

## The evolution of thermal physiology in endotherms

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### TABLE OF CONTENTS

1. Abstract
2. Introduction
3. Adaptation to thermal heterogeneity
4. Thermoregulation
  - 4.1. Patterns of thermoregulatory precision
  - 4.2. Optimal thermoregulation
  - 4.3. Evidence of adaptive thermoregulation in mammals and birds
    - 4.3.1. Effects of energy availability
    - 4.3.2. Effects of air temperature
    - 4.3.3. Effects of huddling
    - 4.3.4. Effects of water availability
  - 4.4. Patterns of avian brooding
5. Thermosensitivity
  - 5.1. Do thermoregulatory strategies impose selection on thermosensitivity?
  - 5.2. Can thermosensitivity respond to selection?
  - 5.3. What patterns of thermosensitivity should evolve?
6. Summary and perspective
7. Acknowledgements
8. References

## 1. ABSTRACT

Biologists usually refer to mammals and birds as homeotherms, but these animals universally experience regional and temporal variations in body temperature. These variations could represent adaptive strategies of heterothermy, which in turn would favor genotypes that function over a wide range of temperatures. This coadaptation of thermoregulation and thermosensitivity has been studied extensively among ectotherms, but remains unexplored among endotherms. In this review, we apply classical models of thermal adaptation to predict variation in body temperature within and among populations of mammals and birds. We then relate these predictions to observations generated by comparative and experimental studies. In general, optimality models can explain the qualitative effects of abiotic and biotic factors on thermoregulation. Similar insights should emerge when using models to predict variation in the thermosensitivity of endotherms, but the dearth of empirical data on this subject precludes a rigorous analysis at this time. Future research should focus on the selective pressures imposed by regional and temporal heterothermy in endotherms.

## 2. INTRODUCTION

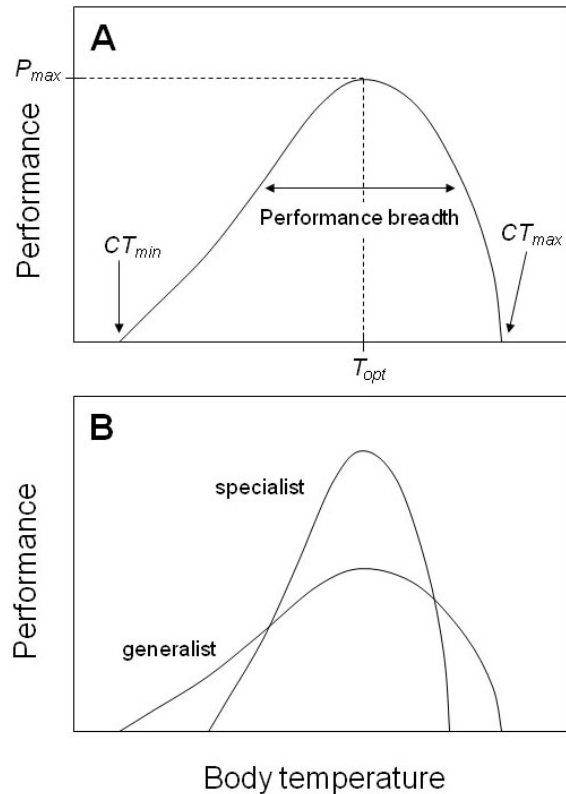
*We may state then that there are no signs so far that body temperature of mammals and birds is adaptive to the different climates on earth. A logical corollary of this is that it cannot have been adaptive to the over-all climatic conditions on earth either. It seems then that the narrow band of body temperature on which both birds and mammals operate is a fundamental, nonadaptive constant in their biochemical setup* (1, p. 261).

-Per Fredrik Scholander *et al.* (1950)

*In order to maintain an untenable position, you have to be actively ignorant* (2).

-Stephen Tyrone Colbert (2007)

Amidst the remarkable diversity of life, mammals and birds display a unique capacity for thermoregulation. Whether they dwell at the equator or the poles, these endothermic animals keep their bodies at high and constant temperatures during activity (1, 3). This impressive feat results from coordinated changes in conductance,



**Figure 1.** A) This hypothetical performance curve shows the stereotypical optimum at an intermediate temperature. The thermal optimum ( $T_{opt}$ ), performance breadth, critical thermal limits ( $CT_{min}$  and  $CT_{max}$ ), and maximal performance ( $P_{max}$ ) are labeled. Adapted from Huey and Stevenson (25) with permission from Oxford University Press. B) A fundamental tradeoff exists between specialists and generalists. Generalists can perform over a wider range of temperatures, but perform poorer than specialists at the optimal temperature.

evaporation, circulation, and metabolism in response to environmental conditions. In particular, the capacity of mammals and birds to regulate conductance and metabolism far surpasses that of other organisms (4, 5). Interestingly, the remarkable uniformity of body temperatures among active mammals and birds has inspired two diametrical views among researchers. On one hand, some researchers have concluded that the body temperatures of these endotherms represent a biophysical constraint; in fact, Scholander and colleagues (1) went as far as to suggest that the body temperature of a mammal or bird is a “nonadaptive constant” (p. 261). On the other hand, other researchers have argued that natural selection has shaped the mean and variance of body temperature in endotherms (6, 7).

In recent decades, the balance of power has shifted toward the adaptive view (8-10). This shift occurred as researchers gradually realized that mammals and birds exhibit far more variation in body temperature throughout their lives than was originally perceived from the study of active individuals. Body temperature, and the physiological processes that maintain it, vary extensively and predictably

along environmental clines. For example, the active body temperatures of mammals tend to increase with increasing latitude (11), presumably because of greater heat production or lesser heat conductance (1, 11-13). Furthermore, the range of body temperatures experienced by individuals varies continuously among avian species (14) and likely does so among mammalian species (15). In light of this evidence, the non-adaptive view has eroded to the point where researchers are now testing hypotheses about the evolutionary maintenance of thermoregulatory strategies in mammals and birds (e.g., see 8, 10).

Despite the mounting effort to untangle the causes of endothermic thermoregulation, no organized attempt has been made to examine the evolutionary impacts of variation in the body temperatures of endotherms. As with ectotherms, the body temperature of an endotherm should determine its capacity to perform vital functions. Yet, we know virtually nothing about this thermosensitivity of performance in mammals and birds. What little we do know comes from studies of young birds (16) or isolated tissues (17-20), which lack the capacity for endothermy. Moreover, these studies lacked theoretical contexts or experimental designs that address microevolutionary processes. Yet even superb thermoregulators, such as adult mammals and birds, can experience considerable variation in body temperature. This variation should affect performance and potentially drive the evolution of thermosensitivity.

In this paper, we ask whether the theory originally designed to understand thermal adaptation in ectotherms can generate insights about thermal adaptation in vertebrate endotherms (hereafter, simply referred to as endotherms). This theory identifies selective pressures on thermoregulation and thermosensitivity in heterogeneous environments (reviewed by 21). Arguably, current models should apply equally well to endotherms as they do to ectotherms. Using these models, we outline a set of predictions about variation in body temperature, variation in thermal sensitivity, and the covariation between these traits. These predictions have been evaluated previously through comparative and experimental studies of ectotherms (reviewed by 21, 22, 23, 24), and here we attempt to draw on similar studies of endotherms. We show that variation in body temperature within mammals and birds often accords with predicted responses to environmental conditions, such as ambient temperature or food availability. Furthermore, the variation in body temperature seems sufficient to exert selective pressures on the thermal sensitivity of physiological performance. Thus, we urge researchers to investigate the evolution of thermal physiology in endotherms, and suggest some promising directions for doing so.

### 3. ADAPTATION TO THERMAL HETEROGENEITY

The laws of physics and chemistry demand that the performance of any organism depends on its body temperature. Traditionally, physiologists have quantified this thermal dependence in the context of a performance curve (25), which describes the nonlinear relationship between an organism’s temperature and its rate of performance (Figure 1A). We can characterize any performance curve by its thermal optimum and thermal

## Evolution of thermal physiology

breadth. The thermal optimum equals the body temperature that maximizes the rate of performance. The thermal breadth equals the range of temperatures over which performance exceeds an arbitrary level (e.g., 80% of maximal performance). Thermal optima and breadths vary among genotypes; individuals with narrow thermal breadths are called specialists, whereas individuals with wide thermal breadths are called generalists. In theory, tradeoffs constrain the variation in performance curves among genotypes. For example, enzymes that function well at high temperatures function poorly at low temperatures, and vice versa (26). Therefore, a generalist must produce multiple forms of key enzymes, resulting in a loss of metabolic efficiency (6). This investment would impose a tradeoff by either reducing the energy available for reproduction or increasing the duration of foraging (27). For a given supply of energy, a specialist should outperform a generalist when compared at the thermal optimum (see Figure 1B).

The inevitable thermosensitivity of performance imposes a selective pressure when microclimates vary over space and time. This selective pressure leads to one of three outcomes. First, a population can adapt such that individuals use some combination of behavior, physiology, and morphology to regulate body temperature near the thermal optimum (evolution of thermoregulation). Second, a population can adapt such that individuals can perform well over a relatively wide range of temperatures (evolution of thermosensitivity). Finally, a population can fail to adapt such that the mean performance of individuals and the mean fitness of the population declines (no response to selection). If genetic variation exists for thermoregulation or thermosensitivity, the third outcome seems unlikely. Rather, some adaptive combination of thermoregulation and thermosensitivity should emerge from natural selection.

Over the last two decades, theorists have combined optimality and genetic models to predict evolution in heterogeneous environments (reviewed by 21, 28). Optimality models define the fitness landscapes for traits, enabling us to predict the direction and strength of selective pressures on thermoregulation and thermosensitivity. Genetic models describe how these traits respond to selection given genetic constraints. Optimal thermoregulation has been modeled as a function of energetic costs and benefits (29, 30). Optimal thermosensitivity has been defined under stochastic (31, 32), abrupt (33), and directional (34, 35) changes in body temperature. Under most scenarios, selection favors genotypes that perform best at the modal body temperature (or very near this temperature). Furthermore, selection favors specialists unless body temperature varies greatly among generations. An organism's capacity to shift its thermosensitivity within its lifetime—usually referred to as acclimation—qualitatively alters the selective pressures on thermosensitivity. Generally, the potential for acclimation favors specialists in environments that might otherwise favor generalists (33, 36). In this way, organisms can maintain superior performance in a changing environment. Theorists have also used genetic models to investigate the

dynamics of evolution given additive alleles (37, 38), developmental noise (32), pleiotropic effects (28), sexual reproduction (38), and gene flow (39, 40). These factors affect the rate of adaptation but do not alter the optimal phenotype (32, 38, 39). Therefore, we can use optimality models to predict the adaptation of thermal physiology when genetic variation persists.

Although selective pressures on thermoregulation and thermosensitivity have been modeled independently, a clear relationship exists between the two (24). Consider the following examples. If we wanted to know whether a specialist or a generalist would achieve greater fitness in a particular environment, we would need to know how that environment affected the distribution of body temperatures. But the thermoregulatory strategy determines these body temperatures. Thus, the optimal thermosensitivity depends on the organism's strategy of thermoregulation. In a similar way, the optimal thermoregulatory strategy depends on the thermosensitivity; for instance, a specialist has a greater incentive to thermoregulate than does a generalist. These considerations imply that certain combinations of thermoregulation and thermosensitivity would confer greater fitness than others (41). Consequently, the coevolution of these traits should generate relationships that would be evident from comparisons among populations or species. First, the mean body temperature during thermoregulation should match the thermal optimum for performance. Second, the variance of body temperature during thermoregulation should relate to the thermal breadth of performance (e.g., see 42). Although these hypotheses were formulated with ectotherms in mind (41), they should also hold for endotherms.

In the sections that follow, we ask whether current models can identify factors that influence the thermoregulatory strategies and thermal sensitivities of mammals and birds. In doing so, we must tailor the optimality models developed for ectotherms to fit the unique features of endotherms. We then compare the results of experiments to the predictions of the models. Rather than present an exhaustive review of the empirical evidence, we intend to illustrate the advantage of organizing data in the context of theory. For this reason, we highlight only those studies that generated the data needed to evaluate current models of thermal adaptation.

## 4. THERMOREGULATION

### 4.1. Patterns of thermoregulatory precision

Although Scholander *et al.*'s (1) data suggested that body temperatures of mammals and birds remain constant, the data collected during the intervening decades supports a resounding conclusion: body temperatures vary universally within and among individuals. Among species of birds, mean body temperatures vary from 36 to 45°C and from 35 to 41°C during activity and rest, respectively (43). Even more variation exists among species of mammals (44). Importantly, this interspecific variation stems from analyses of mean body temperatures, which obscure the appreciable variation that occurs within populations and individuals. In fact, every organism must experience

regional heterothermy—variation in temperature throughout the body—merely as a consequence of heat flux between the body core and the external environment (45). Additionally, temporal heterothermy has been widely documented in the form of diel or seasonal fluctuations in body temperature (8); depending on the duration and intensity, these thermal fluctuations have been described as transitions among the alternative states of normothermia, hypothermia, torpor, or hibernation (15). Yet these terms lack real explanatory power because they require subjective distinctions and carry hidden assumption (see 46). Indeed, the body temperatures of mammals and birds vary continuously within and among species (14, 15, 43, 47). Even classically defined homeotherms such as humans experience diel cycles of body temperature (48). More than half a century after the work of Scholander and his colleagues, we are tempted to conclude quite the opposite of what they were willing to conclude: no species on Earth is a perfect homeotherm, and consequently the body temperatures of mammals and birds must reflect selective pressures operating within physical, genetic, and developmental constraints.

Terms such as homeothermy and poikilothermy have helped to delineate lines of inquiry, but they have also reinforced intellectual barriers that discouraged us from posing important questions about the thermal physiology of endotherms. Is the variation in body temperature within and among individuals adaptive? Does this variation in body temperature impose selective pressures on the thermosensitivity of physiological performance? Have strategies of thermoregulation and thermosensitivity coevolved? These questions become equally relevant to students of endotherms and ectotherms when one recognizes that we cannot label either group as homeothermic or poikilothermic. Strictly speaking, a homeotherm maintains a constant body temperature regardless of the operative environmental temperature (or operative temperature; *sensu* 49), and a poikilotherm always conforms to the operative environmental temperature. In contrast to these theoretical extremes, real endotherms sometimes abandon metabolic or evaporative mechanisms of thermoregulation, and real ectotherms often resort to behavioral or evaporative mechanisms of thermoregulation. Rather than squeeze organisms into the pigeonholes of homeothermy and poikilothermy, we should focus on the causes and consequences of meaningful variables, such as the mean and variance of body temperature. Such an approach would advance our understanding of thermoregulation by mammals and birds and could generate new lines of inquiry about the evolution of their thermal physiology.

The body temperatures of an endotherm depends on the duration of time spent in elevated and depressed metabolic states, as well as behavioral and morphological mechanisms of thermoregulation (5). These regulatory mechanisms impose costs that offset the benefits of a high and constant body temperature. By applying optimality models, we can identify the selective pressures that influence the accuracy and precision of thermoregulation in endotherms. The accuracy of thermoregulation can be

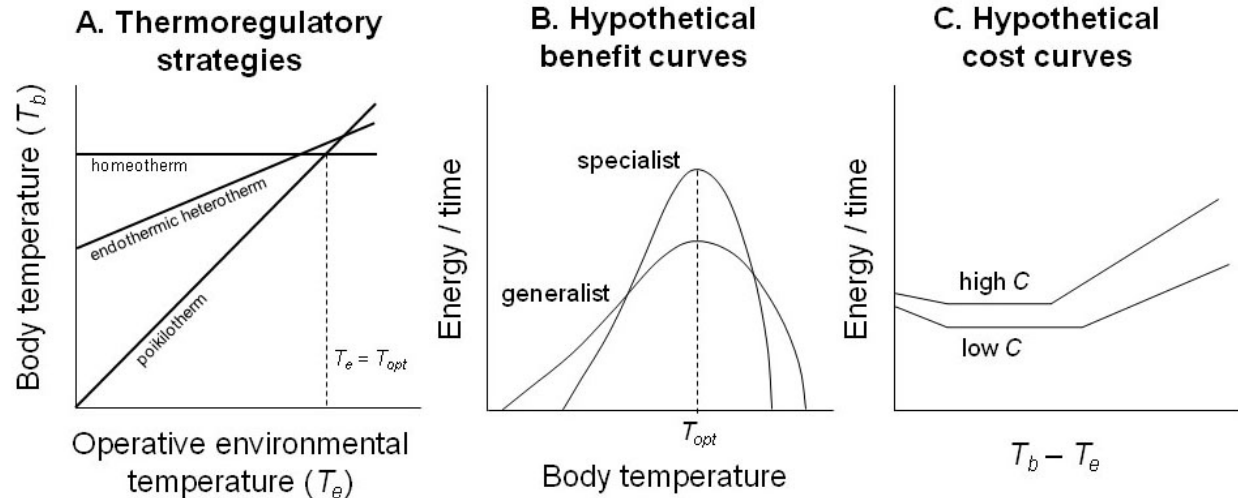
objectively defined as the absolute deviation between the thermal optimum for performance and the mean body temperature (50). The precision of thermoregulation can be represented by the variance of body temperature. As we shall see, the selective pressures that influence endothermic thermoregulation do not differ fundamentally from those that shape ectothermic thermoregulation (reviewed by 21).

### 4.2. Optimal thermoregulation

The relatively high and constant body temperatures of endotherms appear to confer major metabolic advantages. The rates of biochemical reactions depend on the interaction between the structures of macromolecules and the properties of their environment (26, 51, 52). Certain biochemical structures provide functional stability at high temperatures, but they also slow the rate of catalysis. Nevertheless, the rate of molecular collisions increases with increasing temperature. The effects of enzymatic structure and body temperature combine to determine the catalytic rate. When these effects sum, the advantage of a high body temperature more than outweighs the disadvantage of a stable enzymatic structure (26). Seemingly as a consequence, warm-adapted organisms generally outperform cold-adapted organisms, even when compared at their respective thermal optima (21, 53, 54). Hamilton (7) proposed that the high body temperatures of mammals and birds were selected to take advantage of this thermodynamic effect on performance. A low variance of body temperature would also enhance the efficiency of metabolism because cells would have to produce only those macromolecules needed to function within a narrow thermal range (6). This metabolic efficiency underlies the theoretical tradeoff between specialists and generalists (see Figure 1B).

Despite the significant benefits of thermoregulation, selective pressures also depend on the costs of endothermy in a given environment. In other words, selection favors those individuals whose thermoregulatory strategy confers the greatest net benefit. This net benefit must be quantified in some currency that relates to fitness. Energy seems a reasonable currency to consider. We know that energy availability influences survivorship and fecundity, which in turn determine fitness (55). Alternatively, we might directly consider the effects of thermoregulation on survivorship or fecundity. In this way, we could model non-energetic costs, such as predation risk or missed opportunities.

Huey and Slatkin (29) developed a model of optimal thermoregulation that was motivated by observations of ectotherms, but their model applies equally well to endotherms after some modification (Figure 2). They envisioned an organism whose rate of energy gain was a function of its temperature (Figure 2B). In a heterogeneous environment, this organism could enhance its energy gain by regulating the mean and variance of body temperature. Yet, this thermoregulation would impose an energetic cost (Figure 2C). Huey and Slatkin implicitly assumed that this cost stemmed from a behavioral process, such as shuttling between sun and shade. However, we can



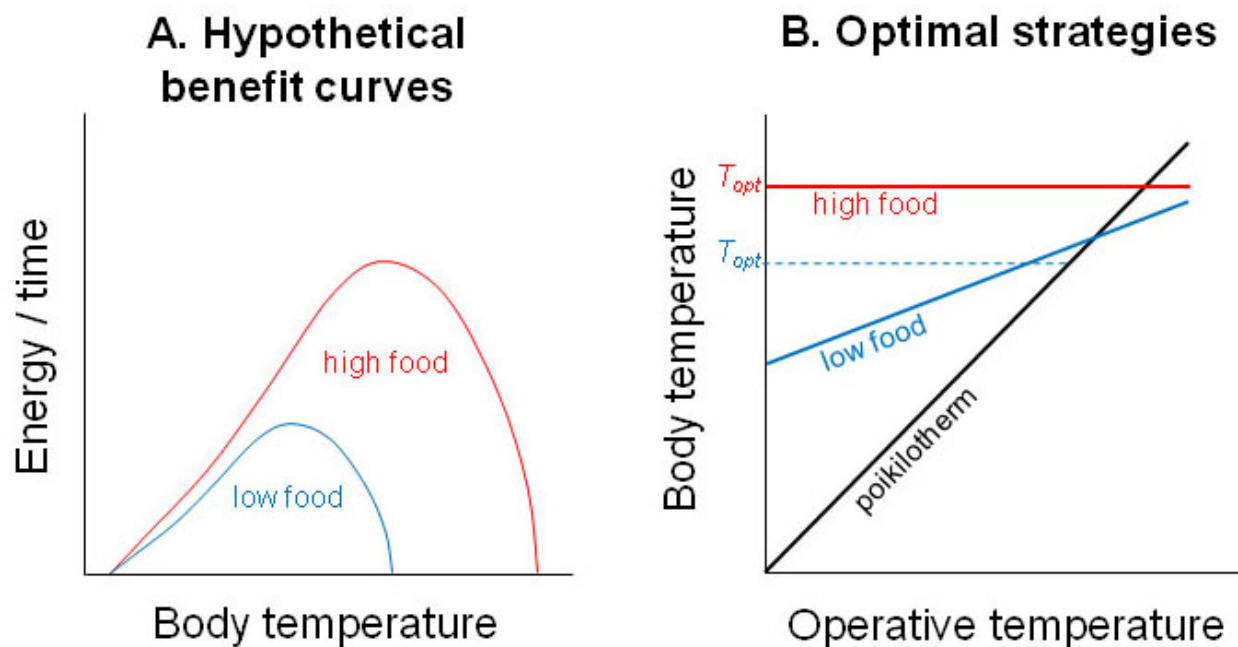
**Figure 2.** Modeling the optimal strategy of thermoregulation requires precise definitions of the potential strategies and their respective costs and benefits. Here, we modified the model of Huey and Slatkin (29) to fit the properties of an endotherm. A) The thermoregulatory strategy was modeled as the relationship between the operative environmental temperature ( $T_e$ ) and the body temperature ( $T_b$ ). The slope of this relationship varies between 0 and 1, with a slope of 0 defining a homeotherm and a slope greater than 0 defining a heterotherm. Heterothermic individuals include ectotherms that do not thermoregulate (ectothermic poikilotherms; slope = 1) and endotherms that thermoregulate inaccurately (endothermic heterotherms;  $0 < \text{slope} < 1$ ). Note that endothermy causes an organism's body temperature to exceed the thermal optimum for performance ( $T_{opt}$ ) when the operative temperature equals the thermal optimum. B) The rate of energy gain was assumed to increase as the body temperature approached the thermal optimum; hypothetical curves for a thermal specialist and a thermal generalist are shown. C) The energetic cost of thermoregulation was assumed to increase as the operative temperature deviates from the set-point body temperature. Hypothetical curves for an animal with high conductance (C) and an animal with low conductance are shown. These cost functions ignore the energy required to produce insulation (e.g., fur, blubber, or feathers) and the energy required for cardiovascular regulation of heat flux.

also imagine that this cost represents physiological processes, namely the metabolic reactions associated with endothermy. Within the thermoneutral zone, an endotherm pays a constant energetic cost determined by its set-point temperature and its minimal conductance. As the operative temperature of the environment falls below the thermoneutral zone, an endotherm must expend more energy to maintain its body temperature at the set point.

The net benefit of thermoregulation depends on the organism and the environment. An organism can adopt any strategy ranging from homeothermy to poikilothermy (Figure 2A). A homeotherm receives a greater gross benefit than does a poikilotherm, but a poikilotherm pays no cost of thermoregulation. For a given strategy, the expected cost and benefit depend on the spatial and temporal distributions of operative temperatures in the environment. Which environments would favor an endotherm that thermoregulates imprecisely? Any factor that decreases the benefit or increases the cost of thermoregulation would shift the optimal strategy toward poikilothermy. Two factors seem to have obvious relevance. First, the availability of food affects the energetic benefit of thermoregulation. High body temperatures enhance the assimilation of energy, but this thermal effect depends on the absorptive state of the organism. When food becomes limiting, energy assimilation proceeds more slowly and growth proceeds best at a lower temperature (e.g., see 56). This change in

the shape of the benefit curve would decrease the net benefit of thermoregulation. Thus, individuals who consume less food should thermoregulate less accurately. Second, the mean operative temperature of the environment affects the energetic cost of thermoregulation. Operative temperature decreases with decreasing air temperature, decreasing solar radiation, and increasing wind speed (57, 58). An organism faced with such conditions could generate more heat to maintain its set-point temperature or suffer a decrease in body temperature and physiological performance. If the cost of thermoregulation rises sufficiently, selection might even favor genotypes that depress their metabolism and temperature, as during torpor or hibernation. For endotherms, a decreasing benefit or an increasing cost of thermoregulation favors one of two responses: a change in the set-point body temperature (inaccurate thermoregulation) or an increase in the variance of body temperature (imprecise thermoregulation). Thus, the states commonly described as normothermia, hypothermia, and hyperthermia could represent optimal strategies for different environmental conditions.

Non-energetic benefits would also influence selective pressures on endothermic thermoregulation. Such benefits include the enhancement of physiological functions, the maintenance of neural integrity, and the prevention of cellular damage (10). For example, when the ability to detect and evade predators depends on body



**Figure 3.** The availability of food affects the optimal strategy of thermoregulation. A) Both the maximal rate and the thermal optimum of energy assimilation decrease with decreasing food availability. B) Environments that are rich in food (high food) favor more precise thermoregulation than do environments that are poor in food (low food).

temperature, thermoregulation would confer a survival benefit in a risky environment. Nevertheless, this benefit must be balanced against the energetic cost of thermoregulation. Pravosudov and Lucas (59) modeled the tradeoff between the survival benefit and the energetic cost of thermoregulation in small birds. They concluded that a bird can maximize survivorship by avoiding nocturnal hypothermia when its energetic supply meets the energetic demand of thermoregulation. As the supply dwindles, an animal must either forage more intensely or face a risk of starvation if it chooses to thermoregulate accurately and precisely. Indeed, some mammals and birds increase their rates and frequencies of feeding as ambient temperature decreases (60). These behaviors could increase the risk of predation during activity (61), which would offset a survival benefit during inactivity.

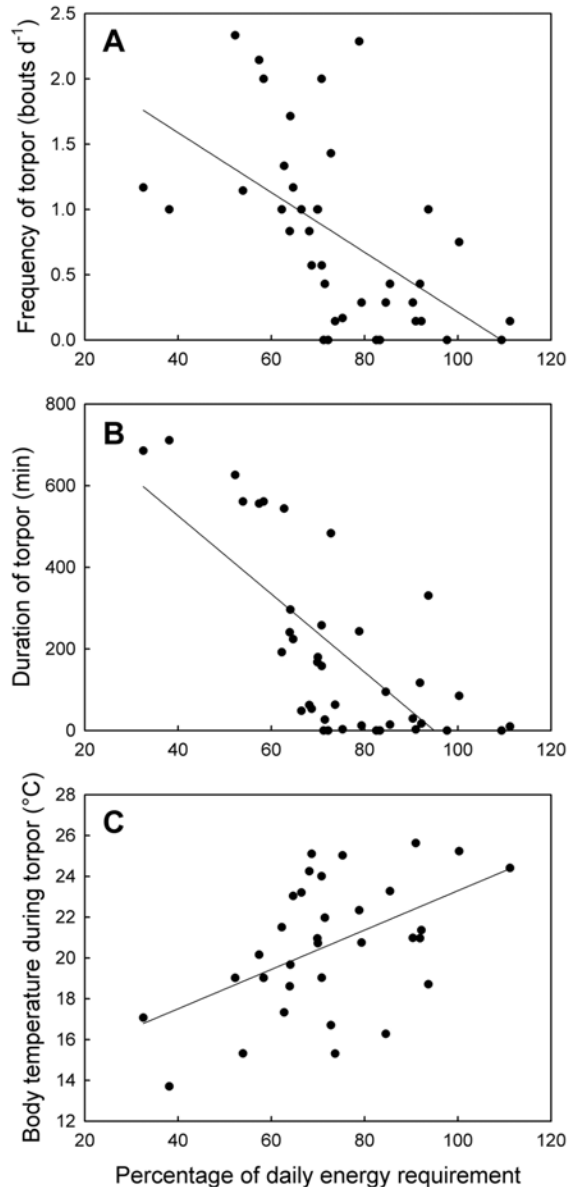
We can use models of optimal thermoregulation to infer the causes of variation in body temperature within mammals and birds. Already, other researchers have argued that physiological and ecological factors influence the use of torpor (8-10). Consider the thermoregulatory consequences of variation in body size among species of birds. Small birds, which would need to generate considerable heat (per gram of body tissue), permit their temperature to drop more during inactivity than do large birds (9). Furthermore, smaller birds experience a wider daily range of body temperatures, as expected from their greater mass-specific cost of homeothermy (43). Such macroevolutionary patterns suggest that adaptation of thermoregulation has occurred, but do not tell us the potential for adaptation on a microevolutionary scale. Yet

even a cursory examination of the literature should lead one to conclude that thermoregulatory strategies vary not only among species but also within species (62-72). In the next section, we focus on variation within and among individuals and populations to see how much insight we can gain from applying the current theory.

### 4.3. Evidence of adaptive thermoregulation in mammals and birds

#### 4.3.1. Effects of energy availability

The rate of feeding affects the optimal strategy of thermoregulation in two ways. First, food consumption directly affects the benefit of thermoregulation. Specifically, a reduction in food simultaneously lowers the thermal optimum for energy gain and the maximal rate of energy gain (Figure 3). Consequently, both the optimal set-point temperature and the net benefit of thermoregulation decrease. Food consumption also indirectly affects the cost of thermoregulation. When food becomes too limited to support growth, thermoregulation would deplete energy stores. A model based on energetic costs and benefits would predict a strategy of poikilothermy, but the non-energetic benefits could favor some thermoregulation even if it results in a net loss of energy (see Section 4.2). Nevertheless, animals likely face risks of mortality as energy stores become depleted. Therefore, a decrease in body condition could cause an animal to thermoregulate less accurately or precisely. Taken together, the direct and indirect effects of feeding lead us to predict a decrease in the mean and minimal body temperatures following food restriction (or an increase in these variables following food supplementation).



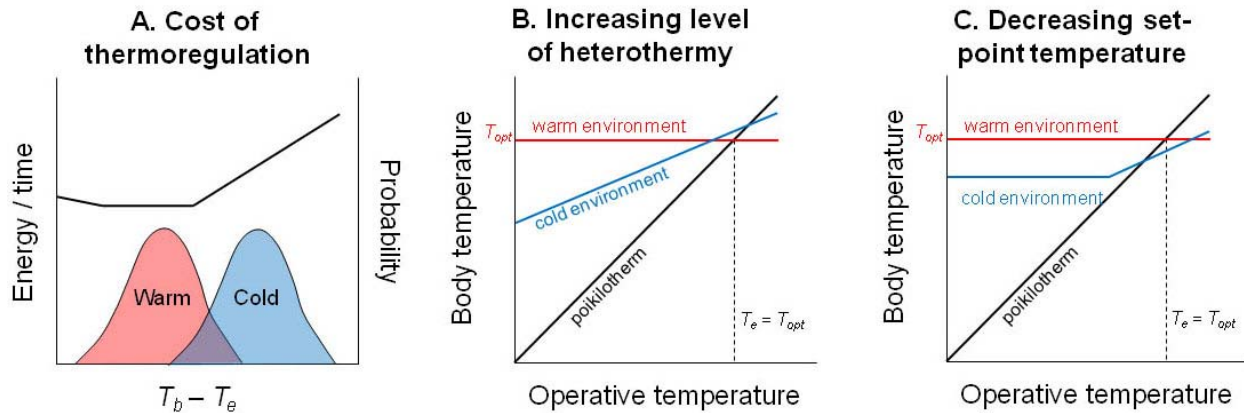
**Figure 4.** The rate of feeding influenced patterns of thermoregulation by Chilean mouse opossums. Animals that consumed a greater percentage of their daily energy requirement exhibited fewer (A) and shorter (B) bouts of torpor. Furthermore, the mean body temperature during torpor increased within increasing energy intake (C). Adapted from Bozinovic *et al.* (77) with kind permission from Springer Science and Business Media. © Springer-Verlag 2007.

Experimental manipulations of feeding rates have generated strong support for the theory of adaptive thermoregulation. Restriction of feeding in mammals and birds generally causes an increase in the frequency and intensity of torpor (65, 73-79). Supplementation of food has the opposite effect. For example, chipmunks whose hoards were enhanced with acorns, sunflower seeds, and peanuts spent less than half as much time in torpor as did

chipmunks with an unmanipulated diet (80, 81). Furthermore, the minimal body surface temperature of supplemented chipmunks was about 7° to 10°C higher than that of control chipmunks. This experimentally induced variation in thermoregulation mirrored natural variation among years that differed in food availability; even during food-rich years, variation in food density among home ranges correlated with the use of torpor (82). In the Chilean mouse opossum (*Thylamys elegans*), the relationship between the rate of feeding and the duration and depth of torpor was roughly linear (Figure 4). In some cases, set-point body temperatures during activity also decreased following food restriction (76, 83, 84). As one might expect, the response to food availability depends on the thermal environment, and hence the time of year. For example, Hiebert (66) restricted feeding by hummingbirds to 70-90% of maximal rates during the spring and the summer; food restriction in both seasons caused birds to become torpid during the night, but the frequency of torpor was greater in spring than in summer. This result suggests that these birds experienced lower energetic costs or greater non-energetic benefits of thermoregulation in the summer.

Laboratory studies of behavioral thermoregulation have provided further evidence that endotherms adaptively respond to food availability. Ostheim (85) created an apparatus that provided access to food for nine seconds whenever a pigeon (*Columba livia*) pecked a key. At the same time, the bird could control the air temperature by flying across light beams that initiated the release of hot or cold air. During the experiment, the potential rate of feeding was progressively lowered by increasing the number of pecks required to access food. Initially, birds increased the duration of feeding to maintain their set-point body temperatures during activity and rest. When feeding became insufficient to maintain body mass, birds decreased their resting body temperatures. After a further loss of mass, birds behaviorally raised the air temperature of their enclosure to 25°C during the night. In a similar experiment, Yoda and colleagues (86) examined the interaction of food deprivation and air temperature on the thermoregulation of rats (*Rattus norvegicus*). Individuals were kept in a cold arena, but could initiate a stream of warm air by entering a specific portion of the arena. The burst of heat lasted 30 s, after which the rat had to leave that area of the arena and then return to reengage the heat source. When the background temperature of the arena was low (3° or 13°C), fed rats spent very little time near the heat source while starved rats repeatedly accessed this area of the arena. When the background temperature of the arena was high (35° or 40°C), both fed and starved rats avoided the heat source. These behaviors enabled rats to keep their body temperatures near 37°C under all conditions. Although these two experiments involved highly artificial environments, they highlight the behavioral and physiological flexibility of thermoregulating endotherms.

Pharmacological manipulations of available energy have provided an independent means of testing the predictions of theory. Several drugs have been used to experimentally lower the actual or perceived supply of energy. Most commonly, 2-deoxy-D-glucose has been used to inhibit the oxidation of glucose, while mercaptoacetate or methyl palmoxirate have been used to inhibit the



**Figure 5.** The probability distribution of operative environmental temperatures affects the cost of thermoregulation. A) The cost of perfect thermoregulation in any particular microenvironment depends on the difference between the set-point body temperature and the operative environmental temperature ( $T_b - T_e$ ). B) In a cold environment, a high cost of thermoregulation can favor heterothermy, as indicated by a change in body temperature with operative temperature. Consequently, body temperature in a cold environment might equal the thermal optimum only at a single operative temperature. C) Alternatively, a higher cost of thermoregulation in a colder environment can favor a lower set-point temperature.

oxidation of fatty acids. In studies of mammals, pharmacologically induced states of glucoprivation and lipoprivation lowered set-point body temperatures (87-89). Glucoprivation also induced torpor (90-92), but lipoprivation had mixed effects on the use of torpor. In placental mammals, lipoprivation via mercaptoacetate did not induce torpor (87, 88, 90), but lipoprivation via methyl palmoixirate induced torpor in some individuals (93). In marsupials, lipoprivation via mercaptoacetate caused an expression of torpor similar to that caused by food deprivation (92). Although mercaptoacetate did not increase the frequency of torpor in placental mammals, this drug did cause bats to select cooler microclimates, which resulted in deeper bouts of torpor (94). The perceived energetic state has been pharmacologically manipulated by supplementing circulating levels of leptin, a hormone produced by adipose tissue (95). Leptin increased the body temperature of juvenile rats, most notably during rest, which in turn reduced the daily amplitude of body temperature (96). Furthermore, leptin eliminated torpor in Siberian hamsters (97) and substantially reduced the duration or depth of torpor in other species (98, 99). These direct manipulations of energetic state bolster the conclusions drawn from indirect manipulations, such as food supplementation and food deprivation.

#### 4.3.2. Effects of air temperature

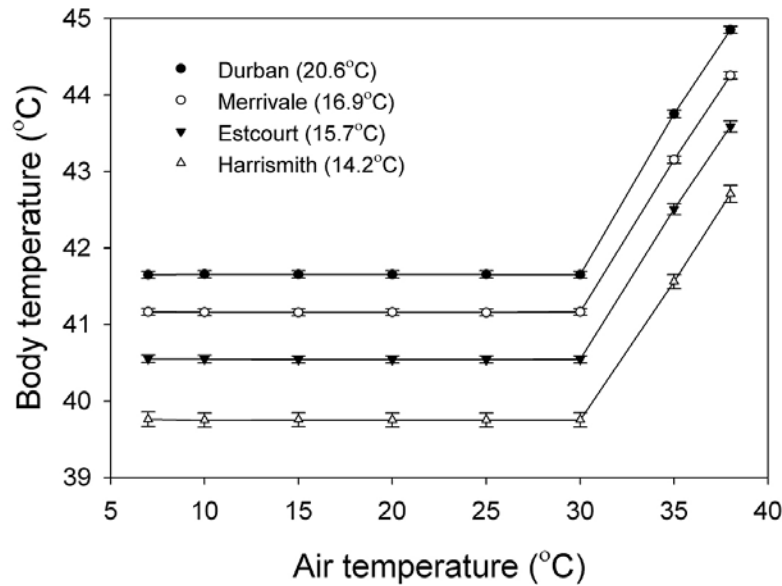
Because operative temperature scales with air temperature (49), the energetic cost of homeothermy increases as the mean air temperature decreases (Figure 5A). Thus, cold environments should favor temporal heterothermy. In the context of Huey and Slatkin's model, this inaccuracy of thermoregulation would be manifested as a positive relationship between operative temperature and body temperature (Figure 5B). Alternatively, we might expect selection to favor a set-point temperature below the thermal optimum for energy gain (Figure 5C). Either strategy would cost less energy

than it would to maintain a set-point temperature that equals the thermal optimum. Both strategies could be interpreted as either hypothermia or torpor, depending on the behavioral or metabolic changes that accompany the change in body temperature (15).

We can determine the support for these predictions by comparing thermoregulatory strategies within and among populations. Changes in air temperature and solar radiation drive temporal and spatial variations in operative temperature (21); therefore, we can make several predictions about the effects of environmental conditions on the accuracy of thermoregulation. Within populations, the accuracy of thermoregulation should decrease during the night, which includes the coolest period of the diel cycle. Furthermore, the accuracy or precision of thermoregulation should decrease as the seasons change from summer to winter. Among populations, body temperatures should vary more in cold environments than in warm environments.

Comparisons of thermoregulatory strategies among seasons have revealed both of the predicted responses to thermal extremes. In cold environments, air temperature will drop below the thermoneutral zone more often during winter than it will during summer. This condition favors a decrease in the accuracy of thermoregulation as the environment cools seasonally. In accordance with this prediction, eastern gray squirrels (*Sciurus carolinensis*) exhibited a greater intensity of nocturnal hypothermia during the winter than they did during the summer (100). Similarly, northern bobwhites (*Colinus virginianus*) lowered their diurnal set-point temperature from 38.9° to 37.7°C between the summer and the winter. Consistent with the pattern depicted in Figure 5C, the body temperatures of bobwhites were unrelated to air temperatures in both seasons (101). In hot environments, the cost of regulating heat loss influences thermoregulation more than the cost of heat production. This condition favors an decrease





**Figure 6.** In some species, environmental temperature affects the set-point body temperature rather than the degree of heterothermy. Fiscal shrikes (*Lanius collaris*) from four sites along an altitudinal gradient in South Africa were homeothermic between 7° and 30°C and were heterothermic at higher temperatures. Despite this general pattern, birds from warmer environments maintained higher set-point temperatures (as in Fig 5C). Error bars depict 95% confidence intervals. The mean air temperature of each site is given in parentheses. Data are from Soobramoney *et al.* (69).

in the accuracy of thermoregulation as the environment warms seasonally. For example, Arabian oryxes (*Oryx leucoryx*) permitted their body temperature to fluctuate more than twice as much during summer days than they did during winter days ( $4.1 \pm 1.7^{\circ}\text{C}$  vs.  $1.5 \pm 0.6^{\circ}\text{C}$ ), presumably because heat storage on hot days minimized energetic and hydric costs (102).

Because morphology interacts with climate to determine the operative temperature of an organism (49), changes in morphology that affect heat exchange should also affect the cost of thermoregulation. For this reason, variation in morphology within and among populations should drive variation in the accuracy of thermoregulation. For instance, smaller individuals should thermoregulate less accurately at low air temperatures when heat loss threatens homeostasis, but should thermoregulate more accurately at high air temperatures when heat gain threatens homeostasis (103). Thus, comparisons within and among populations must account for significant variation in size, shape, color, or insulation among individuals.

A study of springbok illustrates how the phenotype and the environment can interact to influence thermoregulatory strategies (104). The color and absorptivity of a springbok's fur varies from white to black. Darker springbok, which absorb more solar radiation, experience higher operative temperatures in a given environment. Therefore, white springbok will be most likely to experience cold stress, whereas black springbok will be most likely to experience heat stress. In line with this reasoning, diel variation in body temperature increased from summer to winter in white springbok and decreased

from summer to winter in black springbok. Springbok of an intermediate color (tan) experienced no seasonal change in the daily amplitude of body temperature.

Variation in thermoregulatory strategies among populations provides only mixed support for the prediction that endotherms thermoregulate less accurately as energetic costs increase. Shrikes (*Lanius collaris*) from higher elevations maintained lower set-point temperatures, despite that fact that birds from each elevation maintained relatively constant body temperatures at air temperatures ranging from 7-30°C (Figure 6). Likewise, prairie dogs exhibited deeper and longer depressions of body temperature at higher altitudes (70). In contrast to these examples, the relationship between air temperature and body temperature did not differ among populations of stonechats (*Saxicola torquata*) from different latitudes (105). Furthermore, thermoregulatory strategies did not differ between mole rats from high and low altitudes even though metabolic rates did (68). Because these comparisons occurred in the laboratory, the failure to detect variation among populations could reflect plasticity of thermoregulation. A better complement of lab and field studies along latitudinal or altitudinal clines would resolve this issue.

Experimental manipulations of the cost of thermoregulation should control for confounding variables associated with comparative studies. Geiser and Drury (106) lessened the cost of thermoregulation by providing a source of radiation to dunnarts (*Sminthopsis macroura*), small marsupials that often enter torpor. The mean body temperature of resting individuals decreased with

## Evolution of thermal physiology

decreasing air temperature (1.6°C per 10°C), but radiant heating enabled individuals to maintain their body temperatures across the range of air temperatures. Furthermore, heated individuals passively warmed from 21° to 36°C at twice the rate as unheated individuals, which reflected a further reduction in the energetic cost of thermoregulation.

### 4.3.3. Effects of huddling

When mammals and birds live in social groups, they can huddle to conserve energy. Huddling raises the operative temperatures of all individuals in a group by increasing radiative heat gain and decreasing convective heat loss. Consequently, huddling reduces the energetic cost of thermoregulation. Emperor penguins display one of the most impressive examples of this behavior; air temperatures inside tight huddles frequently exceed 35°C when air temperatures outside these huddles are well below 0°C (107). Even in less extreme environments, the ability to huddle should influence thermoregulation. All else being equal, larger groups of individuals should thermoregulate more accurately. This difference could be manifested as either a decrease in heterothermy or an increase in the set-point body temperature with increasing group size (as shown in Figure 5).

Several studies provided concrete evidence that huddling leads to adaptive plasticity of endothermic thermoregulation. Studies of birds focused on patterns of daily torpor in isolated individuals and social groups. In mousebirds (*Colius* spp.), huddling either slowed (108, 109) or prevented (75) cooling during rest. In white-backed mousebirds, cooling slowed as the size of the group increased from 1 to 6 individuals (109). Similarly, woodhoopoes (*Phoeniculus purpureus*) in groups tended to lower their resting body temperatures less than did woodhoopoes in isolation (110). A recent study of seasonal torpor in mammals supported the conclusion drawn from studies of birds. Hwang and colleagues (111) recorded the body temperatures of solitary and grouped skunks during winter. Both the frequency and depth of torpor depended on social conditions. Solitary skunks entered torpor an average of 50 times, whereas grouped skunks did so only six times. Solitary skunks allowed their body temperatures to drop to  $26.8 \pm 0.32^\circ\text{C}$ , whereas grouped skunks dropped to only  $30.9 \pm 0.23^\circ\text{C}$ . Although social living clearly confers thermoregulatory benefits, future research should consider the potential costs, such as greater risks of predation and infection.

### 4.3.4. Effects of water availability

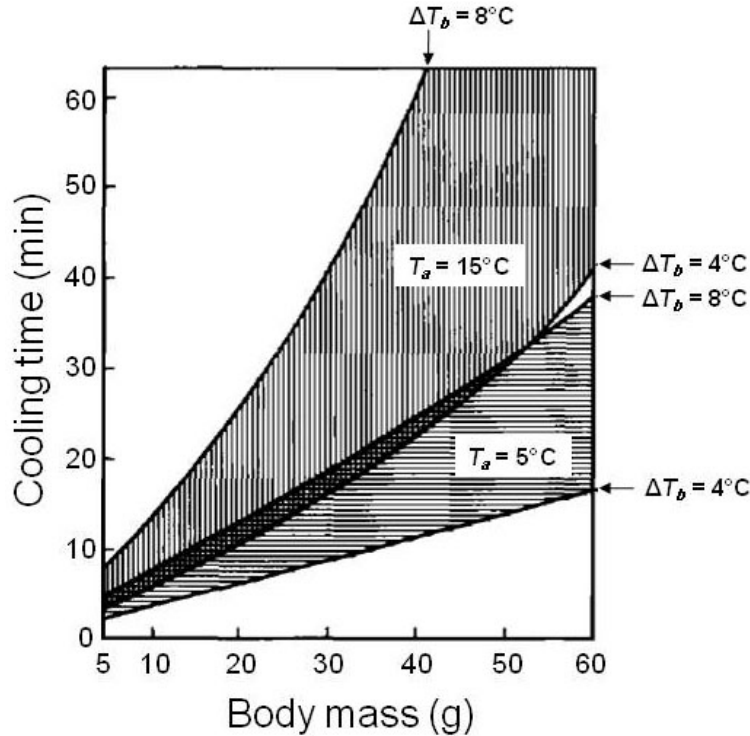
As the operative temperature of the environment approaches the set-point body temperature, an endotherm must shift from conserving heat to dissipating heat. The dissipation of heat depends entirely on evaporative water loss. Terrestrial organisms possess limited capacity for evaporative cooling because dehydration impairs performance and ultimately leads to death. Therefore, the optimal strategy of thermoregulation in a hot environment depends on an individual's state of hydration; more specifically, dehydrated animals should thermoregulate less precisely than hydrated animals, leading to higher maximal daily body temperatures.

Adaptive shifts in thermoregulation during dehydration have been documented in mammals and birds, although this phenomenon has been studied much more extensively in mammals (see reviews by 112, 113). Typically, a period of water deprivation leads to a de-emphasis of evaporative cooling and an increase in the mean or maximal body temperature. For example, emus exposed to 45°C waited twice as long to begin panting when dehydrated than they did when hydrated (114); consequently, the mean body temperature of dehydrated birds exceeded that of hydrated birds (38.7° versus 38.3°C). Similarly, desert ungulates delay the onset of evaporative cooling and permit body temperatures to rise when dehydrated (113). Similar examples of dehydration-induced hyperthermia exist for other wild (115, 116) and domestic mammals (84, 117). When maximal body temperatures increase substantially, some mammals selectively cool their brains. Mitchell and colleagues (112) argued that this behavior inhibits the brain from engaging mechanisms of evaporative cooling, enabling body warming and conserving body water. A study of sheep illustrates the use of this strategy. Without selective brain cooling, hydrated and dehydrated sheep had similar body temperatures. When dehydrated sheep engaged in selective brain cooling, their body temperatures rose higher than those of hydrated sheep (117).

### 4.4. Patterns of avian brooding

Birds commonly brood their offspring during early developmental stages. Brooding raises the temperatures of embryos or chicks (118), which in turn enhances survival, growth, and development (reviewed by 119, 120). At the same time, brooding consumes time and energy that could be used for other purposes. In essence, parents make thermoregulatory decisions for their offspring and incur the associated costs. If we view brooding as a form of thermoregulation, the optimal strategy maximizes the difference between the indirect benefit and the direct cost to the parent. Factors that influence the cost of brooding should affect the mean and variance of the offspring's body temperatures.

The factors that influence the thermoregulation of adult birds also appear to influence maternal brooding. From Section 4.3.2, recall that air temperature directly affects the energetic cost of thermoregulation; warmer environments favor an increase in the accuracy of thermoregulation, exhibited as a decrease in heterothermy or a change in the homeothermic set-point temperature (see Figure 5). Two experiments suggest that this prediction holds for the body temperatures of embryonic birds during brooding. Both experiments involved artificial heating of some nests combined with a control treatment of other nests. Swallows with heated nests spent more time brooding and maintained warmer eggs than did swallows with control (unheated) nests (121). Likewise, sandpipers with heated nests spent nearly one more hour per day brooding than did sandpipers with control nests (122). From Section 4.3.1, recall that individuals with more energy should thermoregulate more accurately. Consistent with this prediction, zebra finches raised on a high protein diet attended their nests more than did finches



**Figure 7.** Body mass determines the time required for a chick to cool from the set-point temperature ( $T_b = 38^\circ\text{C}$ ) to some thermal limit for activity ( $T_b = 34^\circ$  or  $30^\circ\text{C}$ ). For large chicks, a change in the lower limit from  $34^\circ$  to  $30^\circ\text{C}$  more than doubles the time for activity. Calculations are shown for air temperatures ( $T_a$ ) of  $5^\circ$  and  $15^\circ\text{C}$  (horizontal and vertical hatchings, respectively). Adapted from Visser and Ricklefs (139) with permission from the American Ornithologists' Union.

raised on a low-protein diet (123). Finally, species with a higher risk of nest predation visit their nests less frequently, by extending the duration of each on- and off-bout (124). Taken together, these findings support the conclusion that changes in energetic and mortality costs trigger adaptive shifts in brooding behavior. We might significantly advance our understanding of endothermic thermoregulation by tailoring current models to studies of avian brooding.

## 5. THERMOSENSITIVITY

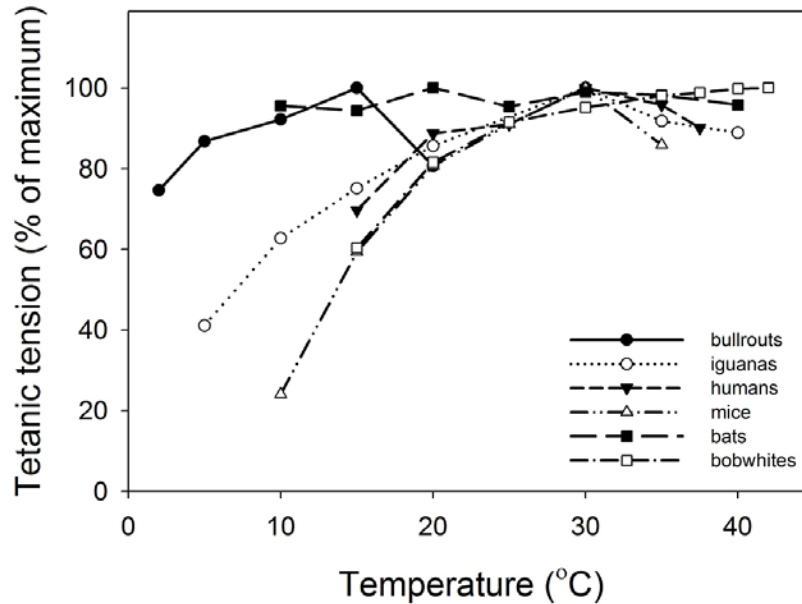
Body temperature determines the capacity for behavioral and physiological performances. This phenomenon has most commonly been documented for ectothermic organisms because of the ease with which one can manipulate their body temperatures. Nevertheless, endothermic organisms experience the same general pattern of thermosensitivity: they perform best over a finite range of temperatures and perform relatively poorly at temperatures beyond this range. In mammals and birds, we can most readily see this thermosensitivity in juveniles, which possess limited potential for endothermic thermoregulation and experience highly variable body temperatures. The best example comes from a pair of studies of young birds conducted by Choi and Bakken (18, 125). These researchers compared the sensitivities of locomotor performance at the organismal and tissue levels. Northern bobwhites ran and jumped faster as their bodies

warmed over the range of  $30^\circ$  to  $42^\circ\text{C}$ . Not surprisingly, their gastrocnemius muscles produced more isometric tetanic force when warmed over a broader range ( $15^\circ$  to  $42^\circ\text{C}$ ). Qualitatively similar sensitivities of locomotor and muscular performances were observed in red-winged blackbirds (*Agelaius phoeniceus*). Logic dictates that performances of ectothermic and endothermic organisms suffer the same thermal constraints, since both rely on proteins and lipids whose structures and functions depend on temperature (26, 126, 127). In fact, studies of rats (128-132), mice (133, 134), rabbits (135) and humans (136-138) indicate that temperature strongly affects cellular performances.

The thermosensitivity of cellular and organismal performances in mammals and birds begs several questions. First, what selective pressures shape the performance curves of endotherms? Second, do populations of endotherms possess the genetic variation in thermosensitivity needed to respond to selection? And finally, what macroevolutionary patterns should we expect to observe among species of mammals and birds? Although we cannot answer these questions at present, we speculate about the answers in the sections that follow.

### 5.1. Do thermoregulatory strategies impose selection on thermosensitivity?

As discussed throughout Section 4, mammals and birds experience diel and seasonal fluctuations in body



**Figure 8.** The thermosensitivity of muscular performance varies among ectothermic and endothermic vertebrates. Data are relative tetanic tensions of muscles or fibers from bullfrogs (148), iguanas (149), humans (150), mice (151), bats (19), and bobwhites (18). Adapted from Rall and Woledge (146) and Choi *et al.* (19).

temperature. The consequences of these fluctuations depend on the thermosensitivity of organismal performances. A thermal specialist would suffer a severe loss of performance when body temperature fluctuates, whereas a thermal generalist would suffer only a mild loss of performance (Figure 1B). Indeed, the lethargy associated with torpor in some species could represent the expected loss of locomotor performance when a thermal specialist cools dramatically. But what if this loss of performance impacts survival or fecundity? Although one could easily envision such a scenario, let's consider a quantitative example to bring the problem into focus. Imagine a precocial chick that alternates between bouts of brooding and foraging. While foraging, the chick's temperature falls steadily according to its biophysical properties. By modeling the cooling of such animals, Visser and Ricklefs (139) discovered that chicks could dramatically extend the duration of foraging if they could tolerate lower body temperatures (Figure 7). If thermosensitivity varies among individuals, some chicks might acquire more food than others. Early differences in food intake affect growth and development, which in turn could influence survival or fecundity. This example should by no means be isolated.

What degree of heterothermy would impose a noticeable selective pressure on thermosensitivity? This seemingly innocent question opens an important and complex line of inquiry. Although all mammals and birds exhibit some degree of heterothermy, their body temperatures vary far less than those of other animals. In some cases, one might even argue that heterothermy has no biologically significant impact on performance. Consider the small degree of diel variation in body temperature exhibited by some species. Body temperatures during the active phase of the diel cycle generally exceed those during

the resting phase (140). For most species studied to date, the amplitude of this cycle does not exceed 3°C (47, 48). Why do these animals bother to warm by such a small margin during activity? Could a difference of a few degrees impact physiological performance enough to affect survival and reproduction? Diel variation might be an unavoidable consequence of heat production during motor activity. However, two pieces of evidence oppose this explanation (48). First, the increase in body temperature actually occurs just prior to activity, rather than at the onset. Second, humans undergo similar cycles of body temperature when abstaining from motor activity. Perhaps diel variation represents a genetic or physical constraint, such as an inextricable link between the neural controls of temperature and activity. But if we refuse to accept an adaptive explanation, we implicitly assume that a slight warming does not enhance performance during activity. If that assumption were true, we should ask ourselves a simple question: why has natural selection failed to lower the mean body temperature by a few degrees? Even this small decrement in body temperature would save energy, which could be used for growth or reproduction. In fact, natural selection should reduce body temperature to the point where a further reduction imposes a performance loss that outweighs the energetic saving. And if natural selection has done so, we should not ignore the possibility that the even small fluctuations in body temperature can impair performance. By corollary, such fluctuations could impose selection for thermal generalization. The challenge will be to uncover which performances have sufficient impacts on survival and reproduction to evolve by natural selection. Digestive, renal, neural, and immunological performances seem like promising choices for investigation. Do endotherms maintain these performances when body temperatures drop, or do they merely sacrifice them during

periods of cooling? At least some species maintain neuromuscular activity at low body temperatures (e.g., see 141, 142-144), suggesting that heterothermy can favor endothermic generalists. Nevertheless, we have much to learn about selective pressures on the thermosensitivities of endotherms.

The evolution of thermosensitivity is further complicated by the fact that some body tissues are warmer than others. Simply put, an organism of reasonable mass cannot simultaneously maintain constant core and surface temperatures; either its core can be defended against thermal fluctuations while its surface temperature varies, or its surface can be defended while its core varies (45). Consequently, tissues in some regions of the body will experience relatively stable thermal conditions while tissues in other regions experience potentially dramatic fluctuations. When surface temperature varies more than core temperature, organs that lie at the periphery of the body, such as skin and muscles, would undergo selection for thermal generalization. At the same time, visceral organs would undergo selection for thermal specialization. The reverse would be true for organisms that defend surface temperature more than core temperature. These considerations lead to a novel prediction: natural selection should produce regional variation in thermosensitivity within individuals that mirrors geographic variation in thermosensitivity within species.

### 5.2. Can thermosensitivity respond to selection?

Even when selective pressures on thermosensitivity exist, evolutionary responses to these pressures require additive genetic variance of thermosensitivity within populations (145). To our knowledge, no one has attempted to quantify the genetic variance of thermosensitivity in a population of endotherms. Yet we have reason to suspect that such variation does exist. In ectotherms, researchers have found some genetic variation in thermosensitivity nearly every time they have looked for it (reviewed by 21, 23). Because the molecular machineries of ectotherms and endotherms resemble one another, they should be subject to similar sources of variation by mutation. Although the magnitude of genetic variation undoubtedly varies widely among populations, some genetic variation in thermosensitivity should exist in any large population.

A comparison of thermosensitivities among mammalian species enables us to infer the potential for evolutionary change. For example, performance curves for muscular contraction vary greatly within and among mammalian species. In a review of published studies, Bennett (17) reports thermal optima for tetanic force that range from 25° to 40°C. Performance breadths also vary among species (19, 146). For example, bats maintained excellent muscular performance between 10° and 40°C, while bobwhites, humans, and mice exhibited strong thermal dependencies; to put these patterns in perspective, mice experienced a nearly five-fold increase in contractile capacity between 10° and 30°C, while bats experienced no statistically significant change over the same thermal range (19). Assuming that some fraction of this phenotypic

variation represents genetic variation, we can view these data as evidence for macroevolutionary patterns of thermotolerance. The existence of such macroevolutionary patterns assures that microevolutionary processes—such as mutation, selection, and drift—have operated in the past. We have no reason to think these processes will cease to shape the thermosensitivities of mammals and birds in the future.

### 5.3. What patterns of thermosensitivity should evolve?

If heterothermy imposes selective pressures on thermosensitivity, how should the performance curves of mammals and birds vary along environmental clines? To answer this question, we must use a model that considers (i) the environmental factor of interest, (ii) the impact of this factor on the distribution of body temperatures, and (iii) the relationship between performance and fitness. Let us consider each of these components in turn.

In Section 4, we identified factors that determine the cost or benefit of thermoregulation, including food availability, air temperature, hydration state, and social behavior. Both temporal and spatial variations in these factors interact to set the optimal thermoregulatory strategy within the bounds defined as homeothermy and poikilothermy. Some of these factors vary predictably over time and space. For instance, animals experience seasonal variations in air temperature and food availability, which are usually more pronounced at higher latitudes. As we discussed in Section 4.3, seasonal and latitudinal variations in these factors affect the use of torpor by birds and mammals. Therefore, we can predict how the distribution of body temperatures should be influenced by changes in thermoregulatory behavior over time and space (see Section 4.2).

The evolution of performance curves depends on the variation in body temperature within and among generations. Variation within generations stems from any degree of heterothermy. Depending on the lifespan of the species, diel, daily, seasonal and annual variations in environmental conditions can increase an individual's variance of body temperature. Diel and seasonal variations are likely more predictable than daily and annual variations. Regardless of its source or predictability, variation within generations increases the range of body temperature that an individual must tolerate. By contrast, variation among generations implies that an individual's descendants must tolerate body temperatures that differ markedly from its own body temperatures. For short-lived species, variation in body temperature among generations stems from seasonal variation in environmental conditions. For annual or longer-lived species, variation in body temperature among generations stems from less predictable climatic events, such as those caused by El Niño and La Niña. As we shall see, quantifying both intragenerational and intergenerational variations in body temperature constitutes an essential step in predicting selective pressures on thermosensitivity.

The selective pressure caused by heterothermy depends on whether the performance of interest contributes

## Evolution of thermal physiology

to survivorship or fecundity. When performance affects survivorship, an individual must exceed some minimal level of performance throughout its entire life; failure to do so results in death. Consequently, variation in body temperature within or among generations favors either genotypes that can perform over a broad range of temperatures (32) or genotypes that can developmentally alter their thermal optimum of performance (33, 36). Such strategies would ensure that a genotype's lineage enjoys a greater geometric mean of fitness over time. When performance affects fecundity, an individual can cease to perform for some period and still reproduce later in life. Consequently, variation in body temperature within generations tends to favor genotypes that can perform over a narrow range of body temperatures (31); the ability to developmentally alter the thermal optimum of performance would favor an additional reduction in the thermal breadth of performance.

Both comparative and experimental approaches have been used to evaluate predictions about the evolution of thermosensitivity (reviewed by 21, 23). For ectothermic species, many researchers have compared sensitivities among genotypes sampled from latitudinal or altitudinal clines. Fewer efforts have been made to document experimental evolution in artificial or natural environments. But to our knowledge, researchers have not used either of these approaches to study the evolution of performance curves in endothermic organisms. The literature contains only a handful of interspecific comparisons (18-20), which lack adequate replication and phylogenetic control. Therefore, we cannot draw sound inferences at this time.

Obviously, the paucity of information about the performance curves of mammals and birds stems from their unique capacity for endothermy. Effective physiological control of body temperature prevents one from readily measuring the thermosensitivity of organismal performance. So how can we test hypotheses about the evolution of thermosensitivity? One solution would be to compare the sensitivities of physiological functions in cells, tissues, and organs. Such studies could be conducted *in vitro* to eliminate the limitations imposed by thermoregulation. The thermosensitivity of muscular performance has been measured in rats, mice, hamsters, bats, cats, and pigs (17). Renal, immune, digestive, and neural functions seem like prime candidates for further studies. This approach would assume that we can ultimately scale from suborganismal performances to organismal ones. Although the validity of this assumption remains undemonstrated, the suborganismal approach seems a reasonable alternative to ignoring this line of inquiry altogether.

## 6. SUMMARY AND PERSPECTIVE

In their provocative review, McKechnie and Lovegrove (9) asked whether the diversity of endothermic physiologies reflects adaptation or constraint. In our minds, this question has a simple answer: endothermic physiologies reflect adaptation within the constraints imposed by genetics, development, and physics (147). The

key to understanding the physiological diversity of endotherms will be to capture these evolutionary constraints in the form of quantitative models. The models that we described here were originally formulated to understand the thermal physiology of ectotherms. Yet, we believe these models provide opportunities for cross-fertilization between subdisciplines, because the selective pressures on thermal physiology should not differ fundamentally between ectotherms and endotherms. Our preliminary effort to apply the models to mammals and birds leads us to draw the following conclusions:

- Both ectotherms and endotherms are heterothermic organisms, even though an endotherm typically experiences a higher mean and lower variance of body temperature.
- Optimality models enable us to conceptually organize empirical patterns of thermoregulation by endotherms; quantitative predictions about thermoregulation require additional information about the performance curves of mammals and birds.
- Regional and temporal heterothermy in endotherms should drive the evolution of thermosensitivity; at present, we know virtually nothing about the thermosensitivity of performance in mammals and birds.
- As we learn more about the thermoregulation and thermosensitivity of endotherms, we should begin to test hypotheses about the coadaptation of these traits.

Despite the similar principles that underlie the evolution of thermal physiology in ectotherms and endotherms, these two groups have taken different evolutionary trajectories. Mammals and birds thermoregulate far more precisely than ectotherms. Even the most heterothermic of species maintains its body temperature above the operative environmental temperature for most of the time. Although set-point temperatures vary predictably with food availability and air temperature, the variation rarely exceeds a few degrees. Theory indicates that a major benefit of precise thermoregulation is the ability to enhance performance through thermal specialization (see Fig 1B). Therefore, we might logically assume that mammals and birds have evolved relatively narrow performance breadths. If this assumption proves correct, the heterothermy of these endotherms would lead to losses of performance during certain periods. Genetic variation in thermosensitivity would enable the evolution of thermal generalists in more heterothermic species. In this way, strategies of thermoregulation and thermosensitivity would coevolve.

Coadaptation should produce a correspondence between thermoregulation and thermosensitivity (41). Two combinations of strategies should confer particularly high fitness: (i) thermal specialists that thermoregulate precisely, and (ii) thermal generalists that thermoregulate imprecisely (24). If we think of these phenotypes as two ends of a continuum, mammals and birds seem to lie more toward the specialist end of this continuum than do ectothermic animals. But three questions regarding the evolution of

thermal physiology remain entirely unresolved. First, do mammals and birds really possess narrower performance breadths than do ectothermic animals? Second, have populations within mammalian and avian species diverged along the phenotypic continuum? Finally, which environmental factors cause the selective pressures that move populations toward either extreme? These questions should guide future research on the evolution of thermal physiology.

A successful theory of thermal adaptation must consider both the costs and the benefits of thermoregulation. Current theory holds that the metabolic efficiency of thermal specialization and the thermodynamic advantages of high temperature promote selection for homeothermy (see Section 4.2). Nevertheless, serious energetic costs offset these benefits, which must impose selection for heterothermy in some populations. The net benefit of thermoregulation determines whether specific environments favor homeothermic specialists or heterothermic generalists. Continued efforts to quantify the costs and benefits of endothermy will ensure that we never revert to the view that body temperature represents a nonadaptive constant.

## 7. ACKNOWLEDGEMENTS

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