to environmental temperature). The population was given genetic variation in the T_o , but performance breadth was the same for all individuals. Under these assumptions, they examined the effects of performance breadth on the evolution of T_o in response to increasing environmental temperature. The T_o always lagged behind environmental temperature, but the magnitude of this lag depended on the rate of change of environmental temperature, the amount of genetic variation in T_o , and the width of the performance breadth. Of great significance is the result that the lag

between the T_o and environmental temperature was greater when the performance breadth was wider. Specifically, the lag between the T_o and environmental temperature was related to the square of the performance breadth. Thus, a relatively wide performance breadth may severely weaken selection on the thermal sensitivity of performance.

Huey and Kingsolver relaxed a number of assumptions of the model to explore the sensitivity of their results. By adding the risk of extinction, it was shown that an intermediate breadth could be optimal. If the performance breadth was too wide, the population was unable to track changes in environmental temperature. If the performance breadth was too narrow, the population quickly became extinct because small changes in environmental temperature dramatically decreased fitness. Incorporating a trade-off between the absolute performance at the T_o and the performance breadth led to selection for a narrower performance breadth, but an intermediate performance breadth was still favored. This result suggests that greater performance at the T_o is favored over a wider performance breadth when a negative genetic correlation exists between the two. Adding stochasticity to changes in environmental temperature favored an increase in the performance breadth, but the optimal breadth was still intermediate.

The model of Huey and Kingsolver (1993) reaffirmed the belief that a wider performance breadth is favored when there is variation in environmental temperature. At the same time, two new predictions were generated: (1) that the T_o should evolve more slowly when the performance breadth is wider, and (2) that fitness should be maximized at an intermediate performance breadth. Although Huey and Kingsolver focused on the evolution of thermal physiology in response to a change in the mean environmental temperature, an equally interesting concern is to understand the consequences of a change in the variance of environmental temperature for the evolution of thermal physiology.

Gilchrist (1995) modeled the effect of variation in environmental temperature on the evolution of thermal physiology to determine whether certain patterns of variation in environmental temperature favored thermal generalists (i.e., individuals with wide performance breadths) or thermal specialists (i.e., individuals with narrow performance breadths). The model differed from previous models of evolution under environmental heterogeneity in several important ways. First, Gilchrist selected an asymmetric performance function, which describes the thermal sensitivity of performance in real ectotherms better than a symmetric function. Second, he assumed that an individual's performance function was completely contained within its tolerance range, so that performance contributed to fitness in an additive fashion rather than a multiplicative fashion. Third, Gilchrist

considered the evolutionary consequences of environmental variation within and among generations. Like others who have modeled evolution in heterogeneous environments (e.g., Levins, 1962), Gilchrist assumed that there is a strong evolutionary trade-off between absolute performance and the performance breadth.

An interesting prediction derived from Gilchrist's model is that wider performance breadths are favored when the thermal heterogeneity among generations increases, but narrower performance breadths are favored when the thermal heterogeneity within generations increases. The opposing effects of thermal heterogeneity within and among generations arises, in part, from the assumption that evolutionary trade-offs are strong. When evolutionary trade-offs are weakened, variation in environmental temperature within and among generations favors the evolution of a wider performance breadth. Thus, understanding the nature and strength of trade-offs associated with the evolution of performance functions is a crucial step in evaluating current theory. When evolutionary trade-offs are strong, generation time can play a key role in the evolutionary response to environmental temperature; organisms with longer generations will probably encounter greater fluctuations in environmental temperature throughout their lifetime, which would favor the evolution of narrower performance breadths.

A major challenge to evaluating these models is to gather accurate estimates of the direction and rate of the evolution of performance functions in response to the thermal environment. When selection is strong and evolutionary constraints are weak, we should see the predicted patterns of variation in thermal physiology among populations or species. Alternatively, when evolutionary constraints are strong, the evolution of thermal physiology will either proceed slowly or counter-intuitively (e.g., the evolution of narrower versus wider performance breadths that is predicted by Gilchrist's model). The direction of evolutionary change is simple enough to quantify, but estimating the rate of this change still poses a problem in many cases because the timing of divergence between taxa is unknown. When the timing of divergence is known, rates of evolution are easily estimated (e.g., see Huey et al., 2000). Unfortunately, many potentially valuable comparisons of the thermal sensitivity of performance have been made without specific knowledge of the phylogenetic relationships and the times of divergence among taxa. Therefore, quantitative estimates of the rates at which performance functions can evolve are presently beyond reach, and will continue to be so until studies of thermal physiology are more firmly united with information about the evolutionary history of the organisms under study.

3. Lability of thermal physiology varies among taxa: evidence from the study of locomotor performance

Bennett (1980) launched a major paradigm for studying the evolution of the thermal sensitivity of performance. In particular, Bennett wanted to know if the T_o for performance corresponded to the average T_b during activity. In the laboratory, he quantified thermal sensitivities of burst speed (also referred to as sprint speed) and treadmill endurance of several species of lizards. A qualitative match between field T_b and the T_o of locomotor performance was found, suggesting that thermal physiology has evolved in response to environmental temperature. More importantly, Bennett's study set the stage for locomotor capacities to become one of the most popular measures of whole-organism performance (reviewed by Bennett and Huey, 1990).

Interspecific comparative analyses of the thermal sensitivity of locomotor performance have provided mixed support for the prediction that the T_o for performance should correspond to T_b 's experienced in nature (Fig. 3). Certain groups exhibit clear associations between T_b 's commonly experienced during activity and the T_o for performance. In *Anolis* lizards, the T_o for sprinting was significantly correlated with the median field T_b (van Berkum, 1986). Likewise, the locomotor performance of amphibians is sometimes related to field T_b . The montane frog *Eleutherodactylus portoricensis*, jumped poorly at a T_b of 30°C but jumped very well at T_b 's of 20° and 25°C, compared to its lowland congener *E. coqui* (Beuchat et al., 1984). Several other species of

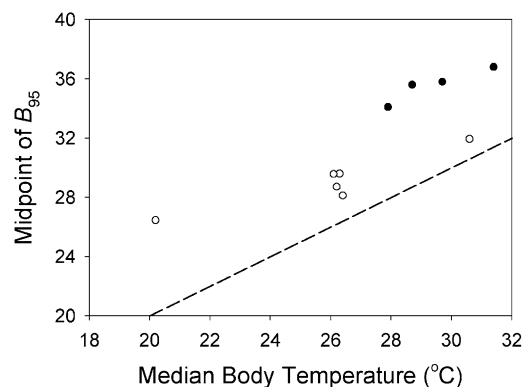


Fig. 3. *Anolis* lizards (open circles) have thermal optima for sprinting that correspond more closely to median field body temperatures than gekkonid lizards (solid circles). The dashed line is provided as a reference; points that are closer to the line signify a closer match between the median field body temperature and the thermal optimum. Thermal optima were estimated by the median of the 95% performance breadth. Data for *Anolis* and gekkonids are from van Berkum (1986) and Huey et al. (1989; *Physiological Zoology*, © 1989 by The University of Chicago), respectively.

frogs were shown to jump maximally at T_b 's that correspond to average field T_b 's (Knowles and Weigl, 1990). Other groups exhibit more conservative patterns of thermal physiology. For example, nocturnal geckos had rather high thermal optima for sprinting despite relatively low T_b 's during activity (Huey et al., 1989). Similarly, thermal optima for sprinting were higher than average T_b 's experienced by agamid lizards; however, these lizards were capable of sprinting at greater than 90% of maximum speed at their average field T_b 's (Hertz et al., 1983). In some instances, such as the case of geckos (Huey et al., 1989), it is clear that there has been a considerable period of time for the evolution of thermal physiology to proceed, even though there is little evidence that an evolutionary response to the thermal environment has occurred. Taken together, these studies support the idea that a given aspect of the thermal physiology, such as the thermal sensitivity of locomotor performance, has been more labile in some taxa than it has in others.

Fewer studies have examined the relationship between variation in T_b and the performance breadth for locomotion, but available studies indicate that this parameter of the performance function is more labile than the T_o . The best evidence comes from interspecific comparisons along latitudinal or altitudinal clines. For example, van Berkum examined the relationships between variation in field T_b and performance breadths for sprinting in representatives from three families of lizards. The interquartile distance of field T_b was correlated with B_{95} in lizards from the Iguanidae, Xantusiidae and Teiidae, but was not correlated with B_{80} (van Berkum 1986, 1988). In these same taxa, the range of thermal tolerance ($CT_{Max}-CT_{Min}$) was positively correlated with the range of field T_b 's (van Berkum, 1988). Data for amphibians also suggests that temporal variation in T_b can impact the evolution of performance breadth. A powerful case study was conducted along an altitudinal cline in the Andes mountains of South America. Navas (1996a, 1997) measured the thermal sensitivity of locomotor performance in frogs from the families Dendrobatidae, Hylidae, Bufonidae and Leptodactylidae. A conspicuous pattern of convergent evolution was observed. In each family, high-elevation species (2600–3500 m) were capable of activity at low temperature that was unparalleled by their low-elevation congeners. The wider performance breadths of high-elevation species were consistent with the greater variation in field T_b 's experienced by these species (Navas, 1996b). Like Andean frogs, temperate frogs exhibit adaptive variation in thermal physiology among species. Holartic tree frogs of the genus *Hyla* jumped better at low temperatures than their southern counterparts, and temperatures that allowed for 80% of maximal performance correlated with the lowest environmental temperature re-

corded in natural environments (John-Alder et al., 1988). These studies indicate that there is considerable lability in the performance breadth for locomotion, such that temporal variation in T_b can be an important determinant of the evolution of thermal physiology.

Even with respect to locomotor performance, our general understanding of the extent to which performance functions can evolve is poor, because only a handful of species from a small set of taxonomic groups have been studied. However, the relatively recent extension of empirical models to insects is beginning to correct this bias. Gibert et al. (2001) compared the thermal sensitivity of walking speed in fruitflies (*Drosophila melanogaster*) from France and Congo. The effect of temperature on the walking speed of adults did not differ significantly between flies from Congo and France. Interestingly, however, flies from Congo walked faster at a given temperature than flies from France did when larval development occurred at high temperatures (25°C and 29°C), but the reverse was true when larval development occurred at a lower temperature (18°C). This result indicates that the response of locomotor performance to thermal acclimation has diverged between these two populations of *D. melanogaster*.

Although Gibert et al.'s comparative study did not produce evidence for the evolution of the thermal physiology in *D. melanogaster*, selection experiments have done so. Gilchrist et al. (1997) examined the thermal sensitivity of walking speed in genetic lines of *D. melanogaster* maintained in three different thermal environments (constant temperatures of 16.5°C, 25°C, and 29°C). After at least 100 generations of selection, the T_o for locomotor performance was positively correlated with the temperature at which flies were maintained during selection. Additionally, performance breadths of flies increased as a result of selection at low temperature. Flies maintained at 16.5°C performed better at low temperatures (relative to flies maintained at 29°C), without a concomitant reduction in performance at intermediate or high temperatures. Gilchrist et al. demonstrated conclusively that the thermal sensitivity of locomotor performance is labile in *D. melanogaster* and that evolutionary trade-offs between performance at different temperatures did not play a major role in the evolution of thermal physiology in this species. Since comparative analyses often generate ambiguous results, selection experiments are a powerful method of investigating the adaptation of thermal physiology to the thermal environment (Bennett and Lenski, 1999; Feder et al., 2000). Unfortunately, selection studies are impractical for many of the organisms that interest evolutionary physiologists, so selection studies are best viewed as a complement to comparative analyses rather than a replacement for them (Feder et al., 2000).

4. Why is thermal physiology more conservative in some ectotherms?

Three factors that govern the evolution of performance functions are the existence of heritable variation in the thermal sensitivity of performance, the relationship between performance and fitness, and evolutionary trade-offs arising from genetic correlations. Theories predicting the direction and magnitude of the evolution of performance functions include assumptions about each of these factors. When the pattern of variation in thermal physiology observed in nature deviates from the pattern predicted by a theory, we should attempt to determine whether one or more of the assumptions have been violated. For example, is the thermal sensitivity of locomotor performance conservative in gekkonids because they lack heritable variation in the T_o for sprinting? Or, is the capacity for locomotor performance unrelated to fitness in this group? Perhaps there are strong evolutionary trade-offs between locomotor performance at low T_b 's and that at high T_b 's. Unfortunately, the assumptions of theory have not been validated for most of the taxa included in comparative analyses. In fact, there are only a handful of disarticulated studies that can be pooled to infer the potential causes for the conservation of thermal physiology in certain taxa. We shall illustrate this point by considering the extent to which studies of locomotor performance have identified factors that are potentially responsible for the evolutionary stasis of performance functions.

4.1. Repeatable and heritable variation

It is thought that locomotor performance is an ideal trait for studies of evolutionary physiology because there is repeatable and heritable variation in locomotor performance among individuals (Bennett, 1990; Bennett and Huey, 1990). Indeed, there is considerable variation among species in the T_o and performance breadth for locomotion (see reviews by Huey, 1982, and Rome et al., 1992). Though how much of this variation is truly repeatable and heritable? Repeatable variation in locomotor performance has been observed over time periods of a week to a year (reviewed by Bennett and Huey, 1990), but it is not known whether locomotor performance is repeatable over the life of an individual. The evidence that maximal sprint speed is repeatable over long periods of time comes from one study of garter snakes (Jayne and Bennett, 1990) and another study of canyon lizards (Huey and Dunham, 1987; Huey et al., 1990). In both of these studies, individuals that were relatively fast in one year tended to be relatively fast in the next year. However, van Berkum et al. (1989) found that sprint speed was not repeatable over long time periods in *Sceloporus occidentalis*, and cautioned investigators to focus on the significance of variation in

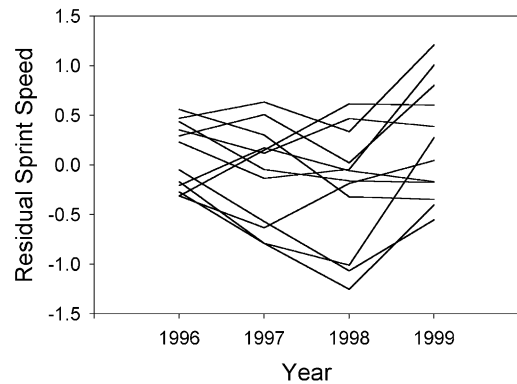


Fig. 4. Sprint speed was not repeatable over a long time period in a California population of the lizard *Petrosaurus mearnsi*. Data are annual measures of size-adjusted sprint speed for 12 individuals (M. Robson, unpublished data), beginning in their first year of life and ending in their fourth year of life. There was little concordance in the rank order of individuals among years (Kendall's coefficient = 0.10, Spearman $r = 0.02$).

locomotor performance observed during short periods of time. This conclusion is supported by long-term studies of locomotor performance in the lizard *Petrosaurus mearnsi*. Robson (2000) made annual measures of sprint speed for a cohort of lizards from ages one to four. There was very little concordance in the rank order of individuals among years, indicating that an individual could be relatively fast when young but relatively slow when old, or vice versa (Fig. 4). Until more is known about the long-term repeatability of locomotor performance, it is best not to assume that performance at one point in time can be used to draw inferences about performance over an individual's lifetime.

Even if there is repeatable variation in locomotor performance among individuals, the heritability of this variation is questionable. Heritable variation in locomotor performance has been documented in garter snakes (Garland, 1988; Brodie, 1989, 1993) and fence lizards (Tsuji et al., 1989). On the other hand, the heritability of sprint speed was found to be low and insignificant in the lizard, *Lacerta vivipara* (Sorci et al., 1995). Because the heritability of performance varies among species, a lack of genetic variation must be considered a plausible explanation for the conservation of thermal physiology in some groups. Furthermore, the heritability of locomotor performance may be lower than available estimates, because few studies have eliminated the possibility of maternal effects. If offspring are obtained from gravid females collected in the field, differences in the early maternal environment might impact locomotor performance. Recently, complex maternal effects on the locomotor performance of juveniles have been identified (Shine et al., 1997; Sorci and Clobert, 1997), stressing the need to consider

potential sources of maternal effects when designing future studies.

What is most needed to understand the evolution of thermal physiology, are data on the heritability of thermal optima and performance breadths, the variables that have been the focus of comparative analyses. However, the need for these data is easier identified than met. Estimating heritabilities of performance functions poses both empirical and analytical challenges. First, estimating the heritability of a performance function requires repeated measures of performance in hundreds of individuals of similar age and known relatedness (Gilchrist, 1996). Consequently, the practicality of such studies are limited to organisms that are very fecund. Second, conventional statistical methods for estimating genetic variation are not ideally suited for the analysis of a function-valued trait, such as a performance function (Kingsolver et al., 2001). Two approaches have been taken: (1) analysis of parameters derived from the performance function (e.g., T_b), and (2) direct analysis of the performance function. Gilchrist (1996) used both approaches to estimate the heritability of the thermal sensitivity of walking speed in the endoparasitic wasp, *Aphidius ervi*. Gilchrist analyzed parameters of the performance function using parametric and nonparametric statistics, but also directly estimated the genetic variation in the performance function using Infinite Dimensional Analysis, a method originally designed for the analysis of reaction norms (Gomulkiewicz and Kirpatrick, 1992). The former approach revealed some heritable variation in the performance breadth but not in the T_b . The latter approach revealed differences in the heritability of performance across a range of temperatures (i.e., low heritability at some temperatures and high heritability at others). Infinite Dimensional Analysis offers several advantages over conventional statistical methods (Kingsolver et al., 2001), and its application to the study of performance functions is a very promising step toward identifying constraints on the evolution of thermal physiology.

4.2. The relationship between performance and fitness

Quite possibly, the importance of maximal locomotor performance in natural populations has been overestimated. The locomotor performance paradigm assumes that sprint speed measured in the laboratory reflects a capacity for performance that is used in nature. Until recently, however, accounts of the frequency with which maximal locomotor performance is used in natural circumstances were mainly anecdotal (Hertz et al., 1988). A pair of clever studies by Jayne and his colleagues (Jayne and Ellis, 1998; Jayne and Irschick, 2000) produced detailed data on preferred speeds of the lizard *Uma scoparia* during undisturbed and escape

locomotion. These investigators realized that the substrate of *U. scoparia*'s habitat made it possible to estimate natural speeds from tracks left in the sand. Their data clearly show that lizards used submaximal speeds during escape locomotion. In fact, these lizards did not even prefer to use escape routes that enhance sprint speed (Jayne and Irschick, 2000). A quantitative analysis of preferred speeds of *Anolis* lizards also indicates that lizards use submaximal speeds for most activities. Of eight species, all moved at speeds less than 40% of maximal speed at least 75% of the time (Irschick, 2000). Though these studies bolster conclusions drawn from more casual observations, there is still a great need for quantitative analyses of the frequency and context of maximal locomotor performance in natural populations. In particular, studies of preferred speed should be combined with the more traditional comparative analyses of performance functions, so that we may better comprehend why the thermal sensitivity of performance is conserved in certain groups.

Amphibians may also use maximal locomotor performance infrequently. During escape, the hylid frog *Scinax hiemalis* jumps distances that are far less than the maximal jumping distance for their T_b . For instance, individuals at 15°C used a jumping distance that could easily be attained at 5°C (Gomes et al., in review). Frogs appear to use “smart jumping” as opposed to “power jumping” to escape predators. Apparently, when the structural habitat is complex, a variety of anuran species choose an escape route and “go for it” in a sequence of well-coordinated but submaximal jumps (C.A. Navas, personal observations). These data highlight an under-explored issue: how does temperature affect the coordination of locomotion and the potential for smart jumping, which may be more important than power jumping in a variety of ecological settings. Additional studies of escape locomotion in natural populations will help to resolve important issues about the survival value of maximal locomotor performance.

Even though individuals may not resort to their maximal speeds often, the use of maximal speed in rare instances can confer a fitness advantage. It is thought that maximal or near-maximal locomotor performance has the greatest impact on fitness during encounters with predators (Hertz et al., 1988). In fact, reptiles are more likely to take evasive action when their T_b 's are relatively high and rely on stationary defenses when their T_b 's are low (Hertz et al., 1982; Crowley and Pietruszka, 1983; Goode and Duvall, 1989; Passek and Gillingham, 1997; Shine et al., 2000). The most direct evidence that maximal locomotor performance is necessary to successfully evade predators comes from a classic study of Galapagos land iguanas (Christian and Tracy, 1981). Land iguanas that had a high enough T_b to permit maximal speed ($> 32^\circ\text{C}$) were significantly more successful in evading hawks than those that had

lower T_b 's. Further support for the importance of locomotor performance comes from a study of garter snakes. Jayne and Bennett (1990) measured the speed of hatchling and juvenile garter snakes and then followed survivorship from year to year. In some years, relatively slow individuals were not as likely to survive as were relatively fast individuals. Extrapolating from this result, one could conclude that the ability of a relatively slow individual to move at its maximal speed would confer a greater probability of survival, thus favoring a match between the average field T_b and the T_o for locomotion. Still, other studies have failed to detect relationships between locomotor performance and survival (reviewed by Bennett and Huey, 1990), leaving doubts as to the general importance of maximal locomotor performance.

Studies of short-term survival in a few species are not adequate to draw a conclusion about importance of maximal locomotor performance, because it is likely that the nature and strength of the relationship between locomotor performance and fitness varies among populations and species. The obvious benefits of enhanced locomotor performance may be balanced by less obvious costs resulting from trade-offs between locomotor performance and other aspects of the phenotype (Clobert et al., 2000). If these costs are manifested as decreased fecundity rather than survival, estimates of lifetime reproductive success will be necessary to establish the fitness consequences of variation in locomotor performance. Although more than a decade has passed since Pough (1989) concluded that the link between organismal performance and fitness needed to be strengthened, our knowledge of this link has not improved much. Experimental manipulations of locomotor performance are desperately needed to determine the relationship between performance and fitness, and recently developed methods for manipulating the locomotor capacities of free-ranging individuals provide powerful new tools to meet this need (Sinervo and Huey, 1990; Miles et al., 2000).

4.3. Evolutionary trade-offs

Evolutionary trade-offs do not appear to have been important constraints on the evolution of locomotor performance. Trade-offs could be manifested in one of two ways: (1) a negative genetic correlation between speed and some other performance, and (2) a negative genetic correlation between speeds at low and high temperatures. The former manifestation is expected from a theoretical standpoint: an increase in the number of glycolytic muscle fibers that would enhance speed may reduce the number of oxidative muscle fibers that would enhance endurance (Garland, 1988). Surprisingly, studies of lizards indicate that sprint speed and endurance are not genetically correlated (Tsuji et al., 1989; Sorci et al., 1995). In fact, Garland (1988)

estimated that the genetic correlation between speed and endurance was positive in garter snakes! Furthermore, there is no evidence of an evolutionary trade-off between performance at high and low temperatures. Huey and Hertz (1984) were the first to point out that evolutionary trade-offs are not universal when they showed that agamid lizards that sprinted relatively fast at one temperature tended to sprint fast at all temperatures. Later, Huey and Kingsolver (1993) showed that the evolution of the T_o and CT_{Max} for locomotor performance in iguanian lizards was not associated with a corresponding change in the CT_{Min} .

Actually, a jack-of-all-temperatures is seldom a master of none. Numerous reports have confirmed that the evolution of enhanced physiological performance at one temperature is not necessarily accompanied by a decrement in performance at another temperature (e.g., Malloy and Targett, 1994; Neat et al., 1995; Navas, 1996a; Schultz et al., 1996; Carrière and Boivin, 1997; Bennett and Lenski, 1999; Imsland et al., 2000; Jonassen et al., 2000; Purchase and Brown, 2000; Birkemoe and Leinaas, 2001; but see Forsman, 1999). This conclusion might prove to be erroneous because it is based primarily on a lack of negative phenotypic correlations, not genetic correlations. Complex genetic correlations can exist when phenotypic correlations are not apparent, and phenotypic correlations are not always indicative of genetic correlations (Gilchrist, 1996). For example, selection studies of foraging performance in the endoparasitic wasp *Trichogramma pretiosum* revealed genetic correlations that were not detected through phylogenetic comparative analyses of phenotypes (Fig. 5). As with other factors that influence the evolution of thermal physiology, our knowledge of evolutionary trade-offs is limited to a few species and must still be considered preliminary. Furthermore, it remains an unexplored possibility that the most important evolutionary trade-offs are those between different kinds of behavioral and physiological performances (at a given temperature), rather than trade-offs between performance at different temperatures (see Carrière and Boivin, 2001).

Interpreting empirical data in light of theoretical models, we can draw some tentative conclusions about the role that evolutionary trade-offs have played in the evolution of thermal physiology. We shall offer two examples. First, consider what we can learn from empirical relationships between average environmental temperature and the T_o for performance. If evolutionary trade-offs were strong, selection for improved performance at extreme temperatures would result in a concomitant decrease in performance at intermediate temperatures. That is, selection will result in a shift in the T_o rather than an increase in the B_{80} . All things being equal, then, the T_o is more likely to track variation in environmental temperature when trade-offs are

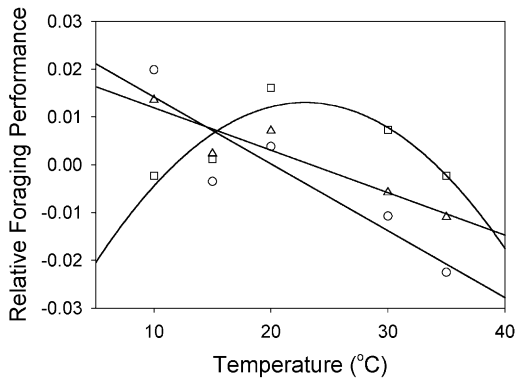


Fig. 5. Mean estimates of the direction of selection for relative performance of endoparasitic wasps, *Trichogramma pretiosum*, searching for oviposition sites (reproduced from Carrière and Boivin, 2001; *The American Naturalist*, © 2001 by The University of Chicago). Lines were selected for foraging performance at 15° (circles), 25° (squares), and 35°C (triangles) for 15 generations. As predicted by the “jack-of-all-temperatures master of none” hypothesis, lines selected for performance at 15°C showed an increase in performance at low temperatures and decrease in performance at high temperatures. Unexpectedly, lines selected for performance at 35°C showed the same trend! These complex genetic correlations between performance at high and low temperatures were not detected by a comparative analysis (Carrière and Boivin, 1997).

strong. The fact that T_o is not correlated with average T_b in certain taxa can be interpreted as evidence that a trade-off in performance among temperatures has not played an important role in the evolution of performance functions in these taxa. As a second example, consider what we can learn from relationships between variation in T_b and performance breadth. If evolutionary trade-offs were strong, variation in the thermal environment within generations should lead to the evolution of thermal specialists (Gilchrist, 1995). Since comparative studies of the thermal sensitivity of locomotor performance in reptiles and amphibians have revealed the opposite trend (see Section 3), one could conclude that genetic trade-offs have not been an important constraint on the evolution of the thermal sensitivity of locomotor performance in these taxa. Certainly there are other interpretations. For example, the poor match between the average T_b and the T_o may be due to a lack of heritable variation in the performance function, or an inaccurate estimate of the average T_b experienced in nature. Our interpretations may be proven false as more data on the thermal physiology of ectotherms are acquired. Yet, they are useful illustrations of the interplay between theory and empiricism that can lead to significant advances in knowledge.

5. Certain aspects of thermal physiology evolve more readily than others

From a theoretical standpoint, the T_o for performance should track changes in environmental temperature more rapidly when the performance breadth is narrow (Huey and Kingsolver, 1993). This prediction is derived from the assumption that there is a direct mapping between performance and fitness (i.e., a given increase in performance results in a proportional increase in fitness). When the mapping between performance and fitness is direct, an individual with a narrow performance breadth will experience a great decrement in fitness when the mean T_b during performance deviates from the T_o . Ultimately, both the performance breadth and the strength of the relationship between performance and fitness should influence the rate at which the T_o evolves. For performances that are relatively insensitive to temperature or those that have only a weak influence on fitness, the T_o would not be expected to respond rapidly to changes in the thermal environment.

Compared to some physiological performances, locomotion is fairly insensitive to T_b . Typically, 80% performance breadths for the sprint speed of lizards span 10–20°C, and include the majority of T_b 's experienced during activity (Bennett, 1980; Hertz et al., 1983; Crowley, 1985; van Berkum, 1986; Huey et al., 1989; Navas, 1996a). In comparison, the growth of ectotherms is usually far more sensitive to T_b . Performance breadths (B_{80}) for growth rate usually span less than 10°C (e.g., see Ji et al., 1995; Kingsolver and Woods, 1997; Jonassen et al., 2000), which is at least twice the thermal sensitivity that is observed for locomotor performance.

Two factors account for the relatively high thermal sensitivity of growth rate. First, the capacity for growth is limited by a number of physiological processes, each of which must occur in sequence: foraging, consumption, digestion, absorption, and anabolism (Weiner, 1992). Each upstream process (e.g., capture and consumption of prey) limits all downstream processes (e.g., digestion, absorption), and vice versa. Second, not all of these processes are equally sensitive to T_b (Van Damme et al., 1991; Ji et al., 1996; Angilletta et al., in press). Consequently, the rate of growth, which relies on the concerted performance of multiple processes (including locomotion), is more sensitive to T_b than any single process involved.

In fact, the thermal sensitivity of growth rate might be even more sensitive to temperature than empirical studies indicate. Growth rate is commonly measured during chronic exposure to constant temperatures, despite the fact that ectotherms are rarely exposed to extreme temperatures for prolonged periods. If chronic exposure to extreme temperatures is stressful, growth

rates at extremes might be reduced and performance breadths will appear artificially narrow. However, empirical estimates of growth during acute versus chronic exposures to a range of temperatures indicate that chronic exposure reduces growth rates at intermediate temperatures, but not at extreme temperatures (Kingsolver and Woods, 1997, 1998). Consequently, estimates of performance breadths for growth rate might be wider than the actual performance breadths. Given the relatively narrow (and potentially even narrower) performance breadths for growth rate, the T_o for growth rate should respond more rapidly than the T_o for locomotor performance to a change in the thermal environment. Note, this prediction is based on the assumption that locomotor performance does not have a greater impact on fitness than growth rate does (see Section 4.2).

Comparative analyses suggest that the thermal sensitivity of locomotor performance does evolve slowly. Although interspecific comparisons have revealed evidence that thermal optima for sprinting have evolved in response to the thermal environment, intraspecific comparisons have failed to do the same. Average field T_b 's of the eastern fence lizard, *Sceloporus undulatus*, differ by several degrees between populations in New Mexico and Colorado, but thermal optima for sprinting were identical for lizards from the two populations (Crowley, 1985). Likewise, field T_b 's of the lizard *Podarcis tiliguerta* differed between low- and high-elevation populations, but both populations had virtually identical thermal optima and performance breadths for sprinting (Van Damme et al., 1989). Northern and southern populations of *Hyla crucifer*, ranging from Florida to New Jersey, exhibited similar thermal sensitivities of swimming performance, an observation that even extended to the physiological properties of isolated muscles (John-Alder et al., 1989). Furthermore, intraspecific comparisons within four families of Andean frogs revealed similar thermal sensitivities of locomotor performance for individuals collected at 2600 and 3500 m (Navas, 1996a), despite major differences in field T_b 's among populations (Navas, 1996b). Although gene flow can limit the rate of evolution within species, the thermal sensitivity of locomotor performance appears to be conservative even when there is clear geographic isolation among populations and variation in the thermal environments is extreme.

The apparent conservation of thermal physiology within species is surprising in light of evidence provided by two interspecific comparative analyses. Huey and Kingsolver (1993) examined the evolution of the T_o for sprinting in the superfamily Iguania. Combining data for 19 species of iguanians from several sources (Bennett, 1980; Crowley, 1985; van Berkum, 1986, 1988; Huey, unpublished data), they detected a sig-

nificant correlation between field T_b and the T_o for sprinting; that is, lizards that experienced high T_b 's during activity tended to have a high T_o for sprinting. Similarly, John-Alder et al. (1988) found significant divergence in the performance breadths for jumping among species of hyliid frogs. Both of these interspecific comparative analyses included species within which the thermal sensitivity of locomotor performance appears to be conservative (i.e., *S. undulatus* in the study by Huey and Kingsolver, 1993, and *H. crucifer* in the study by John Alder et al., 1988). In the iguanian and hyliid lineages, the evolution of thermal physiology is evident among taxa separated by relatively long periods of time but not among taxa separated by shorter periods of time. In general, the discrepancy between the results of inter- and intraspecific analyses may reflect a slow rate of evolution of the thermal sensitivity of locomotor performance.

In contrast, the thermal sensitivity of growth appears to have evolved rapidly in many ectotherms. Comparisons among populations of fish in the North Atlantic Ocean have demonstrated significant evolution of the thermal sensitivity of growth rate within species. In general, fish from high latitudes grow faster at low temperatures than fish from low latitudes (Conover and Present, 1990; Imsland et al., 2000; Jonassen et al., 2000; but see Schultz et al., 1996). The faster growth of fish from high latitudes has been achieved by either an increase in performance breadth or an increase in absolute performance at all temperatures (Fig. 6). Variation in performance persists when all populations are reared in a common environment for one or more generations, confirming that there is a genetic basis for latitudinal variation in growth rate. The evolution of growth rates in fish must have been fairly rapid, considering that populations of fish in the northern Atlantic Ocean diverged at the end of the Pleistocene, perhaps even as late as 12,000 years ago (Blanquer et al., 1992; Pogson et al., 2001; D.O. Conover, personal communication; A.K. Imsland, personal communication). Moreover, the variation in thermal physiology among populations appears to be maintained in spite of considerable gene flow among populations (Conover, 1998).

Studies of other ectotherms have revealed similar trends in the evolution of the thermal sensitivity of growth. At low temperatures, copepods from northern populations grew faster than copepods from southern populations (Lonsdale and Levinton, 1985, 1989). Similarly, the growth of larval swallowtails (*Papilio canadensis*) from Alaska was faster at a low temperature than the growth of individuals from Michigan (Ayres and Scribner, 1994). In a selection experiment conducted in the laboratory, *Drosophila melanogaster* evolved higher growth efficiencies at low temperatures when maintained at a low temperature during selection (Neat et al., 1995). A recent study of garter snakes (*Thamnophis elegans*)

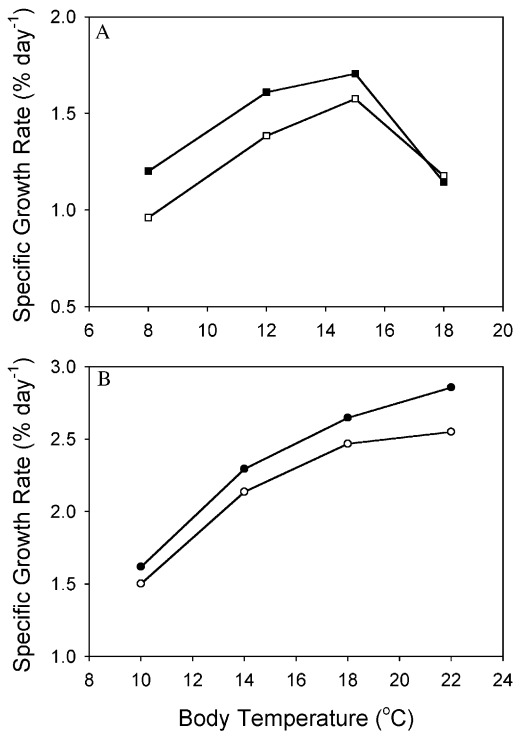


Fig. 6. Over a wide range of body temperatures, fish from northern populations (filled symbols) tend to grow faster than fish from southern populations (open symbols). Data for *Hippoglossus hippoglossus* (A) and *Scophthalmus maximus* (B) are from Jonassen et al. (2000) and Imsland et al. (2000), respectively (*Journal of Fish Biology*, © 2000 by Academic Press). In *H. hippoglossus*, performance breadth has diverged between populations. In *S. maximus*, absolute performance has increased at all temperatures. Performance functions for growth diverged after southern populations re-invaded cold, northern waters following the last ice age.

further confirms that the thermal sensitivity of growth rate can evolve rapidly. Bronikowski (2000) studied snakes from two populations, one from a relatively cool meadow and another from a relatively warm lakeshore. A common environment study, which simulated the two thermal environments (night-time temperatures of 20°C or 25°C), showed that each population grew faster than the other at its respective environmental temperature; the mountain-meadow population grew faster than the lakeshore population at the low night-time temperature, but the reverse was true at the high night-time temperature. It is likely, but not certain, that the differences in performance between populations were genetic because environments were controlled from the beginning of gestation (i.e., prior to birth).

The contrasting results of studies of sprint speed and studies of growth may signify an intrinsic difference between the rates at which these traits evolve. Since

performance breadths for growth rate are narrower than those for sprint speed, the thermal sensitivity of growth may respond more rapidly to natural selection. It is also possible that a given increment in growth rate (e.g., 10%) may have a greater impact on fitness than a given increment in sprint speed. These speculations can only be confirmed or refuted by more intensive investigation of (1) the rates of evolution of performance functions for sprint speed and growth rate, and (2) the relationships between these performances and fitness.

6. Coadaptation of thermoregulatory behavior and thermal physiology

6.1. The coadaptation hypothesis

Some ectotherms use behavioral thermoregulation to reduce the impact of temporal and spatial variation in environmental temperature on T_b (see reviews by Casey, 1981; Avery, 1982, and Hutchison and Dupré, 1992). The thermoregulatory behaviors of ectotherms appear to be governed by distinct thermal preferences, and preferred body temperatures (T_p 's) of individuals can be quantified in the laboratory using various protocols (e.g., Licht et al., 1966; Mac, 1985; Smith et al., 1999). Although many factors are known to affect thermal preference (e.g., nutritional or reproductive state), the T_p is a genuine property of some ectotherms (Licht, 1968; Angilletta and Werner, 1998). Speculation about the significance of the T_p has centered on its relationship with physiological performance. For example, Licht (1966) noted that species of lizards with a higher T_p also had a higher T_o for the activity of myosin adenosine triphosphatase, but no relationship was found between the T_p and the T_o for the activity of alkaline phosphatase. Dawson (1975) conducted a qualitative yet comprehensive survey of the literature on reptiles, and concluded that most physiological processes (e.g., rate of muscle contraction, digestion, sensory perception, immune responses) proceed optimally near the T_p . Beitinger and Fitzpatrick (1979) concluded that the same was true for fish.

The concordance between thermoregulatory behavior and thermal physiology in ectotherms is not thought to be accidental. If fitness is positively related to average performance, individuals that select a T_b that maximizes performance should enjoy greater fitness than those that select other T_b 's. Therefore, an evolutionary shift in the thermal sensitivity of performance should provide selective pressure for a subsequent shift in the T_p , and vice versa (Huey and Bennett, 1987). Over many generations, natural selection would ensure that thermoregulatory behavior and thermal physiology were coadapted. The coadaptation hypothesis predicts that

T_p will correspond to the T_o for physiological performance.

6.2. Evidence of coadaptation

It was more than a decade after Dawson's review before the first quantitative test of the coadaptation hypothesis was conducted. Huey and Bennett (1987) hypothesized that the T_p and the T_o for sprint speed would evolve synchronously in lizards. They measured the thermal sensitivities of sprint speed and T_p 's of 11 species of Australian skinks. Phylogenetic comparative analysis of their data suggested partial coadaptation; although the T_o was significantly correlated with T_p , the T_p evolved at a much faster rate than the T_o . However, reanalysis with a more appropriate statistical model failed to uphold the relationship between T_p and T_o (Garland et al., 1991). Subsequent studies have also provided mixed support. Huey et al. (1989) found that nocturnal geckos had high thermal optima, typical of diurnal lizards, despite the fact that T_p 's were 4–7°C lower. On the other hand, Bauwens et al. (1995) found a significant correlation between the T_p and the T_o for sprint speed among 13 species of lacertid lizards.

The plasticity of T_p provides some evidence that thermoregulatory behavior and thermal physiology are coadapted. It is well established that the T_o for growth depends on the rate of food intake. High temperatures maximize growth when food intake is high, but the opposite is true when food intake is low (Brett, 1971; Elliot, 1982; Cui and Wootton, 1988; Woivode and Adelman, 1991; Letcher and Bengtson, 1993; Russell et al., 1996; Graynoth and Taylor, 2000). Adaptive plasticity in T_p would permit ectotherms to couple their T_b to the T_o , such that T_b is elevated following ingestion and depressed when digestion is completed. As predicted, lake charr (*Salvelinus namaycush*) selected a lower T_b when reared on low rations than when reared on high rations (Mac, 1985). The plasticity of T_p exhibited by lake charr enhanced growth but did not maximize it, because the T_p under restricted rations was still slightly higher than the T_o . In contrast, Atlantic salmon (*Salmo salar*) selected a higher T_b when fasted than when fed in excess (Morgan and Metcalfe, 2001), which is the exact opposite of the expected result.

Vernal migrations of aquatic ectotherms may serve to optimize both food intake and growth efficiency (McLaren, 1963). For example, sockeye salmon (*Oncorhynchus nerka*) migrate daily in the water column between warm, surface water and deeper, cold water, spending most of the day in colder water (Brett, 1971). Rates of consumption and growth are maximized at 15°C when rations are unlimited, but the T_o for growth approaches 5°C with decreasing food availability. These data suggest that fish forage at warm temperatures that maximize the potential for consumption, then return to

cold temperatures that maximize growth rate given limited food. Results of experiments are also consistent with this idea; large mouth bass (*Micropterus salmoides*) grew fastest when maintained at high-low cycles of temperature and were fed at onset of high temperature (Diana, 1984).

Dorcas et al. (1997) tested the hypothesis that plasticity in thermoregulatory behavior is coadapted to the thermal sensitivity of digestive performance. Some species of snakes are known to select higher T_b 's when digesting a meal (Peterson et al., 1993; Blouin-Demers and Weatherhead, 2001). Based on this observation, Dorcas and his colleagues predicted that the T_p of digesting rubber boas would enhance digestive performance, relative to the T_p of fasted snakes. They measured the thermal sensitivity of digestion and T_p 's of fed and fasted individuals. Rubber boas selected a significantly higher T_b when digesting and this T_b maximized the passage rate of food. However, digestion of food at the T_p was significantly reduced, indicating that snakes traded digestive efficiency for passage rate. This result raises the point that there may be complex trade-offs among performances with different thermal optima. A trade-off between the rate and efficiency of energy assimilation can have major consequences for thermoregulatory behavior when food intake is limited by the risk of predation. When predation risk is high, individuals should opt to feed less and maintain a T_b that maximizes digestive efficiency instead of passage rate. The widespread plasticity of thermoregulatory behavior in ectotherms offers many opportunities to test hypotheses about coadaptation.

6.3. Constraints on coadaptation

If T_b exerts such pronounced effects on performance, why is there mixed evidence that thermoregulatory behavior and thermal physiology are coadapted? One possibility is that the evolution of thermoregulatory behavior is constrained, even when the thermal sensitivity of performance is labile. Despite the evidence that T_p 's vary among genera (Licht et al., 1966; Dawson, 1975; Angilletta and Werner, 1998), virtually nothing is known about the rate at which T_p 's evolve or constraints on their evolution (e.g., heritability, genetic correlations). Though the fact that T_p 's are usually conserved within genera (Bogert, 1949; Licht et al., 1966; Angilletta and Werner, 1998) indicates that some evolutionary constraints may exist. In some species, the T_p may reflect a primitive condition rather than an adaptation to the current thermal environment (Angilletta and Werner, 1998; Fig. 7). Studies of coadaptation would benefit from efforts to define the evolutionary constraints on both thermoregulatory behavior and thermal physiology in groups that do not exhibit a close match between T_p and T_o .

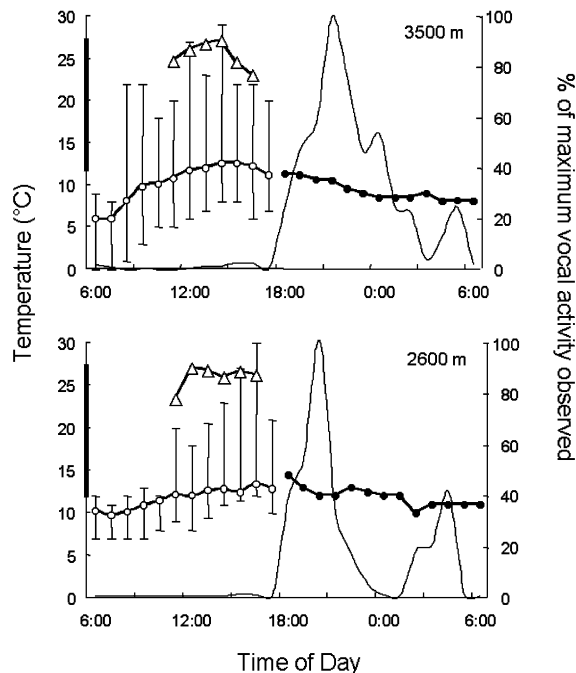


Fig. 7. The Andean tree frog, *Hyla labialis*, prefers a body temperature that maximizes locomotor and calling performances, but cannot attain its preferred body temperature in nature (Navas, unpublished data). Data for frogs from two elevations (2600 and 3500 m) are shown. Triangles indicate average preferred body temperatures measured in a laboratory thermal gradient. Hollow circles indicate average temperatures of the soil surface and error bars denote total ranges. Solid circles are water temperatures on the surfaces of ponds. Thin solid lines show the proportion of males that are vocally active. The thick black bars on the y-axes indicate the 95% performance breadths for swimming speed. The minimum body temperature that permits 95% of maximal calling rate is 11.6°C.

Another factor to consider is that the T_p may not reflect the average T_b of individuals in nature. Preferred body temperatures are usually measured in a laboratory thermal gradient, which enables an individual to move within a wide range of microclimates without risk or constraint. However, advantages of thermoregulation may be offset by the availability of preferred microclimates and costs associated with thermoregulatory behavior (Huey, 1974; Huey and Slatkin, 1976). Costs of thermoregulation include the energetic expense of shuttling between microclimates (Withers and Campbell, 1985), greater exposure to predators (Downes and Shine, 1998), and reduced foraging efficiency (Avery et al., 1982). Some species choose not to thermoregulate in cool environments because such behavior is too costly (Hertz, 1974, 1981; Huey and Webster, 1976). Since the costs of thermoregulation depend on the spatial and temporal availability of microclimates, the extent to

which the T_p is actually maintained by an individual can vary hourly, seasonally, or geographically. An individual may opt to be active at a T_b that is higher or lower than the T_p (Grant, 1990) or limit activity to times when the T_p can be maintained (Grant and Dunham, 1988; Bashey and Dunham, 1997). For example, nocturnal geckos are typically active at T_b 's that are far below their T_p 's (Huey et al., 1989; Angilletta and Werner, 1998), which can reduce the energy expended on maintenance and activity (Autumn et al., 1994). For species in which the T_p and the average field T_b differ, the T_p provides little information about the consequences of field T_b 's for performance (Huey and Stevenson, 1979).

Although environmental constraints on thermoregulation are clearly worth considering, there is little reason to suspect that they explain the failure of previous studies to detect coadaptation. Many lizards do thermoregulate accurately and precisely in nature, despite strong temporal and spatial constraints on thermoregulation (Bauwens et al., 1996; Díaz, 1997; Angilletta, 2001). Even nocturnal geckos have been shown to behaviorally thermoregulate within refuges during the day (reviewed by Avery, 1982; Kearney and Predavec, 2000). Certainly, another explanation for the lack of evidence of coadaptation is necessary.

A potentially serious problem is that each study of coadaptation has focused on a single physiological performance (e.g., sprint speed). Many physiological processes occur simultaneously, and these processes may differ both in their thermal sensitivity and in their impact on fitness. Differences in T_o and performance breadth among physiological processes can influence coadaptation. In some species, many performances can be optimized at a single T_b (Huey, 1982; Stevenson et al., 1985; Ji et al., 1995; Du et al., 2000), but in others the thermal optima differ among physiological performances (Van Damme et al., 1991; Ji et al., 1996). As discussed above, one solution is to temporally vary T_p such that all competing processes can proceed at a maximal rate for some duration. Another solution is to target a single T_b that permits all physiological processes to proceed at a moderate rate. When this strategy is adopted, the relative impact of each process on fitness will determine the T_p favored by natural selection. The T_p will represent a compromise between maximizing each of many processes (similar to the optimal compromise described by Beuchat and Ellner, 1987). If performance breadths vary among traits, thermoregulatory behavior should coevolve with the most thermally sensitive of physiological performances. For example, the T_p of *Sceloporus undulatus* is more closely related to the thermal sensitivity of energy assimilation than that of either sprint speed or endurance (Fig. 8). When performances differ in their thermal sensitivity, detecting coadaptation of thermoregulatory behavior and thermal

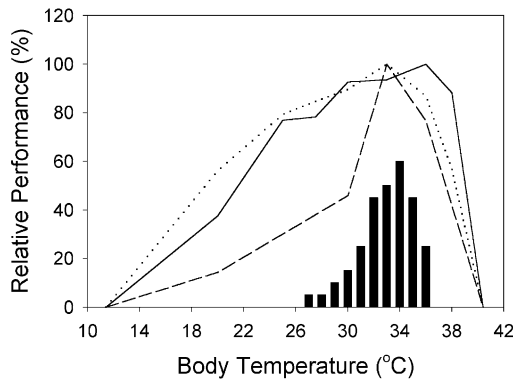


Fig. 8. Thermal sensitivities of sprint speed (solid line), endurance (dotted line), and metabolizable energy intake (dashed line) in the eastern fence lizard, *Sceloporus undulatus* (reproduced from Angilletta et al., in press). Neither sprint speed nor endurance varied significantly over the range of 28°–36°C, but metabolizable energy intake was significantly greater at 33°C than it was at 30° and 36°C (Angilletta, 2001). The distribution of preferred body temperatures in this species is depicted by the solid bars (the scale is relative).

physiology will be more difficult unless the different performance functions and the relationships between performance and fitness are known.

7. Future directions

It is clear that more is known about the evolution of the thermal sensitivity of locomotor performance than is known about the evolution of other physiological performances. Comparisons of performance functions have been made within and among species and these analyses have formed the core of an active field of research (see reviews by Huey and Kingsolver, 1989; Bennett 1990; Bennett and Huey, 1990). Results of these and other studies illustrate that each aspect of thermal physiology in each taxon lies somewhere along a continuum, ranging from conservative to labile. However, phylogenetically-based comparative analyses are few (e.g., Huey and Bennett, 1987; Huey and Kingsolver, 1993; Bauwens et al., 1995) and represent a narrow set of taxa (i.e., lizards). Have existing studies revealed general patterns or have they been focused on exceptional properties of exceptional ectotherms? Determining the generality of evolutionary processes and patterns will require the study of many aspects of the thermal physiology in a diversity of ectotherms.

When choosing additional performances for study, theory should be our guide. Certain performances are more likely to evolve rapidly in response to changes in environmental temperature and coevolve readily with thermoregulatory behavior. Specifically, the evolution of

T_o should be most evident for traits that have a narrow performance breadth (Huey and Kingsolver, 1993). If one's aim is to observe microevolutionary processes, performances that are relatively insensitive to T_b and have a weak or tentative relationship with fitness (e.g., locomotor performance) should not be the primary focus. On the other hand, investigating the evolution of multiple performances in a phylogenetic context would certainly increase our understanding of the relative rates at which different aspects of thermal physiology evolve. When thermal sensitivities vary among performances, more elaborate models will be needed to predict the direction and magnitude of evolution (Beuchat and Ellner, 1987).

If certain theoretical predictions are to be tested, it will be necessary to move beyond comparative analyses to experimental studies. For example, the prediction that natural selection favors intermediate performance breadths is best tested by selection experiments. In the last decade, two pioneers in the area of evolutionary thermal physiology shifted to systems that have enabled them to address evolutionary questions with experimental studies, in addition to comparative analyses. Recent work with *Drosophila melanogaster* (e.g., Huey et al., 1991; Gilchrist et al., 1997; Gilchrist and Huey, 1999), and *Escherichia coli* (e.g., Bennett et al., 1992; Bennett and Lenski, 1993; Mongold et al., 1996) has provided a vital extension of the progress that began with comparative analyses. Selection experiments have provided rare glimpses of the heritability of performance functions, evolutionary trade-offs between thermal optima and performance breadths, and the adaptation of thermal physiology to environmental temperature (Huey and Kingsolver, 1993; Bennett and Lenski, 1999; Carrière and Boivin, 2001). Selection studies of ectotherms with short generation times are valuable complements to the traditional comparative analyses because they allow one to validate assumptions of theory that have been difficult to validate in long-lived ectotherms (see Section 4). The development of additional empirical models would be beneficial, especially if processes observed in the laboratory could be related to patterns observed in nature (e.g., see Bronikowski et al., 2001).

Further development of theory is also essential. In the twenty years since evolutionary physiologists heralded a paradigm for studying the evolution of thermal physiology, empirical work has far outstripped theoretical work. Recent models (Huey and Kingsolver, 1993; Gilchrist, 1995) provide a long-awaited foundation upon which to build. For example, thermal physiology will not evolve as predicted by available theories if fitness is not directly proportional to performance. Given that the relationship between performance and fitness is so poorly characterized for most physiological processes, assessing the sensitivity of predictions to this

assumption is a task that merits immediate attention. Ideally, theory will be expanded to allow the inclusion of multiple performances that differ both in thermal sensitivity and in their relationship to fitness. Continued efforts to synthesize modeling and experimental approaches will increase our understanding of the evolution thermal physiology in ectotherms.

Finally, we encourage a stronger interaction among evolutionary biologists, comparative physiologists, and biochemists. Despite the wealth of evidence that thermal physiology does vary within and among species, the biochemical adaptations that enable improved performance at extreme temperatures or eurythermy are known for only a few species (see reviews by Somero et al., 1996, and Fields, 2001). Studies at the biochemical level identify proximate constraints on performance (Marsh and Bennett, 1985; Navas et al., 1999; Watkins, 2000, 2001; Ressel, 2001), shed light on the cellular and molecular modifications that underlie changes in the performance function (Dode et al., 2001; Ressel, 2001), and provide a mechanistic basis for generating predictions about the evolution of thermal physiology in response to the thermal environment (Crawford et al., 1999). Identifying the factors that facilitate or constrain the evolution of performance functions in specific lineages will result in a deeper appreciation of the processes that shape the evolution of thermal physiology in ectotherms. Both proximate and ultimate constraints on the evolution of thermal physiology deserve much greater attention than they have received.

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