Coadaptation: A Unifying Principle in Evolutionary Thermal Biology*

Michael J. Angilletta Jr.[1],[+]
Albert F. Bennett[2]
Helga Guderley[3]
Carlos A. Navas[4]
Frank Seebacher[5]
Robbie S. Wilson[6]

[1]Department of Ecology and Organismal Biology, Indiana State University, Terre Haute, Indiana 47809; [2]Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697; [3]Département de Biologie, Université Laval, Québec, Québec G1K 7P4, Canada; [4]Departamento de Fisiologia, Instituto de Biociências, Universidade de São Paulo, São Paulo 05508-900, Brasil; [5]School of Biological Sciences, Heydon Laurence Building A08, University of Sydney, Sydney, New South Wales 2006, Australia; [6]School of Life Sciences, Goddard Building, St. Lucia Campus, University of Queensland, Brisbane, Queensland 4072, Australia

ABSTRACT

Over the last 50 yr, thermal biology has shifted from a largely physiological science to a more integrated science of behavior, physiology, ecology, and evolution. Today, the mechanisms that underlie responses to environmental temperature are being scrutinized at levels ranging from genes to organisms. From these investigations, a theory of thermal adaptation has emerged that describes the evolution of thermoregulation, thermal sensitivity, and thermal acclimation. We review and integrate current models to form a conceptual model of coadaptation. We argue that major advances will require a quantitative theory of coadaptation that predicts which strategies should evolve in specific thermal environments. Simply combining current models, however, is insufficient to understand the responses of organisms to thermal heterogeneity; a theory of coadaptation must also consider the biotic interactions that influence the net benefits of behavioral and physiological strat-

---

egies. Such a theory will be challenging to develop because each organism's perception of and response to thermal heterogeneity depends on its size, mobility, and life span. Despite the challenges facing thermal biologists, we have never been more pressed to explain the diversity of strategies that organisms use to cope with thermal heterogeneity and to predict the consequences of thermal change for the diversity of communities.

Introduction

Forty years after Heath (1964) placed beer cans in the sun to caution against a simplistic approach to the study of thermoregulation, thermal biology has become a thriving area of research based on mathematical theories, sophisticated technologies, and model organisms. Much of this research is still designed to help us understand the causes and consequences of thermoregulation, but the evolution of thermal reaction norms (for definitions of this and other thermal biology terms, see Table 1) has also become a major focus. The core assumptions of thermal biology are (1) temperature is one of the most pervasive state variables affecting biological processes, and (2) the laws of thermodynamics define the direction and rate of biochemical processes that underlie the performance of whole organisms (Haynie 2001; Brown et al. 2004). Given these core assumptions, thermal biologists have concluded that the environment exerts strong selective pressures on all organisms and that knowledge of thermal biology is the key to explaining many physiological, ecological, and evolutionary patterns.

Adaptive responses to thermal heterogeneity involve all levels of biological organization from the expression of genes to the behavior of the organism, but these responses occur on different temporal scales (Fig. 1). We think of the interactions among levels of organization that link these responses as a mechanistic cascade, which flows from the biochemical to the organismal levels and is nested within a feedback loop. In other words, the expression of genes shapes the behavior of the organism, but this behavior causes a change in physiological state that determines subsequent gene expression. Thus, the relationships among thermal responses at various levels of organization are likely to be complex, and thermal responses at biochemical levels cannot be used to predict changes at higher levels of organization (Huey and Stevenson 1979; Chaui-Berlinck et al. 2004). The challenge for biologists is to define the mechanistic links between thermal responses at different levels and to identify their impact on fitness—in other words, to understand the evolution of the mechanistic cascade.

Table 1: Definition of terms in thermal biology

Term	Definition
Coadaptation	The coevolution of traits within a population via natural selection
Developmental acclimation	Irreversible plasticity of a physiological trait in response to an isolated environmental variable, such as temperature, which is experienced during ontogeny
Eurythermy	The ability to function over a broad range of body temperatures
Operative temperature	The temperature of an inanimate object of zero heat capacity with the same size, shape, and color as the animal
Seasonal acclimation	Reversible plasticity of a physiological trait in response to a seasonal change in an isolated environmental variable, such as temperature
Stenothermy	The restriction of function to a narrow range of body temperatures
Thermal reaction norm	A mathematical function relating environmental temperature (or body temperature) to the phenotype expressed by a given genotype; includes thermal performance curves, which describe the thermal sensitivities of behavioral or physiological rates, and thermal tolerance curves, which describe thermal sensitivities of fitness
Thermal sensitivity	The slope (or derivative) of a thermal reaction norm
Thermoregulation	The maintenance of a mean or variance of body temperature that differs from the mean or variance of operative environmental temperatures, by means of behavioral, physiological, or morphological strategies

Note. See Mercer (2001) for additional clarification of terminology.

At the organismal level, strategies for coping with thermal heterogeneity vary along a continuum with two dimensions. The first dimension describes the strategy of thermoregulation, from organisms that maintain a nearly constant body temperature despite thermal heterogeneity to those that conform to environmental temperature. The second dimension describes the strategy of thermal sensitivity, from organisms whose performance is very sensitive to temperature (stenotherms) to those whose performance is relatively insensitive to temperature (eurytherms). All organisms fall somewhere within the continuum bounded by these axes. Many endotherms, such as mammals and birds, are thermoregulators that are stenothermic, but many ectotherms also regulate their body temperature using somewhat different mechanisms. Certain fish, such as carp, are good examples of thermoconformers that are eurythermic. The position of an organism along this continuum can be altered by acclimation; in fact, an individual can be stenothermic during specific seasons but eurythermic over the course of a year. Finally, evolution by natural selection alters both acute and acclimatory responses to temperature. Thus, ecological responses involve reversible or nonreversible forms of phenotypic plasticity, and evolutionary responses involve a change in the reaction norms of genotypes in a population (see Levins 1963 for a generalized discussion of these strategies).

Given that organisms have many options for dealing with thermal heterogeneity, why does each species adopt certain strategies over others? To answer this question, we must consider the costs and benefits of each strategy in a range of environments; such considerations range from purely verbal models to complicated mathematical ones. Levins (1962, 1963) was the first to advance models of evolution in heterogeneous environments, and many models of thermal adaptation were undoubtedly inspired by the work described in his classic book (Levins 1968). Here, we review current models and draw on recent studies of fish, reptiles, and amphibians to evaluate them. We then combine the ideas generated from these models to form a conceptual model of coadaptation that predicts the optimal suite of strategies given mean, variance, and predictability of environmental temperature. We argue that coadaptation is a unifying principle of thermal biology because it emphasizes the simultaneous evolution of thermoregulation and thermal sensitivities.

Adaptive Responses to Thermal Heterogeneity: Theory and Evidence

When the temperature of the environment varies spatially and temporally, one of four conditions must occur: (1) body temperature is regulated by behavior and physiology; (2) body temperature fluctuates, but performance is not impaired; (3) body temperature fluctuates, and performance is initially impaired but is restored later by acclimation; or (4) body temperature fluctuates, and performance is impaired and is not restored by acclimation. As we shall discuss, any of these outcomes could be adaptive in certain environments. Because each outcome results from a combination of behavioral and physiological strategies, natural selection should produce organisms with suites of traits that are coadapted to the environment.
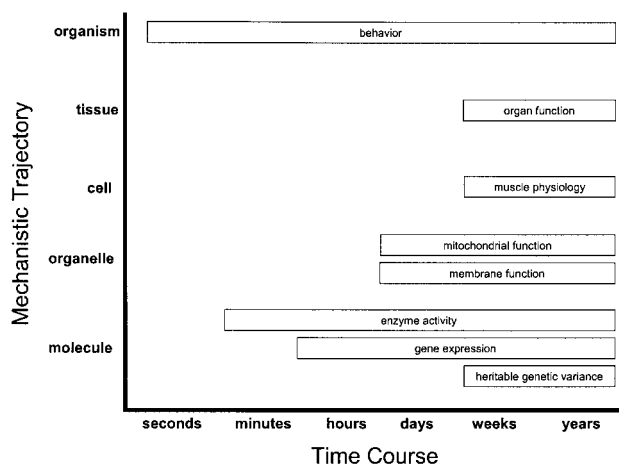
Figure 1. A cascade of mechanisms operating from cellular to organismal levels is responsible for adaptive responses to thermal heterogeneity. These mechanisms alter commonly measured properties of organisms, from gene expression to behavior, on different temporal scales.

Given the complexity of this process, how can we develop a theory of coadaptation to explain the diversity of strategies that are manifested in nature? To answer this question, we must first consider existing theories of thermal adaptation and their empirical support.

Thermoregulation

What factors determine the degree to which an individual should thermoregulate and the mechanisms it should use to do so? Huey and Slatkin (1976) modeled the optimal degree of thermoregulation given energetic costs and benefits. They assumed that the rate of energy gain was a unimodal function of temperature. Although they modeled an energetic cost of thermoregulation, they noted that other costs are certainly plausible; for example, thermoregulators might incur a greater risk of predation and fewer opportunities for territorial defense or courtship, reducing fitness via survival and fecundity, respectively. The model makes several predictions: (1) thermoregulation should be greater in patchy environments, where thermal heterogeneity enables heating and cooling with a low cost of shuttling; (2) stenotherms should thermoregulate more carefully than eurytherms; and (3) individuals in colder environments should have a lower mean body temperature than individuals in hotter environments when all other factors are equal.

Reptiles provide ample evidence that the costs and benefits of thermoregulation influence the body temperatures of animals. Many species of diurnal lizards maintain relatively high and constant body temperatures during activity, which tend to maximize capacities for performance (Huey 1982; Hertz et al. 1983; Adolph 1990; Angilletta et al. 2002a). Anyone who

watched these lizards could appreciate the tremendous significance of behavioral mechanisms of thermoregulation, which include shuttling between microhabitats, perching on objects, and orienting the body toward solar radiation (Heath 1965; Hertz and Huey 1981; Christian et al. 1983; Adolph 1990; Bauwens et al. 1996). Because solar radiation is the primary source of heat for ectotherms, thermoregulation is presumably more costly for species that are nocturnal or inhabit dense forests (Huey 1974, 1982; Huey and Slatkin 1976). Indeed, body temperatures of nocturnal geckos during activity are significantly lower than those of diurnal lizards, even though these low temperatures impede locomotor performance (Huey et al. 1989). For some species of geckos, relatively low body temperatures during activity are undoubtedly caused by costs or constraints imposed by nocturnal activity because the same species maintain relatively high and constant body temperatures in artificial thermal gradients (Huey et al. 1989; Angilletta and Werner 1998). Some nocturnal geckos thermoregulate as accurately and effectively during the day as diurnal lizards, particularly in late spring and summer, when considerable thermal heterogeneity exists within and among sites of retreat (Kearney and Predavec 2000; Rock et al. 2002). Transplant experiments also reveal the influence of costs and constraints on thermoregulation. For example, *Chamaeleo schubotzi*, which inhabits the foggy slopes of Mount Kenya (3,300 m), maintained its preferred body temperature (33°C) for only an hour on clear days and never approached this body temperature on most days (Bennett 2005); yet, individuals transplanted to a lower elevation near Nairobi (1,700 m) maintained body temperatures above 30°C throughout the day (Fig. 2). These examples demonstrate the profound flexibility of thermoregulatory behavior in reptiles.

As predicted by theory, comparative studies over space and time indicate that mean body temperatures of ectotherms are lower in colder environments. Within species, this phenomenon is manifested in one of two ways: individuals in colder environments (1) maintain lower body temperatures while they are active (Hertz 1981; Hertz et al. 1983; Van Damme et al. 1989; Adolph 1990; Grant and Dunham 1990; Christian and Weavers 1996) or (2) maintain elevated body temperatures for shorter durations each day (Angilletta 2001; Sears and Angilletta 2004). Despite these differences in behavior in natural environments, preferred body temperatures measured in artificial thermal gradients often do not differ among populations when field body temperatures do (Van Damme et al. 1989; Angilletta 2001). Interspecific comparative analyses have provided mixed support for the hypothesis that body temperatures will be lower in colder environments. Among species of *Chamaeleo*, mean body temperature decreased with decreasing minimal and maximal air temperatures (Bennett 2005). Among tropical species of *Sceloporus* and *Liolaemus*, mean body temperature during activity decreases by 1°C per 1,000 m of elevation (Andrews 1998; Navas 2002). Tropical anurans exhibit more pronounced
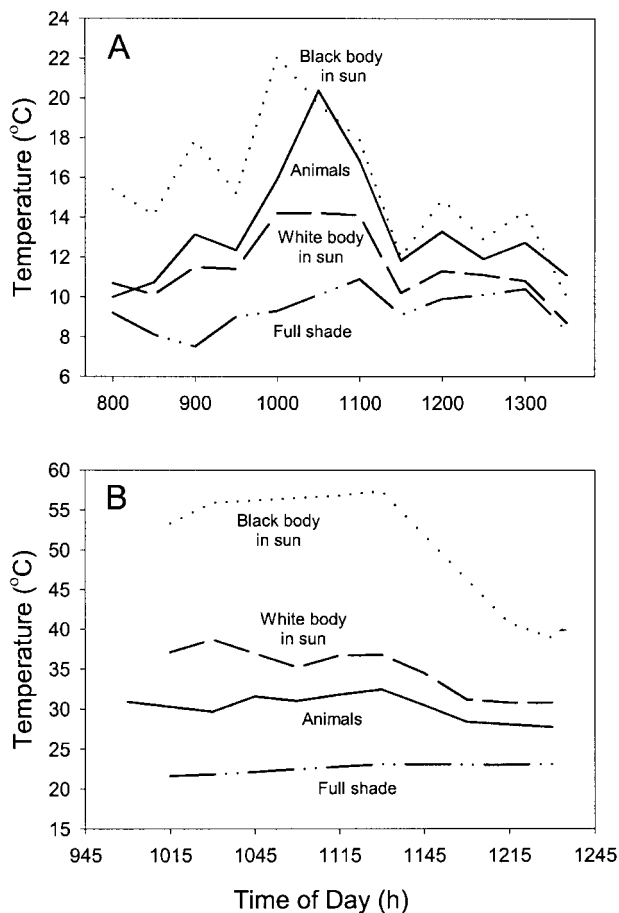
Figure 2. Thermoregulation by (*A*) native and (*B*) transplanted cha-meleons (*Chamaeleo schubotzi*) in Kenya. Data are mean body tem-peratures and mean operative temperatures measured in the sun and shade; operative temperatures in the sun were measured with hollow copper tubes painted white or black. *A*, Individuals in the native habitat of Mount Kenya (*N* = 4) never attained body temperatures above 23°C. *B*, Individuals transplanted to Nairobi (*N* = 6) maintained body temperatures above 30°C most of the day. Data are from A. F. Bennett (unpublished manuscript).

elevational clines, with mean body temperature decreasing by 5°C per 1,000 m of elevation (Navas 2002). Yet, no elevational trend in body temperature was evident among temperate spe-cies of *Sceloporus* (Andrews 1998); this observation does not necessarily contradict the prediction of theory because tem-perate species in colder environments usually maintain pre-ferred body temperatures for shorter durations per day (Sears and Angilletta 2004). Thus, lizards in colder environments maintain lower mean body temperatures over the course of their lives.

Experimental studies of thermoregulation under perceived risks of predation also support a model of thermoregulation based on costs and benefits. Downes (2001) used chemical cues to alter the perception of risk by garden skinks (*Lampropholis guichenoti*) in experimental enclosures. Skinks surrounded by a high density of scent markings became active later and became inactive earlier than lizards surrounded by a low density of scent markings. Consequently, the mean body temperature of these skinks was lower and their growth was slower. Addition-ally, velvet geckos (*Oedura lesueurii*) preferred warm retreats in the absence of predators but chose cool retreats when warm retreats were marked by the chemical cues of a predator (Downes and Shine 1998). Clearly, the risk of predation and its effect on body temperature depend on the specific mech-anisms of thermoregulation. Behavioral mechanisms (e.g., shut-tling and posturing) might make an individual more conspic-uous to predators, whereas physiological mechanisms (e.g., shunting blood and changing color) might not increase risk. Large reptiles can effectively exploit physiological mechanisms of thermoregulation, but small reptiles could be forced to rely largely on behavioral mechanisms (Bartholomew 1982; Dzi-alowski and O'Connor 2004). Furthermore, the relationship between thermoregulation and predation risk is complicated because the ability of prey to escape predators probably depends on body temperature (reviews in Hertz et al. 1988; Angilletta et al. 2000*b*).

Thermal Sensitivity

When body temperature varies, natural selection is expected to shape the thermal sensitivity of performance. The direction of evolution should depend greatly on the manner in which an individual's performance contributes to its fitness. If perfor-mance contributes additively to fitness (i.e., the sum of per-formance over time determines fitness), stenotherms are fa-vored under most patterns of temporal variation; eurytherms are more fit than stenotherms only if environmental temper-ature varies greatly among generations and little within gen-erations (Gilchrist 1995). A greater degree of eurythermy, how-ever, would be favored if environmental temperature changed systematically with time (Huey and Kingsolver 1993). Thus, the relative magnitude of variation within and among gener-ations determines the optimal thermal sensitivity when per-formance contributes additively to fitness. If performance con-tributes multiplicatively to fitness (i.e., the product of performance over time determines fitness), optimal thermal sensitivities are determined more by variation within genera-tions than by variation among generations; stenothermy is fa-vored in constant environments, and eurythermy is favored in variable environments (Lynch and Gabriel 1987). The generality of these conclusions depends on the validity of a critical as-sumption: an increase in performance at one or more tem-peratures necessitates a decrease in performance at other tem-peratures. In other words, a jack-of-all-temperatures is assumed to be a master of none (Huey and Hertz 1984). This trade-off between specialization and generalization, originally proposed

by Levins (1968), is a common assumption of evolutionary theories in general.

Both comparative and experimental studies have shown that eurythermy evolves far more often than predicted by theory. Thermal sensitivities of growth rate have been compared among populations of marine fish distributed along latitudinal clines. If we assume that growth contributes additively to fitness, current theory predicts that natural selection should produce stenotherms that perform best at the mean water temperature. In most cases, however, genetic divergence along latitudinal clines has produced eurytherms that perform equally well or better than stenotherms at any temperature (review in Angilletta et al. 2002b). These genetic differences among populations persist despite considerable gene flow among populations (Conover 1998), which suggests that natural selection can produce jacks-of-all-temperatures that are masters of all. Semi-natural selection of *E. coli* under various thermal regimes has provided mixed support for the theory of thermal adaptation. Selection at 37°C during 20,000 generations improved fitness at 27°–39°C but reduced fitness at extreme temperatures (Fig. 3). Nevertheless, a series of selection experiments with *E. coli* (Bennett and Lenski 1999; Pörtner et al. 2006) and a comparative study of *Daphnia pulicaria* (Palaima and Spitze 2004) have shown that a trade-off between fitnesses at high and low temperatures is not a necessary outcome of evolution. These comparative and experimental results cast doubt on the generality of current theory.

One possible explanation for the lack of thermal specialization within natural populations is that physiological performances contribute both additively and multiplicatively to fitness. Consider the number of genes that must underlie a complex trait such as growth rate. Some fraction of these genes could also code for proteins that enhance maintenance, repair, and, hence, survival. Such genes would cause growth rate to evolve in correlation with thermal tolerance. Because environmental temperature tends to vary more at higher latitudes, natural selection should produce broader thermal tolerances at these locations (e.g., van Berkum 1988). Thus, correlated evolution of thermal sensitivities of growth rate and thermal tolerance might explain the countergradient variation observed in fish (Conover and Schultz 1995). Selection experiments can be used to explore potential genetic correlations between the tolerance of extreme temperatures and performance at less extreme temperatures (Mongold et al. 1999). The identification of mechanistic cascades that produce variation in organismal performances would shed light on the network of genes shared between performance and tolerance.

Acclimation of Thermal Sensitivity

Many ectotherms modify thermal sensitivities of performance throughout their lifetimes. These modifications can be non-reversible responses to temperatures experienced during on-
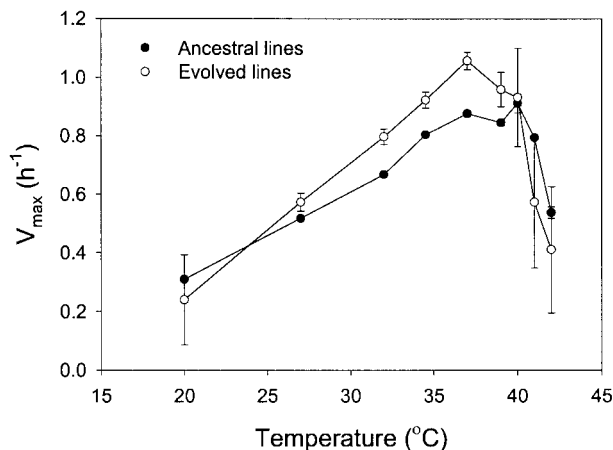

Figure 3. Maximal growth rates (V_{max}) of ancestral (*filled circles*) and selected (*open circles*) populations of *E. coli*. Selected populations were maintained at 37°C for 20,000 generations. Error bars are 95% confidence intervals. Adapted from Cooper et al. (2001).

togeny (developmental acclimation) or reversible responses to gradual changes in temperature among seasons (seasonal acclimation). The distinction between developmental and seasonal acclimation is important when discussing the evolutionary significance of phenotypic plasticity (Kingsolver and Huey 1998). Both developmental and seasonal acclimation involve a cascade of processes, which can include the detection of environmental signals, a signal transduction pathway (or pathways), and the activation of the production machinery of the cell (e.g., structural genes, polymerases, ribosomes) leading to a change in physiology. During developmental acclimation, the process involves morphogenesis that is irreversible. Small effects of developmental temperature early in ontogeny can lead indirectly to larger effects on the phenotype later in ontogeny. Thus, developmental acclimation can produce changes that are distinct from those observed during seasonal acclimation of the same physiological systems (I. A. Johnston and R. S. Wilson, unpublished data).

Precht (1958) divided patterns of acclimation into five categories based on the degree to which the rate of performance is maintained during environmental change; these categories are overcompensation, perfect compensation, partial compensation, no compensation, and inverse compensation. All of these responses have been interpreted as adaptive strategies for coping with thermal fluctuations (Huey and Berrigan 1996). For example, when faced with seasonal cooling, an ectotherm can (1) slow physiological capacity by submitting to Q_{10} effects (e.g., O'Steen and Bennett 2003); (2) depress physiological capacity by enhancing thermal effects (e.g., St. Pierre and Boutilier 2001); or (3) offset Q_{10} effects by maintaining capacities through partial compensation, perfect compensation, or overcompensation (e.g., Rome et al. 1984; Guderley and St. Pierre 1999).

Patterns of acclimation are enriched by nature's complexity; for example, when environmental warming is accompanied by a depletion of resources (e.g., food, oxygen), some ectotherms initiate a metabolic depression that alleviates Q_{10} effects (Hand and Hardewig 1996; de Souza et al. 2004; review in Guppy and Withers 1999). The presumption that these compensatory responses enhance the fitness of an organism is known as the beneficial acclimation hypothesis (Leroi et al. 1994).

Critics of the adaptationist program noted alternatives to adaptive explanations for acclimatory responses (Garland and Carter 1994; Feder et al. 2000), and others argued that the evolutionary significance of such responses has rarely been established (Huey and Berrigan 1996; Kingsolver and Huey 1998; Huey et al. 1999). Huey et al. (1999) encouraged the application of strong inference (Platt 1964) and advanced four hypotheses as alternatives to the beneficial acclimation hypothesis. Although we agree that strong inference is a powerful approach, we contend that current hypotheses have limited power to increase our understanding of the evolution of acclimation. First, these hypotheses stem from verbal models that consider isolated mechanisms rather than quantitative models that consider multiple causality; for example, the hypothesis that "colder is better" is based on the common observation that organisms reach larger body sizes at lower temperatures, whereas the hypothesis of developmental buffering is based on a mechanism that is independent of body size (Huey et al. 1999). Because these hypotheses are not mutually exclusive and neither leads to quantitative predictions about the magnitude of acclimation, one cannot easily design crucial experiments to distinguish between them (see Quinn and Dunham 1983). More importantly, these hypotheses do not stem from an explicit consideration of the variance and predictability of environmental temperature. A quantitative model, however, would provide the explicit analysis of costs and benefits that is needed to predict the optimal capacity for acclimation given the mean, variance, and predictability of environmental temperature. Furthermore, such a model would enable investigators to make a priori predictions about the acclimation of thermal sensitivity when multiple mechanisms (or constraints) are involved.

Currently, only one quantitative model can be used to infer the optimal acclimation of thermal sensitivity. This model, constructed by Gabriel and Lynch (1992), describes the evolution of an environmental tolerance curve, which can be thought of as the relationship between temperature and fitness. As with a performance curve, a tolerance curve can be characterized by an optimum and a breadth. The model predicts that the net benefit of acclimation increases with increasing variation in body temperature among generations and decreasing variation in body temperature within generations. This result, however, follows from the fact that fitness is zero if body temperature falls outside of the tolerance curve at any point during the life of an organism (i.e., once you're dead, you're dead). The optimal acclimation of performance curves would differ quali-

tatively from that of tolerance curves if performance contributes additively to fitness rather than multiplicatively (see "Thermal Sensitivity").

Despite the limitations of current theory, experimental studies of acclimation have generally rejected the beneficial acclimation hypothesis (Leroi et al. 1994; Zamudio et al. 1995; Huey and Berrigan 1996; Bennett and Lenski 1997; Huey et al. 1999; Gibert et al. 2001). Given that these studies used rigorous experimental designs to test and reject a long-held assumption within evolutionary physiology, they confirm the need to critically evaluate adaptive explanations for phenotypic plasticity. Much of the rigorous nature of these experiments was afforded by the careful selection of model organisms, such as *E. coli* and *Drosophila melanogaster*. Huge numbers of replicates, short generation times, and comparatively simple procedures of maintenance were all important advantages of using these species. In the majority of these studies, however, organisms were raised at different temperatures for one or more generations. A consequence of this experimental design was that reversible and irreversible forms of acclimation might have been confounded (Wilson and Franklin 2002).

Our understanding of acclimation comes mostly from hundreds of descriptions of seasonal acclimation and its underlying mechanisms (Prosser 1979). Although recent experiments have focused on developmental acclimation in organisms with short generations, the benefits of seasonal acclimation still remain to be investigated (Guderley and St. Pierre 2002; Wilson and Franklin 2002). This gap in our understanding of acclimation is surprising when one considers that many model organisms in thermal biology have generations that span one or more years and are therefore routinely exposed to seasonal changes in temperature. One key to better understanding the evolution of either developmental or seasonal acclimation will be the careful selection of a trait that has a clear connection to survival or reproduction. For example, Wilson and Johnston (2005) studied the thermal acclimation of mating success of males of *Gambusia holbrooki*. Males of this species copulate entirely through sneaky encounters because females always resist mating. When tested at 18°C, males acclimated to this temperature swam faster, maneuvered better, and had greater mating success than males acclimated to 30°C; the converse was true for tests conducted at 30°C (Fig. 4). Because mating success is likely to correlate strongly with fitness, this experiment provides some evidence for the benefits of seasonal acclimation.

Even when compensation would seem beneficial, failure to compensate perfectly could reflect costs of acclimation (Hoffmann 1995; Guderley 2004). Acclimation of thermal performance curves would seem beneficial if (1) fluctuations in temperature within generations are predictable, (2) the time lag required for compensation is short relative to the rate of change in temperature, and (3) the energetic or survival cost of compensation is less than the loss of energy or reduction of survivorship that is caused by a failure to compensate (see DeWitt
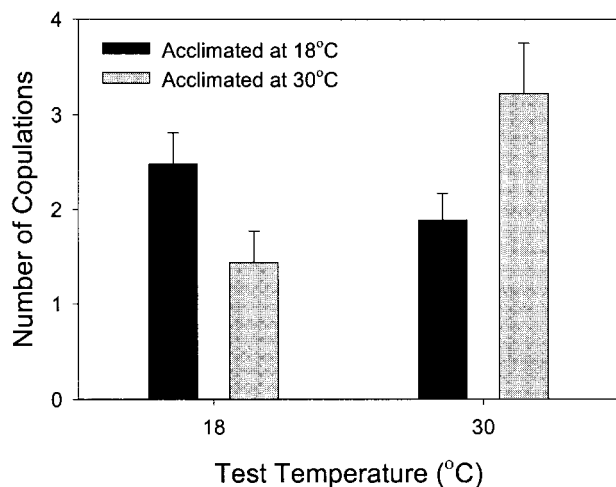
Figure 4. Effect of thermal acclimation on the number of copulations obtained by males of *Gambusia holbrooki* at 18° and 30°C. Copulations were recorded during 5 min of exposure to two females in an aquarium. Significant differences were detected between groups at both test temperatures ($N = 20$ for each group). Data are means ± SE. Adapted from Wilson and Johnston (2005).

et al. 1998). Perfect compensation of performance is costly because of the time and energy required to synthesize new enzymes, modify membranes, and redistribute resources. For example, compensation of muscular function during exposure to low temperature can involve increases in the concentrations of enzymes (Sänger 1993), the expression of myosin isoforms (Johnston and Temple 2002), the fluidity of cellular membranes (Hazel 1995), and the oxidative capacity or volume of mitochondria (Guderley and St. Pierre 1999). These changes require time as well as energy; for example, the compensatory response of rainbow trout (*Oncorhynchus mykiss*) is biphasic and requires a minimum of 6 wk to stabilize (Bouchard and Guderley 2003). Beyond the obvious costs of producing these changes, the energetic cost of "primed" mitochondria and the deleterious effects of the reactive oxygen species generated during electron transport are additional costs of compensation (review in Guderley 2004). Furthermore, natural covariation between temperature and other resources can enhance the costs of compensation. A seasonal decrease in temperature is usually accompanied by a reduction in the availability of food, which could favor reverse compensation rather than partial or perfect compensation (Clarke 1993). Indeed, the nutritional state of an animal has marked effects on the aerobic and glycolytic capacities of its muscles (Pelletier et al. 1993*a*, 1993*b*; Dutil et al. 1998). More effort must be expended to determine the net benefits of acclimation in natural environments (Huey and Berrigan 1996), and cooperation between physiologists and ecologists will be invaluable in this undertaking (Kingsolver and Huey 1998).

A Theory of Coadaptation

Although the coadaptation of thermoregulation and thermal reaction norms has been appreciated for over 20 yr (Huey and Slatkin 1976; Huey and Bennett 1987), this appreciation has not led to an understanding of why some organisms modify behavior, physiology, and biochemistry in certain combinations. Consider the two most commonly tested hypotheses regarding thermal coadaptation: (1) the mean (or preferred) body temperature of an organism should match the thermal optimum for performance, and (2) the variance in body temperature should correlate with the thermal performance breadth. These predictions deal with covariation between phenotypes but say nothing about which phenotypes should be observed in a given environment. Do some organisms, such as tropical anurans (Navas 1996), use mainly biochemical modifications of thermal sensitivity because the cost of thermoregulation is too high? Are other organisms, such as temperate lizards (Sears and Angilletta 2004), more likely to use thermoregulation because its costs are lower in their environments? And what are the causes of variation along this continuum within major groups of ectotherms?

Currently, no theory of coadaptation links phenotypic strategies to thermal environments because models of thermoregulation assume a thermal reaction norm and models of thermal reaction norms assume a profile of body temperatures. Optimal thermal reaction norms depend on temporal variation in body temperature (Huey and Kingsolver 1993; Gilchrist 1995). The benefit of thermoregulation depends on thermal reaction norms for all phenotypes that contribute to fitness; benefits are high for thermal specialists and low for thermal generalists (Huey and Slatkin 1976; Huey 1982). Each body of theory makes assumptions about the other; therefore, one must view the evolution of thermoregulation and thermal sensitivities of performance as a coadaptive process (Huey and Bennett 1987). Current theories enable us to understand the covariation between thermoregulation and thermal physiology, but they do not enable us to predict which suites of traits will evolve in particular environments.

How can one unify current theories of thermal adaptation to produce a more powerful theory of coadaptation? We start by offering a conceptual model, which can be further developed quantitatively. Two assumptions pervade current theories (Huey and Kingsolver 1989): (1) a jack-of-all-temperatures is a master of none (i.e., a trade-off exists between performance at a given temperature and the thermal breadth of performance), and (2) hotter is better (i.e., performance at the thermal optimum is greater when the thermal optimum is higher). If the first assumption is valid, a stenotherm with a constant body temperature that is equal to its thermal optimum should have a higher fitness than a eurytherm with any distribution of body temperatures (Gilchrist 1995). If the second assumption is valid, a stenotherm with a high and constant body

temperature should have a higher fitness than a stenotherm with a low and constant body temperature. Using these two assumptions, we can predict the strategies produced by coadaptation. In the simplest case, an organism in a stable environment obviously must thermoconform and should be a specialist for the modal temperature (see Janzen 1967). But what about organisms in variable environments? Here, the cost of thermoregulation might be the primary driver of coadaptation (Fig. 5). Environments in which the cost of thermoregulation is low will favor specialists that thermoregulate precisely. The preferred body temperature (or preferred range of body temperatures) should depend on the cost-benefit ratio of thermoregulation, the effect of temperature on absolute performance (i.e., whether hotter truly is better), and physical constraints on the stability of cellular and molecular structures. Alternatively, environments in which the cost of thermoregulation is high will favor either specialists or generalists that thermoconform; organisms whose generation is long should be specialists, whereas organisms whose generation is short should be generalists. This conclusion follows from the fact that the optimal thermal sensitivity is determined by the relative magnitude of within-generation versus among-generation variation in temperature (see "Adaptive Responses to Thermal Heterogeneity"). Note that eurythermy on a generational scale might be achieved by developmental plasticity or acclimatization, which would appear to be stenothermy on a shorter temporal scale. If a trade-off between specialization and generalization is not universal, the process of coadaptation might be more complex. Yet, our current understanding of biochemical adaptation (Hochachka and Somero 2002; Guderley 2004) leads us to conclude that this trade-off must occur at the biochemical

level, even if it can be masked at the organismal level (see Angilletta et al. 2003).

Putting the Game into Theories of Thermal Adaptation

Evolutionary thermal biologists have made great strides in discovering the processes that operate at or below the organismal level but have generally underappreciated the biotic arena in which organisms employ their behavioral and physiological strategies. This oversight is hardly punishable, considering that ecologists have only just begun to appreciate the role of environmental temperature in shaping the dynamics of communities (Panikov 1999; Rooney and Kalff 2000; Al-Rabai'ah et al. 2002; Garvey et al. 2003; McClanahan and Maina 2003; Genner et al. 2004). In nature, temperature is likely to influence the quantity and quality of competitors, predators, and mutualists. These other players must also find strategies for coping with thermal heterogeneity while dealing with their own set of competitors, predators, and mutualists. The result is a rich web of interactions among species that must ultimately shape the process of thermal coadaptation within species (see Magnuson et al. 1979).

This game-theoretic perspective offers more than a macroscopic view of thermal adaptation. Indeed, the interactions among species are likely to produce emergent phenomena that differ qualitatively from the predictions of current theories (e.g., Davis et al. 1998). In other words, one cannot understand thermal adaptation in a community of species by studying the evolution of each species in isolation. We draw this conclusion for two reasons: (1) the net benefits of thermoregulation and thermal acclimation depend on the strategies adopted by other
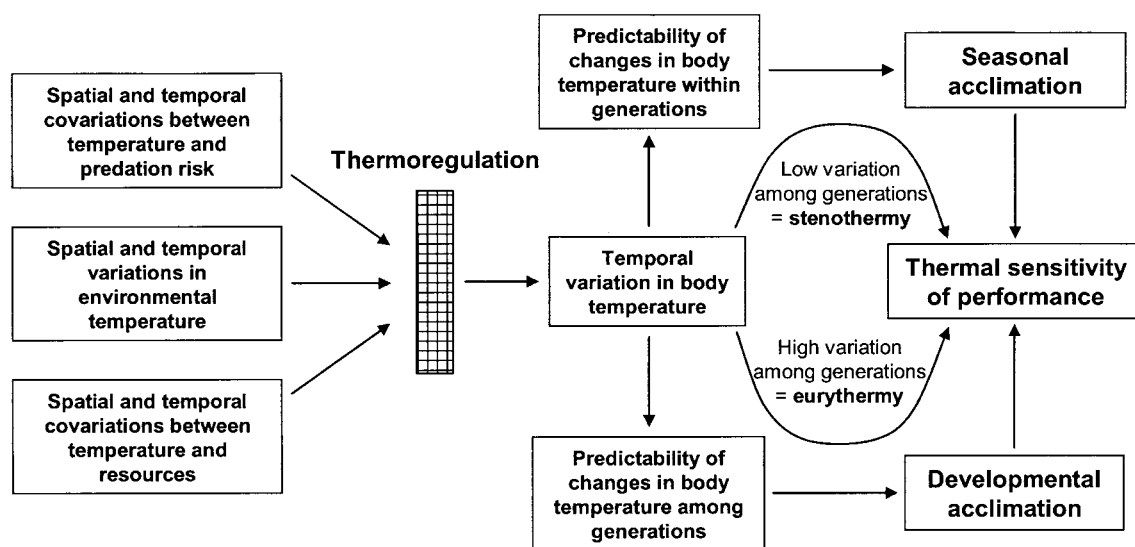

Figure 5. Conceptual model illustrating how thermoregulation and the thermal sensitivity of performance coevolve in ectotherms.

organisms, and (2) species within a community are expected to have different thermal sensitivities of performance. The first point should be obvious from studies of thermoregulation under perceived risks of predation (see "Adaptive Responses to Thermal Heterogeneity"). Whether predators are capable of activity under a thermal condition affects the cost of thermoregulation by their prey (Huey and Slatkin 1976; Huey 1982). The same coevolutionary dynamic applies to seasonal acclimation; whether a species should compensate for seasonal changes or submit to a decrease in physiological function depends on whether their predators and prey are doing so because the net benefit of compensation depends on the availability of resources (Clarke 1993). The expectation that species in a community will have different thermal sensitivities of performance follows from the recognition that all species perceive the thermal environment differently. For example, consider an environment in which temperature cycles daily and annually (Fig. 6). Species with generations of a few weeks (or less) will experience less variation within generations and more variation among generations; moreover, variation among generations will be unpredictable because temperature fluctuates stochastically within seasons (hence the terms "cold snap" and "heat wave"). Species with generations of a few months will experience moderate variation within and among generations; however, variation among generations will be caused by predictable changes in season. Finally, species with generations of a year or more

will see more variation within generations than among generations; much of the variation within generations will be caused by predictable changes in season. Spatial variation is also perceived differently because small and large species at the same location can have very different body temperatures (Stevenson 1985); this problem is exacerbated by differences in mobility between small and large species (or between plants and animals; Bradshaw 1972; Huey et al. 2002). These differences in the perception of temporal and spatial variation among species should influence the evolution of thermal sensitivities and acclimatory responses and hence should have consequences for the ecological and evolutionary dynamics of communities.

The Need for Immediate Progress in Evolutionary Thermal Biology

A theory of thermal coadaptation should have impacts beyond the realm of basic science. Over 99% of all organisms are ectothermic, and global climate change has and will continue to pose thermal challenges to these organisms. On a regional basis, some environments have warmed by as much as 2°C in the last 30 yr, while other environments have cooled by a similar degree (Walther et al. 2002). These thermal changes have altered the growth, phenology, and distribution of many plants and animals (Atrill and Power 2002; Beaugrand et al. 2002; Walther et al. 2002; Parmesan and Yohe 2003). Because temperature
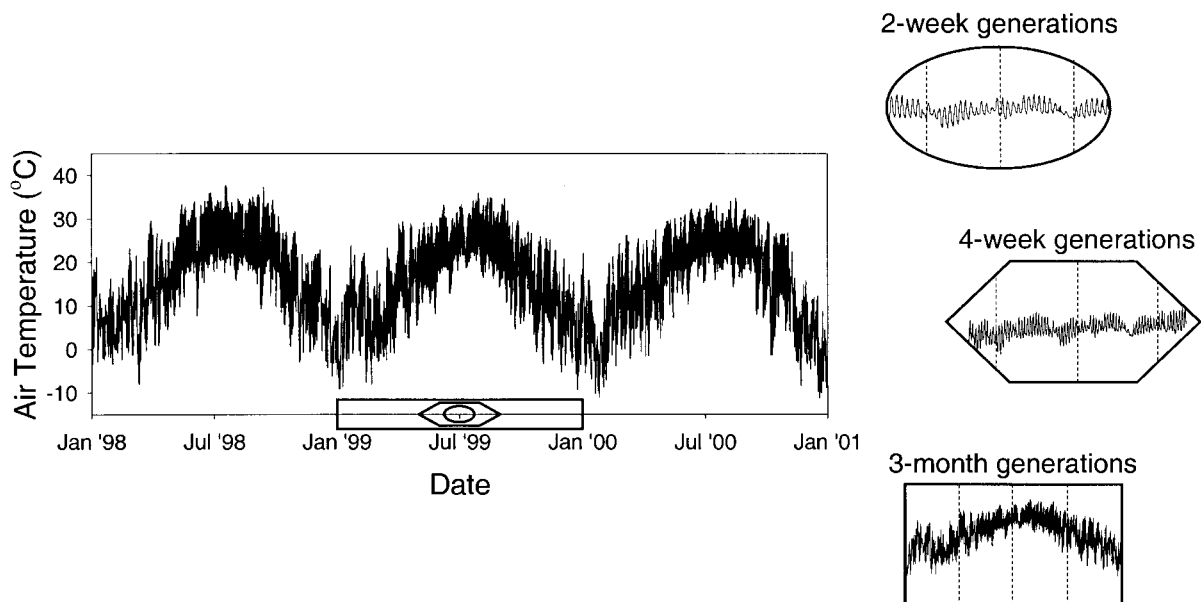

Figure 6. Variation in environmental temperature is perceived differently by each species in a community. Species that live one or more years experience more variation within generations than they do among generations, whereas those that live only a few weeks experience more variation among generations than within generations. This point is illustrated by data from Oak Ridge, Tennessee (36°00′05″N, 84°14′56″W; elevation 266 m), recorded by the National Oceanic and Atmospheric Administration. The effect of generation time is shown by expanding several periods of the year 1999, ranging from 6 wk (*oval frame*) to the entire year (*rectangular frame*).

affects many traits that determine the interactions among species (Garvey et al. 2003; Jiang and Morin 2004), the structure and dynamics of communities will likely be perturbed by global climate change. These perturbations will be particularly problematic when responses to thermal change are asynchronous among species whose interactions are normally in a dynamic equilibrium (e.g., Fitter and Fitter 2002).

The development of a game theory of thermal coadaptation could offer a major advantage to applied ecologists. Although great effort has been expended to understand the ecological consequences of global climate change, the evolutionary consequences remain less clear. Yet, evolutionary responses will determine the interactions among organisms in future ecosystems. This interplay between ecological and evolutionary responses will be complex because certain species will evolve more rapidly than others. Knowledge of the rates and magnitudes of potential evolutionary responses could help us to assess the long-term consequences of global climate change. Thus, a game theory of thermal coadaptation might ultimately lead to insights that will enable us to manage biodiversity successfully in the coming decades.

Acknowledgments

Literature Cited

Adolph S.C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71:315–327.

Al-Rabai'ah H.A., H.L. Koh, D. DeAngelis, and H.L. Lee. 2002. Modeling fish community dynamics in the Florida Everglades: role of temperature variation. Water Sci Technol 46:71–78.

Andrews R.M. 1998. Geographic variation in field body temperature of *Sceloporus* lizards. J Therm Biol 23:329–334.

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

Angilletta M.J., T. Hill, and M.A. Robson. 2002a. Is physio-logical performance optimized by thermoregulatory behavior? a case study of the eastern fence lizard, *Sceloporus undulatus*. J Therm Biol 27:199–204.

Angilletta M.J., P.H. Niewiarowski, and C.A. Navas. 2002b. The evolution of thermal physiology in ectotherms. J Therm Biol 27:249–268.

Angilletta M.J. and Y.L. Werner. 1998. Australian geckos do not display diel variation in thermoregulatory behavior. Copeia 1998:736–742.

Angilletta M.J., R.S. Wilson, C.A. Navas, and R.S. James. 2003. Tradeoffs and the evolution of thermal reaction norms. Trends Ecol Evol 18:234–240.

Atrill M.J. and M. Power. 2002. Climatic influence on a marine fish assemblage. Nature 417:275–278.

Bartholomew G.A. 1982. Physiological control of body temperature. Pp. 167–211 in C. Gans and F.H. Pough, eds. Biology of the Reptilia. Vol. 12. Academic Press, New York.

Bauwens D., P.E. Hertz, and A.M. Castilla. 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. Ecology 77:1818–1830.

Beaugrand, G., P.C. Reid, F. Ibañez, J.A. Lindley, and M. Edward. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692–1694.

Bennett A.F. 2005. Thermoregulation in African chameleons. Pp. 234–241 in S. Morris and A. Vosloo, eds. Animals and Environments: Proceedings of the Third International Conference of Comparative Physiology and Biochemistry. Elsevier, Amsterdam.

Bennett A.F. and R.E. Lenski. 1997. Evolutionary adaptation to temperature. VI. Phenotypic acclimation and its evolution in *Escherichia coli*. Evolution 51:36–44.

———. 1999. Experimental evolution and its role in evolutionary physiology. Am Zool 39:346–362.

Bouchard P. and H. Guderley. 2003. Time course of the response of mitochondria from oxidative muscle during thermal acclimation of rainbow trout, *Oncorhynchus mykiss*. J Exp Biol 206:3455–3465.

Bradshaw A.D. 1972. Some of the evolutionary consequences of being a plant. Evol Biol 5:25–47.

Brown J.H., J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Chaui-Berlinck J.G., C.A. Navas, L.H. Monteiro, and J.E. Bicudo. 2004. Temperature effects on a whole metabolic reaction cannot be inferred from its components. Proc R Soc Lond B 271:1415–1419.

Christian K.A., C.R. Tracy, and W.P. Porter. 1983. Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). Ecology 64:463–468.

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

Clarke A. 1993. Seasonal acclimatization and latitudinal com-

pensation in metabolism: do they exist? Funct Ecol 7:139–149.

Conover D.O. 1998. Local adaptation in marine fishes: evidence and implications for stock enhancement. Bull Mar Sci 62:477–493.

Conover D.O. and E.T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends Ecol Evol 10:248–252.

Cooper V.S., A.F. Bennett, and R.E. Lenski. 2001. Evolution of thermal dependence of growth rate of *Escherichia coli* populations during 20,000 generations in a constant environment. Evolution 55:889–896.

Davis A.J., J.H. Lawton, B. Shorrocks, and L.S. Jenkinson. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. J Anim Ecol 67:600–612.

de Souza S.C., J.E. de Carvalho, A.S. Abe, J.E. Bicudo, and M.S. Bianconcini. 2004. Seasonal metabolic depression, substrate utilisation and changes in scaling patterns during the first year cycle of tegu lizards (*Tupinambis merianae*). J Exp Biol 207:307–318.

DeWitt T.J., A. Sih, and D.S. Wilson. 1998. Costs and limits to phenotypic plasticity. Trends Ecol Evol 13:77–81.

Downes S. 2001. Trading heat and food for safety: costs of predator avoidance in a lizard. Ecology 82:2870–2881.

Downes S. and R. Shine. 1998. Heat, safety or solitude? using habitat selection experiments to identify a lizard's priorities. Anim Behav 55:1387–1396.

Dutil J.-D., Y. Lambert, H. Guderley, P.U. Blier, D. Pelletier, and M. Desroches. 1998. Nucleic acids and enzymes in Atlantic cod (*Gadus morhua*) differing in condition and growth rate trajectories. Can J Fish Aquat Sci 55:788–795.

Dzialowski E.M. and M.P. O'Connor. 2004. Importance of the limbs in the physiological control of heat exchange in *Iguana Iguana* and *Sceloporus undulatus*. J Therm Biol 29:299–305.

Feder M.E., A.F. Bennett, and R.B. Huey. 2000. Evolutionary physiology. Annu Rev Ecol Syst 31:315–341.

Fitter A.H. and R.S.R. Fitter. 2002. Rapid changes in flowering time in British plants. Science 296:1689–1691.

Gabriel W. and M. Lynch. 1992. The selective advantage of reaction norms for environmental tolerance. J Evol Biol 5:41–59.

Garland T., Jr., and P.A. Carter. 1994. Evolutionary physiology. Annu Rev Ecol Syst 56:579–621.

Garvey J.E., D.R. Devries, R.A. Wright, and J.G. Miner. 2003. Energetic adaptations along a broad latitudinal gradient: implications for widely distributed assemblages. Bioscience 53:141–150.

Genner M.J., D.W. Sims, V.J. Wearmouth, E.J. Southall, A.J. Southward, P.A. Henderson, and S.J. Hawkins. 2004. Regional climatic warming drives long-term community changes of British marine fish. Proc R Soc Lond B 271:655–661.

Gibert P., R.B. Huey, and G.W. Gilchrist. 2001. Locomotor performance of *Drosophila melanogaster*: interactions among developmental and adult temperatures, age, and geography. Evolution 55:205–209.

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

Grant B.W. and A.E. Dunham. 1990. Elevational covariation in environmental constraints and life histories of the desert lizard, *Sceloporus merriami*. Ecology 71:1765–1776.

Guderley H. 2004. Metabolic responses to low temperature in fish muscle. Biol Rev 79:409–427.

Guderley H. and J. St. Pierre. 1999. Seasonal cycles of mitochondrial ADP sensitivity and oxidative capacities. J Comp Physiol B 169:474–480.

———. 2002. Going with the flow or life in the fast lane: contrasting mitochondrial responses to thermal change. J Exp Biol 205:2237–2249.

Guppy M. and P. Withers. 1999. Metabolic depression in animals: physiological perspectives and biochemical generalizations. Biol Rev 74:1–40.

Hand S.C. and I. Hardewig. 1996. Downregulation of cellular metabolism during environmental stress: mechanisms and implications. Annu Rev Physiol 58:539–563.

Haynie D.T. 2001. Biological Thermodynamics. Cambridge University Press, Cambridge.

Hazel J.R. 1995. Thermal adaptation in biological membranes: is homeoviscous adaptation the explanation? Annu Rev Physiol 57:19–42.

Heath J.E. 1964. Reptilian thermoregulation: evaluation of field studies. Science 146:784–785.

———. 1965. Temperature regulation and diurnal activity in horned lizards. Univ Calif Publ Zool 64:97–136.

Hertz P.E. 1981. Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): field thermal biology and physiological ecology. J Zool (Lond) 195:25–37.

Hertz P.E. and R.B. Huey. 1981. Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. Ecology 62:515–521.

Hertz P.E., R.B. Huey, and T. Garland Jr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles Olympians or body scouts? Am Zool 28:927–938.

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

Hochachka P.W. and G.N. Somero. 2002. Biochemical Adaptation. Oxford University Press, Oxford.

Hoffmann A.A. 1995. Acclimation: increasing survival at a cost. Trends Ecol Evol 10:1–2.

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

———. 1982. Temperature, physiology, and the ecology of rep-

tiles. Pp. 25–74 in C. Gans and F.H. Pough, eds. Biology of the Reptilia. Vol. 12. Academic Press, New York.

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

Huey R.B. and D.A. Berrigan. 1996. Testing evolutionary hypotheses of acclimation. Pp. 205–237 in I.A. Johnston and A.F. Bennett, eds. Animals and Temperature: Phenotypic and Evolutionary Adaptation. Society for Experimental Biology Seminar Series. Cambridge University Press, Cambridge.

Huey R.B., D. Berrigan, G.W. Gilchrist, and J.C. Herron. 1999. Testing the adaptive significance of acclimation: a strong inference approach. Am Zool 39:323–336.

Huey R.B., M. Carlson, L. Crozier, M. Frazier, H. Hamilton, C. Harley, A. Hoang, and J.G. Kingsolver. 2002. Plants versus animals: do they deal with stress in different ways? Integr Comp Biol 42:415–423.

Huey R.B. and P.E. Hertz. 1984. Is a jack-of-all-temperatures a master of none? Evolution 38:441–444.

Huey R.B. and J.G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends Ecol Evol 4:131–135.

———. 1993. Evolution of resistance to high temperature in ectotherms. Am Nat 142(suppl.):S21–S46.

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

Huey R.B. and M. Slatkin. 1976. Cost and benefits of lizard thermoregulation. Q Rev Biol 51:363–384.

Huey R.B. and R.D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: discussion of approaches. Am Zool 19:357–366.

Janzen D.H. 1967. Why mountain passes are higher in the tropics. Am Nat 101:233–249.

Jiang L. and P.J. Morin. 2004. Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. J Anim Ecol 73:569–576.

Johnston I.A. and G.K. Temple. 2002. Thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behaviour. J Exp Biol 205:2305–2322.

Kearney M. and M. Predavec. 2000. Do nocturnal ectotherms thermoregulate? a study of the temperate gecko Christinus marmoratus. Ecology 81:2984–2996.

Kingsolver J.G. and R.B. Huey. 1998. Evolutionary analyses of morphological and physiological plasticity in thermally variable environments. Am Zool 38:545–560.

Leroi A.M., A.F. Bennett, and R.E. Lenski. 1994. Temperature acclimation and competitive fitness: an experimental test of the beneficial acclimation assumption. Proc Natl Acad Sci USA 91:1917–1921.

Levins R. 1962. Theory of fitness in a heterogenous environment. I. The fitness set and adaptive functions. Am Nat 96:361–373.

———. 1963. Theory of fitness in a heterogenous environment. II. Developmental flexibility and niche selection. Am Nat 97:75–90.

———. 1968. Evolution in Changing Environments. Princeton University Press, Princeton, NJ.

Lynch M. and W. Gabriel 1987. Environmental tolerance. Am Nat 129:283–303.

Magnuson J.J., L.B. Crowder, and P.A. Medvick. 1979. Temperature as an ecological resource. Am Zool 19:331–343.

McClanahan T.R. and J. Maina. 2003. Response of coral assemblages to the interaction between natural temperature variation and rare warm-water events. Ecosystems 6:551–563.

Mercer J. 2001. Glossary of terms for thermal physiology. Jpn J Physiol 51:245–280.

Mongold J.A., A.F. Bennett, and R.E. Lenski. 1999. Evolutionary adaptation to temperature. VII. Extension of the upper thermal limit of Escherichia coli. Evolution 53:386–394.

Navas C.A. 1996. Metabolic physiology, locomotor performance, and thermal niche breadth in Neotropical anurans. Physiol Zool 69:1481–1501.

———. 2002. Herpetological diversity along Andean elevational gradients: links with physiological ecology and evolutionary physiology. Comp Biochem Physiol 133A:469–485.

O'Steen S. and A.F. Bennett. 2003. Thermal acclimation effects differ between voluntary, maximum, and critical swimming velocities in two cyprinid fishes. Physiol Biochem Zool 76:484–496.

Palaima A. and K. Spitze. 2004. Is a jack-of-all-temperatures a master of none? an experimental test with Daphnia pulicaria (Crustacea: Cladocera). Evol Ecol Res 6:215–225.

Panikov N.S. 1999. Understanding and prediction of soil microbial community dynamics under global change. Appl Soil Ecol 11:161–176.

Parmesan C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Pelletier D., H. Guderley, and J.-D. Dutil. 1993a. Does the aerobic capacity of fish muscle change with growth rate? Fish Physiol Biochem 12:83–93.

———. 1993b. Effects of growth rate, temperature, season and body size on glycolytic enzyme activities in the white muscle of Atlantic cod (Gadus morhua). J Exp Zool 265:477–487.

Platt J.R. 1964. Strong inference. Science 146:347–353.

Pörtner H.O., A.F. Bennett, F. Bozinovic, A. Clarke, M.A. Lardies, M. Lucassen, B. Pelster, F. Schiemer, and J.H. Stillman. 2006. Trade-offs in thermal adaptation: the need for a molecular to ecological integration. Physiol Biochem Zool 79:295–313.

Precht H. 1958. Concepts of the temperature adaptation of unchanging reaction systems of cold-blooded animals. Pp.

50–78 in C.L. Prosser, ed. Physiological Adaptations. American Physiological Society, Washington, DC.

Prosser C.L. 1979. Comparative Animal Physiology. Wiley, New York.

Quinn J. and A.E. Dunham. 1983. On hypothesis testing in ecology and evolution. Am Nat 122:602–617.

Rock J., A. Cree, and R.M. Andrews. 2002. The effect of reproductive condition on thermoregulation in a viviparous gecko from a cool climate. J Therm Biol 27:17–27.

Rome L.C, P.T. Loughna, and G. Goldspink. 1984. Temperature acclimation: improved sustained swimming performance in carp at low temperatures. Science 228:194–196.

Rooney N. and J. Kalff. 2000. Inter-annual variation in submerged macrophyte community biomass and distribution: the influence of temperature and lake morphometry. Aquat Bot 68:321–335.

Sänger A.M. 1993. Limits to the acclimation of fish muscle. Rev Fish Biol Fish 3:1–15.

Sears M.W. and M.J. Angilletta. 2004. Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. Integr Comp Biol 44:433–442.

Stevenson R.D. 1985. Body size and limits to the daily range of body temperatures in terrestrial ectotherms. Am Nat 125:102–117.

St. Pierre J. and R.G. Boutilier. 2001. Aerobic capacity of frog skeletal muscle during hibernation. Physiol Biochem Zool 74:390–397.

van Berkum F.H. 1988. Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. Am Nat 132:327–343.

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

Walther G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Wilson R.S. and C.E. Franklin. 2002. Testing the beneficial acclimation hypothesis. Trends Ecol Evol 17:66–70.

Wilson R.S. and I.A. Johnston. 2005. Combining studies of comparative physiology and behavioural ecology to test the adaptive benefits of thermal acclimation. Pp. 201–208 in S. Morris and A. Vosloo, eds. Animals and Environments: Proceedings of the Third International Conference of Comparative Physiology and Biochemistry. Elsevier, Amsterdam.

Zamudio K.R., R.B. Huey, and W.D. Crill. 1995. Bigger isn't always better: body size, developmental and parental temperature and male territorial success in *Drosophila melanogaster*. Anim Behav 49:671–677.