Adaptive Thermoregulation in Endotherms May Alter Responses to Climate Change

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Synopsis  Climate change is one of the major issues facing natural populations and thus a focus of recent research has been to predict the responses of organisms to these changes. Models are becoming more complex and now commonly include physiological traits of the organisms of interest. However, endothermic species have received less attention than have ectotherms in these mechanistic models. Further, it is not clear whether responses of endotherms to climate change are modified by variation in thermoregulatory characteristics associated with phenotypic plasticity and/or adaptation to past selective pressures. Here, we review the empirical data on thermal adaptation and acclimatization in endotherms and discuss how those factors may be important in models of responses to climate change. We begin with a discussion of why thermoregulation and thermal sensitivity at high body temperatures should be co-adapted. Importantly, we show that there is, in fact, considerable variation in the ability of endotherms to tolerate high body temperatures and/or high environmental temperatures, but a better understanding of this variation will likely be critical for predicting responses to future climatic scenarios. Next, we discuss why variation in thermoregulatory characteristics should be considered when modeling the effects of climate change on heterothermic endotherms. Finally, we review some biophysical and biochemical factors that will limit adaptation and acclimation in endotherms. We consider both long-term, directional climate change and short-term (but increasingly common) anomalies in climate such as extreme heat waves and we suggest areas of important future research relating to both our basic understanding of endothermic thermoregulation and the responses of endotherms to climate change.

Introduction

Anthropogenic climate change is one of the greatest conservation issues facing biologists, land stewards, and governments and has become a central topic in biological research. Considerable effort is being invested in determining the best methods to measure the current impacts of climate change and model the future effects (Chown et al. 2010). One of the most obvious results of climate change is that environmental temperatures are changing at a rate much faster than seen during natural climatic fluctuations (IPCC 2007). Rapidly changing environmental temperatures will alter the selective pressures acting on all animals because temperature is one of the most important factors affecting energy and water balance; thus, climate change has the potential for severely affecting the fitness of many species. Despite the crucial role of energy balance in determining fitness and the feasible impacts of climate change on energy balance, ecological physiology (the field of study most directly concerned with environmental effects on energy expenditure) has been underutilized until recently (Helmuth et al. 2005; Chown et al. 2010).

Endothermic species (at least classically defined homeotherms) are often thought to maintain relatively high body temperatures ($T_b$) within a narrow range by means of heat produced from metabolic processes. Endothermic metabolic rates are several times higher than those of ectotherms, and metabolic heat production is regulated in response to
environmental temperature fluctuations (adaptive thermogenesis; Lowell and Spiegelman 2000). This specialized form of thermoregulation means that controlling $T_b$ constitutes a large portion of the energy expended by endotherms when environmental temperatures ($T_a$) deviate from the thermoneutral zone (TNZ) (McNab 2002). Thus, climate change and the associated warming trend found in many areas may strongly affect endotherms (especially terrestrial mammals and birds) and it may have a fundamentally different impact on endotherms than on ectotherms. Thermoregulatory flexibility may afford multiple pathways for ectotherms to cope with a changing climate. Some endotherms, on the other hand, may be so thermally specialized that their only option is to increase energy expenditure to maintain a constant $T_b$ as $T_a$s increasingly deviate from the animal’s TNZ, thereby lessening energy available for other fundamental functions such as growth and reproduction. This oversimplified view of endothermic thermoregulation echeos an historically prominent view (Scholander et al. 1950), but it is gradually being replaced as additional research suggests adaptive variation in $T_b$ is common among endotherms.

In a recent paper, Angilletta et al. (2010) defined adaptive thermoregulation as any thermoregulatory pattern that is launched to counteract an environmental stressor, whether that pattern arises from genetic changes across generations (i.e., adaptation) or phenotypically plastic responses within a lifetime (i.e., acclimatization). Predictions about adaptive thermoregulation in endotherms can be made by expanding the framework commonly used in the literature on ectotherms (Huey and Slatkin 1976; Angilletta et al. 2006). They argued that performance in endotherms is related to $T_b$ in a manner similar to performance in ectotherms and can therefore be described using thermal performance curves. A performance curve describes the nonlinear relationship between some physiological trait, in this case $T_b$, and a measure of performance. A performance curve can be described by the maximal level of performance, the optimal $T_b$ for performance, the performance breadth, and the minimum and maximum critical $T_a$s (Fig. 1). The relative characteristics of a species’ performance curve will describe how a species reacts to changes in $T_a$ and thus provides a convenient framework in which to make predictions about when and why an endotherm should allow its $T_b$ to vary. Their stated goal was to provide a general conceptual framework of thermoregulatory patterns in endotherms. Here, we attempt to apply these ideas to the problem of predicting the effects of climate change on endotherms.

Our goals in this article are 3-fold. First, we briefly review the themes found in current literature predicting the responses of endotherms to climate change, focusing on studies that have a physiological component. Second, we review the available literature on the responses of endotherms to high $T_a$s. Finally, we discuss how the effects of climate change on endotherms will vary with varying thermal physiologies, using the concepts of thermoregulation and thermal sensitivity, as well as co-adaptation between them.

Previous research on responses of endotherms to climate change

As interest in the effects of climate change has increased over the past two decades, the number of studies on responses of mammals and birds to a generally warming climate has grown steadily. As with other organisms, most studies have employed a correlative approach, which focuses on changes in the environment and not on specific characteristics of the organisms of interest (Kearney and Porter 2009; Buckley et al. 2010). These models assume that a species’ multidimensional niche space is fixed and that the subset of climatic conditions an organism currently occupies is an accurate predictor of its range under future climates, i.e., an organism will shift its range to find suitable habitat as climate changes. For example, many studies have used...
climate-envelope models to predict shifts of range in endotherms (e.g., Thomas and Lennon 1999; Both and Visser 2001; Parmesan 2006; Coetzee et al. 2009). Generally speaking, these studies have reported latitudinal shifts (generally poleward shifts), altitudinal shifts, or range contractions, in response to climate change. Other papers have reported phenological shifts (especially migrants arriving earlier) in endothermic species (e.g., Inouye et al. 2000).

Of more interest herein are papers that have focused on physiological processes underlying responses to climate change by endotherms, which are rare compared to papers taking this approach with ectotherms (Helmuth et al. 2005). Such mechanistic approaches can be directly contrasted to the simple correlative models described above because they include biophysical, physiological, behavioral, or ecological characteristics of the organism of interest in addition to information about the environment. Mechanistic models have many advantages over simple correlative methods, but are more complex and thus more difficult to parameterize (Helmuth et al. 2005; Buckley 2008; Helmuth 2009; Buckley et al. 2010; Fuller et al. 2010; Kearney et al. 2010). While they are still relatively rare compared to correlative approaches, there has been a recent increase in the number of papers using mechanistic approaches to predict the effects of climate change on endotherms by examining physiological characteristics of the organism and some interaction between these characteristics and environmental characteristics (e.g., Humphries et al. 2002; Humphries et al. 2004; Monahan 2009; Kearney et al. 2010; McKechnie and Wolf 2010; Molnár et al. 2010; Porter et al. 2010).

To date, authors of such mechanistic models have viewed physiological traits as fixed within an individual and species, and the possibility of adaptive physiological responses as climates change have rarely been considered (Atkins and Travis 2010; Chevin et al. 2010; Chown et al. 2010). While these static models may offer more information than do correlative approaches, the next progression in these models will be to include genetic adaptation within populations, intraspecific and interspecific variation in physiological traits, and the possibility of within-individual acclimatization to a changing climate. A number of studies have shown some level of genetic adaptation in response to recent climate change (Bradshaw and Holzapfel 2006; Bradshaw and Holzapfel 2008; Husby et al. 2011), but data are still relatively limited, especially with respect to how fast physiological traits can respond to changing environments. Endotherms show considerable variation in traits related to physiological maintenance, such as energetic requirements (metabolic rate), thermoregulation, and thermal tolerance, and we argue that the potential for traits being flexible in response to changing environments (including both genetic changes in populations as well as within-individual plasticity of traits), needs to form an intricate part of predicting species’ responses.

The co-adaptation of thermoregulation and thermal sensitivity in endotherms

The idea that performance of all systems from biochemical to organismal should be affected by temperature is not new. One possible advantage of endothermy, and more specifically homeothermy, is that maintaining a narrow range of $T_b$ allows biochemical systems to perform maximally at normal $T_b$ (Heinrich 1977; Hochachka and Somero 2002). However, maintaining a high and constant $T_b$ is energetically expensive and thus we should expect some variation in $T_b$, either temporally or regionally within the body, for all endotherms (Arnold et al. 2004; Angilletta et al. 2010). If variation occurs in all endotherms, we should further expect thermoregulation and thermal sensitivity (i.e., the magnitude of change in a measured performance across a range of $T_b$s) of an organism to be co-adapted in a way that maximizes fitness. In other words, the optimal temperature for performance should coincide with the most commonly displayed active $T_b$ and thermal specialists (i.e., species strongly affected by changes in $T_b$) should maintain a relatively narrow range of $T_b$s while thermal generalists (i.e., species weakly affected by changes in $T_b$) should display larger fluctuations in $T_b$ (Levins 1968; Huey and Hertz 1984; Angilletta et al. 2006; Angilletta et al. 2010). Thus, a specialist–generalist trade-off may exist with specialists performing at a high level at a specific $T_b$ while generalists perform at some lower level, but across a wider range of $T_b$s. Differing environmental pressures will change the relative benefit of being a specialist as opposed to being a generalist thermoregulator. As a point of clarification, we do not view thermal specialists and thermal generalists as a true dichotomy of thermoregulatory patterns. Instead, we view the thermoregulatory landscape as a continuum and use the terms “specialist” and “generalist” only in relative terms. While it may be argued that these terms are interchangeable with “homeotherm” and “heterotherm”, we only use those terms when specifically discussing past research based on those definitions because of the inherent
baggage they have accumulated over many years of research.

Biochemical rates have a thermal optimum at which the activities of enzymes are maximized (Daniel et al. 2010), and it may be that thermal optima of enzymes and, hence, performance are matched to the modal $T_b$ in homeothermic species (Morrison et al. 2008). Humans are a good example of a species in which $T_b$ is tightly regulated, and in which performance in muscle, neurobehavioural, and cognitive functions co-vary with $T_b$ to be maximal at the active $T_b$ (Kleitman et al. 1938; Kleitman and Jackson 1950; Wright et al. 2002; Dodd et al. 2006; Racinais and Oksa 2010). Data from humans have likely contributed to the rise of the paradigm that performance is optimized at the $T_b$ most commonly experienced by organisms. Surprisingly, however, this paradigm remains largely untested in other endotherms, and data on the relationship between thermal performance breadth and thermoregulatory patterns are sparse. Tissue-level examinations have revealed that interspecific variation occurs in the thermal breadth of muscle performance (e.g., Bennett 1984; Choi et al. 1998), and while it appears qualitatively that the thermal breadth of muscle performance increases as the level of heterothermy expressed by a species increases, explicit tests are still needed to verify this conclusion (Angilletta et al. 2010). Other functions, such as immune responses, are also likely to vary with thermoregulatory patterns and we would expect species with large variation in $T_b$ (e.g., hibernators) to be able to mount at least some immune response across a wider range of $T_b$s than could a species exhibiting small variations in $T_b$ (e.g., daily heterotherms). There is evidence that hibernators greatly reduce, but probably do not completely abandon, immune function during hibernation (Bouma et al. 2010); however, comparative data across species displaying a range of thermoregulatory patterns are lacking.

The effect of $T_b$ on whole-organism performance has received relatively little attention in endotherms, although it might be possible to draw some conclusions by examining muscle-level performance. For example, in humans, a decrease in $T_b$ strongly affects performance; for example, a 1°C decrease in muscle temperature corresponds to a 2–5% decrease in performance (Racinais and Oksa 2010). In contrast, Wooden and Walsberg (2004) showed that $T_b$ did not affect running speed or force production in highly heterothermic round-tailed ground squirrels (Spermophilus tereticaudus) across a wide range of tested $T_b$s ($\sim$30–42°C). Future work in this area is obviously important, but will likely require pharmacological manipulations, especially in homeotherms, to test performance across a wider range of $T_b$s.

With the exception of these few studies, which support the idea of co-adaptation of thermoregulation and thermal sensitivity in endotherms, no explicit work has been carried out on the subject, despite the important role this relationship might play in modeling the effects of climate change on endotherms. While we can provide no new evidence that thermoregulation and thermal sensitivity are co-adapted in endotherms, we do attempt to provide some of the groundwork for such experiments. Specifically, we hope to fill a gap left by Angilletta et al. (2010) on the possibility of an individual or species adaptively altering thermal sensitivity in response to thermal stress. If physiological responses to high temperatures and heat stress are adaptive in endotherms, there should be some variation in physiological responses among individuals, populations, and species to $T_a$ above the TNZ (although variation may also occur for nonadaptive reasons). In other words, variation in thermoregulatory responses is necessary (but not sufficient) evidence of adaptive alterations in thermal sensitivity in endotherms under thermal stress. Here, we focus on the limited evidence for variation in response to high temperatures because they will be more applicable to climate change, although a similar exercise would also be useful in reference to low temperatures.

**Evidence of variation in thermal sensitivity at high temperatures**

**Tolerance of high body temperatures**

Endotherms must respond to temperatures above the TNZ by either increasing $T_b$ or thermoregulatory effort to maintain a constant $T_b$ within the preferred range. It is unclear whether endotherms will be able to shift their ranges fast enough to avoid such $T_b$s, especially given that relatively small changes may be highly detrimental to some species (Tewksbury et al. 2008). Thus, it is important to consider responses to high $T_b$s. Facultative increases in $T_b$ in response to high $T_a$ are relatively widespread among birds (Tieleman and Williams 1999), with reported values for $T_b$ during facultative hyperthermia varying between 41.1°C and 45.8°C among species (Tieleman and Williams 1999). However, far less is known about upper lethal limits or how physiological performance decreases with increasing $T_b$. Dawson (1954) found that towhees (Pipilo spp.) lost the capacity for coordinated movement at $T_b >45°C$ and died at $T_b \approx 47°C$. Lethal $T_b$ values for four breeds of
chicken were in the range of 45.9–46.2°C (Arad and Marder 1982), although higher values ranging from 46.0 to 47.8°C have also been reported (Randall 1943). California Quail (Lophortyx californicus) tolerated $T_b = 46°C$ for short periods (Brush 1965), and Common Starlings (Sturnus vulgaris) exhibited $T_b = 45.8°C$ at $T_a = 45°C$ (Dmi’el and Tel-Tzur 1985). Lethal $T_is$ for mammals appear generally lower than those for birds: 43.4°C, 42.5°C, and 41.7°C for rabbits, rats, and dogs, respectively (Adolph 1947), 41.9°C in a single long-nosed bat (Leptonycteris yerbabuenae) (Carpenter and Graham 1967), and 43.5°C in Antrozous pallidus, Tadarida brasiliensis, and Myotis yumanensis (Licht and Leitner 1967).

**Tolerance of high environmental temperature**

There also appears to be considerable interspecific variation in the extent to which endotherms can tolerate high environmental temperatures. In birds, for instance, fatal hyperthermia in towhees exposed to $T_a$ of 39–43°C (Dawson 1954), and Zebra Finches exposed to $T_a$ of 45–46°C (Cade et al. 1965) contrasts with the maintenance of $T_b < 42.5°C$ in Houbara Bustards exposed to $T_a$s of 50–55°C (Tieleman et al. 2002), and $T_is$ of 41–42°C at $T_a = 60°C$ in heat-acclimated Rock Doves (Marder and Arieli 1985). Henderson (1971) noted that Gambel’s Quail (Lophortyx gambelli) survived short-term exposure to $T_a = 45°C$ better (two of three birds) than did Scaled Quail (Callipepla squamata) (one of five birds). Likewise, behavioral responses to hot weather can show striking variation among species. Birds breeding in the Salton Sea during summer experience extremely high $T_a$ and a lack of shaded microsites (Grant 1982). At this site, charadriiform adults shared incubation duties, relieving each other more frequently during the hottest part of the day, thereby allowing for more frequent visits to water for drinking and belly-soaking (Grant 1982). In Black-necked Stilts, for instance, the average length of an incubation bout decreased from 57 min at $T_is$ of 15–20°C to just 13 min at $T_is$ of 40–44°C (Grant 1982). In stark contrast, female Lesser Nighthawks incubated throughout the day without leaving the nest to drink or belly-soak, even during extremely hot weather (Grant 1982), suggesting a high tolerance for dehydration and/or a pronounced capacity for facultative hyperthermia.

The capacity of caprimulgids to tolerate extremely high environmental temperatures has been noted by several authors (Bartholomew et al. 1962; Dawson and Fisher 1969; Grant 1982). Since this group of birds is also one of the most heterothermic avian taxa (Brigham et al. 2000; McKechnie et al. 2007), we asked whether the caprimulgids’ capacity for heat tolerance reflects a generalist $T_b$ phenotype, with caprimulgids exhibiting labile $T_b$ both above and below the normothermic range. Somewhat surprisingly, the limited data available suggest the opposite, with caprimulgids tending to defend $T_b$ within a narrower range of values in very hot environments than do many other species. Spotted Nightjars (Eurostopodops argus), for instance, defended $T_b < 43°C$ even at $T_a > 50°C$ (Dawson and Fisher 1969). This leads to several important questions about the characteristics of thermal performance curves that should be addressed for endotherms. First, is the entire performance curve of a generalist species shifted toward colder $T_is$s compared with thermal specialists, such that the lower critical limit, upper critical limit, and thermal optimum are all lower than those of specialists (Fig. 2A)? Conversely, are thermal generalists able to maintain a wider overall range of $T_is$s, such that the lower critical limit is lower, and the upper critical limit higher, than in specialists (Fig. 2B)? No explicit tests have been conducted on this topic, but published literature may give some clues. In a comparison of responses to heat stress by four similarly-sized species of bird, Lasiewski and Seymour (1972) found that the Common Poorwill (Phalaenoptilus nuttalli), a highly heterothermic species, exhibited much smaller increases in $T_b$ at $T_a > 40°C$ than did three other more homeothermic species, namely Village Weavers (Ploceus cucullatus), Chinese painted quails (Exsclactoria chinensis), and Inca doves, (Scardafella inca), apparently as a result of a higher ratio of evaporative heat loss to metabolic heat production. The observations that a highly heterothermic group of birds (i.e., caprimulgids) appears to maintain lower $T_b$s during heat stress than do many less heterothermic groups suggests that upper critical limits of thermal generalists might be lower than those of specialists (Fig. 2A).

Among mammals that inhabit hot sub-tropical deserts, large species that cannot avoid high $T_is$s by seeking shelter in microsites such as burrows may regularly endure $T_is$ values well above their $T_b$. In these species, thermoregulatory responses to very hot weather primarily involve increases in the amplitudes of circadian $T_b$ cycles, rather than increases in mean $T_b$ (Taylor 1969; Ostrowski et al. 2003; Ostrowski and Williams 2006; Hetem et al. 2010). Air temperatures $\geq 40°C$ were associated with circadian $T_b$ cycles of 6°C in captive Beisa oryx (Oryx gazelle beisa) (Taylor 1969), 7.7°C in free-ranging...
Arabian oryx (*Oryx leucoryx*) (Hetem et al. 2010), and 2.3 °C in Arabian sand gazelles (*Gazella subgutturosa marica*) (Ostrowski and Williams 2006). However, we are not aware of data showing interspecific or intraspecific variation in tolerance of high environmental temperature in large mammals.

It appears that considerable variation exists in the thermal responses of endotherms above the TNZ. Again, this is necessary, but not sufficient, to argue that the responses are adaptive. Unfortunately, evidence is still too scarce to determine whether this variation occurs in predictable ways, as would be expected given the past selective pressures on a population or species, or if the variation is driven by phylogenetically-related differences in the cellular functioning among species, for example, in the composition of membranes and the expression of heat shock proteins (Hazel 1995; Feder and Hofmann 1999). When considering the possibility that responses are adaptive, it is important to consider both large-scale climatic effects and local ecological effects. For example, large mammals such as ungulates in desert environments might *a priori* be expected to exhibit more pronounced thermoregulatory responses to high temperatures simply because they have little choice but tolerate them, whereas small mammals can avoid them by using cool microclimates.

**What patterns of thermoregulation and thermal sensitivity should we expect among endotherms?**

The concept of co-adaption between thermoregulation and thermal sensitivity has been well studied in ectotherms (Angilletta 2009; Kingsolver 2009) and to a lesser extent in homeothermic endotherms (especially humans) (Benzinger 1961; Wright 2002). However, few attempts have been made to generalize the concept to encompass all endothermic species across the entire gradient of thermoregulatory patterns (Angilletta et al. 2010). In very general terms, homeothermic individuals, populations, or species should have narrower thermal performance curves than do heterothermic individuals, populations, or species. Thus, a hibernator should be able to maintain some level of performance (even if it is very low) over a wider range of $T_b$'s than should a highly homeothermic species. Likewise, if expression of the trait is highly plastic, the performance breadth should widen during the season in which the animal displays the widest range of $T_b$, which can vary even within a species (Hetem et al. 2009).

An interesting comparison of the relationships between thermal sensitivity and thermoregulation may also come from examining species with varying migratory patterns. Highly migratory or nomadic species should largely avoid harsh environmental conditions and periods of low availability of energy; thus, we expect these species to display performance curves with narrow breadths. Conversely, nonmigrants must cope with a wider range of $T_b$'s and availabilities of energy, and should therefore be less sensitive to changes in $T_b$. If thermoregulation and thermal sensitivity are co-adapted, we would therefore expect migrants to be relatively less heterothermic compared to closely related nonmigratory species. Note that the presence of heterothermic migrants (e.g., hummingbirds and some bats) does not negate this prediction. If fact, it will be of interest to determine whether the most migratory species in these groups are also the most thermally specialized.

![Fig. 2](https://academic.oup.com/icb/article-abstract/51/5/676/627708)

Fig. 2 A trade-off may exist such that a thermal specialist can perform at a high level, but across a narrow range of body temperatures while a thermal generalist can perform across a wide range of body temperatures, but at a low level at all temperatures. Research is needed to determine the relative characteristics of the performance curves describing generalist and specialist endotherms. This figure represents two examples of how the relative characteristics may vary.
Can characteristics of thermal performance be used to predict relative responses to climate change?

Thermoregulation, thermal sensitivity, and the co-adaptation of the two will play an important role in how populations or species of endotherms will respond to a changing climate. For example, others have speculated that plasticity of physiological responses used by heterothermic endotherms might put them at a competitive advantage over homeothermic endotherms in a changing environment (Canale and Henry 2010). Bioenergetic models suggest that seasonally heterothermic mammals may increase in abundance relative to homeothermic species as rising temperatures allow hibernators to shift into some high latitude areas (Humphries et al. 2004) and phylogenetically-independent analyses suggest that heterothermic thermoregulation might lead to decreased risk of extinction (Liow et al. 2009). Such discussions about how variation in thermoregulatory characteristics will affect a species’ response to climate change are important and lead us to ask several deceptively simple questions: Will sympatric endotherms with different thermal characteristics display different responses to a warming climate? What roles will future adaptation and phenotypic plasticity play in responses by endotherms and what are the limits of these factors in mediating responses to climate change? What effects can we expect short-term, but increasingly common, anomalies in weather to have on endotherms?

Here, we ask what effect differences in thermal characteristics of species will have on the species’ responses to climate change. For simplicity, let us first assume that thermal performance curves do not vary intraspecifically and that endotherms have no capacity to adapt or acclimatize to climate changes in the future (i.e., thermal performance curves are fixed, at least relative to the speed of environmental change) and that two species in the same environment experience change in the same way. These are likely unrealistic assumptions (Jiguet et al. 2010; Sears and Angilletta 2011), but these simplifications provide a convenient starting point for the discussion. Several factors may affect these responses, including the relative characteristics of the thermal performance curves of the species in question. For example, assume that a single value of $T_b$ represents the thermal optimum of both a thermal specialist and a thermal generalist, but they differ in thermal breadth. The principles of Jensen’s Inequality (Ruel and Ayres 1999; Martin and Huey 2008; Boyles and McKechnie 2010) predict that the skewed relationship between $T_a$ and thermal performance may lead to a larger relative decrease in performance in a thermal specialist than in a thermal generalist as $T_b$ exceeds the optimum. In this scenario, the specialist may have to increase the time and/or energy spent on thermoregulation substantially, whereas the generalist may have to spend less time and/or energy on thermoregulation, thereby gaining a relative advantage over the specialist. Thus, either long-term directional increases in $T_a$ or short-term weather events that drive $T_a$ above the TNZ should favor generalist thermoregulators over their more specialized competitors.

The response will also vary according to the seasonal timing of increases in temperature associated with climate change. If it is during summer in a warm area where $T_a$s are likely to be within or above the TNZ, warmer environmental temperatures will necessarily cause either an increase in $T_b$ or an increase in the energy or time (or both) devoted to thermoregulation to maintain $T_b$ near optimal levels. Therefore, the relative responses should be similar to those described above. Conversely, if the increases in temperature occur during winter or in temperate regions (IPCC 2007) when $T_a$s are below the TNZ, a thermal specialist could gain an advantage relative to a thermal generalist because the time and energy required to maintain $T_b$ within a narrow range will decrease, which is likely to be more beneficial to homeothermic species than to heterothermic species.

These predictions can be extended to shifts in range as well. For example, in a hot desert environment, an increasing maximum $T_a$ may exert stronger selective pressure on a thermal specialist than on a generalist, making a shift in range more likely for the specialist. In environments in which endotherms experience both $T_a>T_b$ and scarce, unpredictable water resources, the physiological conflict between evaporative cooling and conservation of water will exacerbate selective pressure on thermal specialists that maintain $T_b$ within a very narrow range. Conversely, a warming winter in a cold temperate climate may impose a cost on a generalist (e.g., if it warms enough to make torpor less efficient energetically but not warm enough to allow heterotherms to completely avoid it) while lessening the pressure on specialists (e.g., by lessening the cost of maintaining a high $T_b$). In this scenario, the generalist species is likely to gain more benefit from a poleward shift in range than is the specialist.
The role of phenotypic plasticity
Acclimation and acclimatization

Mammals and birds exhibit considerable phenotypic plasticity in physiological parameters related to thermoregulation. Most of the available data focus on phenotypic flexibility (i.e., short-term, reversible phenotypic adjustments), rather than on developmental plasticity (i.e., nonreversible developmental adjustments) (Piersma and Drent 2003). Phenotypic flexibility has been most commonly investigated in the context of acclimation or acclimatization to cold; many mammals and birds respond to cold environments by increasing the capacity for heat production (Klingenspor et al. 1996; McKechnie 2008; Glanville and Seebacher 2010b), although in mammals the direction of seasonal body mass and metabolic adjustments is strongly related to body mass (Lovegrove 2005). However, phenotypic flexibility manifested through acclimatization can also potentially influence endotherms’ capacity to tolerate high environmental temperatures in several ways. First, endotherms may be able to increase mean normothermic $T_b$ in response to hot environments. Such a response would be particularly advantageous if the thermoregulatory system were ineffective in maintaining $T_b$ within a normothermic range. There is some evidence that $T_b$s change in response to acclimation temperatures (Shido et al. 1989; Shido et al. 1991; Buono et al. 1998; Glanville and Seebacher 2010a), but the overall picture that emerges is that acclimation to heat does not lead to increases in mean $T_b$ and in fact often leads to the opposite. Human subjects acclimated to exercising in a hot, humid environment ($T_a = 35^\circ C$, 75% relative humidity) exhibited a small but significant decrease in $T_b$ during rest, which was correlated with lower $T_b$ at the end of exercise sessions (Buono et al. 1998). Lower $T_b$ may be advantageous by improving at least aerobic exercise performance (Ranalli et al. 2010). In birds, the available evidence also suggests that phenotypic adjustments to heat do not involve increases in $T_b$. Heat-acclimated chickens maintained lower $T_b$ than did control birds (Hillerman and Wilson 1955), and heat-acclimated White-winged Doves maintained lower $T_b$ at $T_a = 45^\circ C$ than did individuals acclimated to room temperature (McKechnie and Wolf 2004). These data suggest an endothermic thermoregulatory system is generally effective in maintaining normothermia at high temperatures.

An endotherm’s hydration state should also be important in the expression of facultative hyperthermia (Angilletta et al. 2010), although data on the role of water in thermoregulation are rare (especially in free-living endotherms). Hydrated endotherms should be able to maintain $T_b$ within a narrow range, but if water is scarce it may become more beneficial to allow $T_b$ to increase at higher temperature, thereby reducing the risk of dehydration. Thus, a second way in which heat acclimation or acclimatization may affect endotherms are alterations to heat-loss avenues which, in at least some birds, concerns the partitioning of evaporative heat loss into respiratory and cutaneous components. Columbiform birds (doves and pigeons), in particular, appear to be able to significantly vary the relative contributions of respiratory and cutaneous avenues of evaporative heat loss (Hoffman and Walsberg 1999; McKechnie and Wolf 2004). In desert White-winged Doves (Zenaida asiatica mearnsii), heat-acclimated individuals exhibited significantly higher rates of cutaneous evaporative water loss (CEWL) than did individuals acclimated to room temperature, with these responses reflecting reduced cutaneous resistance to diffusion of water vapor in heat-acclimated birds (McKechnie and Wolf 2004). The benefit of higher CEWL in these doves appeared to relate to the energetic cost of increasing respiratory evaporative water loss (REWL) through mechanisms such as panting and gular flutter; at $T_a = 45^\circ C$ the metabolic rate of heat-acclimated doves was 35% lower than that of cool-acclimated birds (McKechnie and Wolf 2004). Avian adjustments in CEWL are driven by changes in the skin’s structure and lipid composition (Menon et al. 1988, 1989, 1996; Peltonen et al. 1998; Haugen et al. 2003) and by adjustments in blood flow that result in elevated hydrostatic pressures in the skin’s microvasculature (Ophir et al. 2002).

Facultative hyperthermia

As noted above, some birds and mammals respond to very high $T_a$s by means of facultative, reversible periods of hyperthermia during which $T_b$ increases above normothermic values, and which serve to reduce evaporative water loss by reducing the $T_a$–$T_b$ gradients that need to be maintained by evaporative heat loss. In mammals, these responses may involve increased amplitudes of circadian $T_b$s with increases in diurnal $T_b$ as well as decreases in nocturnal $T_b$ (Taylor 1969; Ostrowski and Williams 2006; Hetem et al. 2010).

In the most thorough recent review of this avian facultative hyperthermia, Tieleman and Williams (1999) critically evaluated laboratory studies in which avian EWL was measured at $T_a \geq 45^\circ C$, and
concluded that in many cases, $T_b$ was increasing, and values of EWL were not representative of steady-state $T_a$ conditions. By modeling heat storage and changes in dry heat transfer at high $T_a$, these authors estimated that during a 5-h hyperthermic bout ($T_b = 44^\circ C$) at $T_a = 45^\circ C$, savings of water associated with facultative hyperthermia were strongly dependent on body mass, with 10 g birds saving ~50% of TEWL, but 1000 g birds incurring a net loss of water (Tieleman and Williams 1999). The $T_a$ of 45$^\circ C$ used by these authors closely approximates the current $T_a$ maxima typical of sites in several subtropical deserts (for instance, Yuma AZ, USA and Birdsville, Australia (44.6 and 44.0$^\circ C$, respectively)—see McKechnie and Wolf (2010)]. However, the relative water savings bird can achieve via facultative hyperthermia are likely to decrease rapidly as air temperature increases above 45$^\circ C$. The mean hyperthermic $T_b$ for 28 species was 43.5 ± 1.2$^\circ C$, with a maximum value of 45.8$^\circ C$ (Tieleman and Williams 1999), and it is likely that biochemical constraints preclude the possibility of birds maintaining $T_b$s much higher. Thus, whereas facultative hyperthermia may permit substantial savings in water at current air temperature maxima of about 45$^\circ C$, such savings will rapidly decrease as air temperatures increase.

Coping with short-term anomalous heat waves

For endotherms, one of the most detrimental, yet understudied, aspects of anthropogenic climate change may be the increasing frequency of extreme climatic events, including heat waves and droughts (Parmesan et al. 2000; McKechnie and Wolf 2010). Examples of mass die-offs of birds and bats have been reported several times over the past century (Finlayson 1932; Miller 1963), but the number of reports seems to have increased in the past decade (Welbergen et al. 2008; McKechnie and Wolf 2010). These short, but extreme, heat waves and droughts impose very different pressures on endotherms than does a slowly warming climate (Parmesan et al. 2000). During heat waves, the most important consideration is survival, often at the expense of reproduction, growth, or other necessary functions. Thus, thermoregulation with the goal of maintaining $T_b$ below the upper lethal temperature should be of primary importance.

If short-term weather anomalies severe enough to lead to sudden die-offs are sufficiently rare, the selective pressure imposed by these events should be relatively low. However, increasing frequency of such extreme events will increase the selective pressure favoring individuals with the ability to cope with them (e.g., thermal generalists should be at an advantage). If extreme climatic events selectively kill some individuals, changes in frequencies of genotypes within the population will occur. For example, Welbergen et al. (2008) found that mortality during heat waves was greater among tropical black flying-foxes (Pteropus alecto) than among temperate gray-headed flying-foxes (Pteropus poliocephalus). In addition to this variation in mortality rates between species, they also found considerable variation in mortality rates among genders and age classes. This variation will obviously affect the demography of the populations. Depending on the relationship between tolerance above and tolerance below the TNZ within an individual, these changes in demographic structure and the associated truncating of genetic diversity caused by very high temperatures may lead to populations less capable of dealing with low temperatures or other normal weather events.

Adaptation and phenotypic plasticity among heterothermic endotherms

Climate change will affect heterothermic endotherms including daily heterotherms and hibernators. Since conservation of energy is such an important aspect of torpor, it was long thought that most species maximized the expression of torpor and hibernation, regardless of environmental conditions (Humphries et al. 2003b). However, evidence is mounting that heterotherms, especially hibernators, instead vary the expression of hibernation in an adaptive manner, adjusting it to fluctuating environmental, ecological, and physiological conditions (Humphries et al. 2003a; Munro et al. 2005; Boyles et al. 2007; Wojciechowski et al. 2007; Landry-Cuerrier et al. 2008). Therefore, it is important to consider the possibility that adaptive thermoregulation and plasticity in the expression of heterothermy might mediate responses to climate change. Recent evidence suggests there is variation between populations in thermoregulation and in the metabolic rates of hibernating endotherms, and that the patterns are predictable along latitudinal gradients (Munro et al. 2005; Fenn et al. 2009; Dunbar and Brigham 2010; Zervanos et al. 2010) (Fig. 3). It appears that at least some of that variation is conserved even under common garden conditions, suggesting some genetic component to the patterns (Fenn et al. 2009). Thus, different populations may respond differently to similar changes in climate, which may be especially important in widely ranging species. Counteracting this adaptation may be the relationship between $T_a$ and energy expenditure.
during hibernation, which increases exponentially with a $Q_{10}$ of 2–3. While this relationship may be modified by metabolic inhibition, generally speaking, a southerly population (in the northern hemisphere) is likely hibernating at warmer temperatures than are northerly conspecifics, and thus an increase in the temperature of hibernacula will lead to a larger expenditure of energy in the southern population than in the northern one (Dunbar and Brigham 2010).

**Limits to adaption in endothermic thermoregulation**

While adaptation and phenotypic plasticity will undoubtedly buffer the effects of climate change on endotherms, there are fundamental physiological limits to how much, and how quickly, organisms can respond to a changing climate. Endothermic thermoregulation produces considerable metabolic heat. Under normal circumstances, excess heat energy is dissipated through evaporative, radiative, conductive, or convective cooling. However, as environmental temperature increases, dissipation of heat becomes increasingly difficult and $T_b$ will necessarily increase. It has been suggested that humans (and other endotherms) can adapt to environmental temperatures only up to the point at which dissipation of heat is impossible (Sherwood and Huber 2010). Evaporative cooling, for instance, is the most efficient route of dissipation of heat when environmental temperature exceeds the $T_b$ of an endotherm, but endotherms face fundamental limitations to the efficiency of using evaporative cooling to lose heat. There are biophysical limits to the rates of heat loss via evaporative cooling, and these rates depend heavily on the differential in water vapor between the surface of the organism and the air. Evaporative cooling can only occur when the surface temperature of the endotherm is higher than the environmental wet-bulb temperature, and evaporative heat loss is severely curtailed at high humidities. To adapt to more humid and hotter environments, endotherms would need to increase their $T_b$ to maintain a negative $T_b-T_a$ gradient. However, since most endotherms regulate $T_b$s near lethal or physiological limits, there is likely a limited scope for thermal adaption in this sense.

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*Fig. 3 Body temperature across the season of hibernation for three populations of woodchucks (*Marmota monax*) across a latitudinal gradient in North America (Maine: 43°42' N; Pennsylvania: 40°22'N; South Carolina: 34°40'N). Reproduced from Zervanos et al. (2010) with permission from The University of Chicago Press.*
Increasing $T_b$ beyond the limits within which acclimation and adaptation are effective will slow enzyme activities by shifting the equilibrium between active and inactive states, and ultimately by denaturing proteins (Daniel et al. 2010). Additionally, cellular function will be disrupted by damage to the membranes of cells and organelles (Hazel 1995). Even if membranes were not directly affected by temperature, an increase in $T_b$ may cause an increase in the production of reactive oxygen species (ROS), which will damage mitochondrial membranes and affect organelle’s function (Brand et al. 2004). Reactive superoxide ($O_2^{•−}$) is produced in the high-energy environment of the inner mitochondrial membrane, and mitochondria possess a natural, enzymatic defense system. Superoxide dismutase turns superoxide into the less reactive hydrogen peroxide ($H_2O_2$). Catalase and glutathione peroxidase break-down hydrogen peroxide into water and molecular oxygen ($H_2O + O_2$) thereby eliminating the threat from ROS. However, the system is not perfect, and secondary radicals, particularly hydroxyl radicals (•OH), form from superoxide. These radicals react with the mitochondrial membrane, disrupting its proper function. Heat stress increases ROS production and thereby performance in mammals and birds (Zuo et al. 2000; Azad et al. 2010), but it is likely to be a mechanism that can facilitate negative effects of climate change on animal function. For example, ROS can cause a decrease in telomere length and thereby shorten lifespan and decrease fitness (Monaghan et al. 2009). Furthermore, increases in $T_b$ can affect the efficacy of ATP production if the thermal sensitivities of mitochondrial proton leak and oxidative phosphorylation shift so that an increasing proportion of the electromotive force across the inner mitochondrial membrane is released as heat rather than being converted into ATP (Abele et al. 2002; Seebacher et al. 2010). The consequences would be that heat load would increase thereby exacerbating already existing heat stress, and that the cells would be starved of ATP.

**Conclusions**

While much is known about endothermic thermoregulation, we know unfortunately little about how variation in $T_b$ characteristics of individuals, populations, and species will interact with the effects of climate change to determine the response of endotherms. We have already addressed the quickly growing body of literature using mathematical modeling to address the effects of climate change on endotherms. Future efforts along these lines will undoubtedly lead to new insights in the field, but will be vastly improved by including the types of variation we address in this review. As a simple example, McKechnie and Wolf (2010) modeled the survival time of birds exposed to increased frequencies of extreme heat waves. They assumed physiological parameters were fixed for birds of a given body mass and therefore predict that all birds of a given size will be equally stressed under the same conditions. However, species’ responses will be influenced by interspecific variation in trade-offs between tolerance to dehydration tolerance and the risk of hyperthermia. For instance, variation in the rate at which EWL increases with increasing environmental temperatures will mean that, for a given body mass, some species will reach their limits of tolerance to dehydration more rapidly than will others. Such variation may be expected to directly affect selection on tolerance of high $T_b$ and will be vital in future modeling efforts.

It appears increasingly clear that thermoregulatory characteristics of endotherms are adaptive and have been shaped by past and current selective pressures when exposed to temperatures below the TNZ. However, little research has explicitly addressed the possibility that responses to high temperatures vary among and between populations and species in a manner consistent with the predictions of the concept of adaptive thermoregulation (Angilletta et al. 2010). Furthermore, a vital line of future enquiry in climate research will be to determine the extent to which endotherms can acclimate and acclimatize to rapidly changing selective pressures associated with anthropogenic climate change and how important those shifts will be in terms of fitness. Recent evidence suggests that climate change has led to shifts in phenology and morphology and subsequently increased fitness in some endotherms (Ozgul et al. 2010). However, other authors have argued that evolutionary processes have done little to stave off extinctions associated with climate change (Parmesan 2006).

Research on adaptive thermoregulation and thermal sensitivity in endotherms in a manner relevant to climate change will be difficult for several reasons. First, long generation times and relatively slow reproductive rates make mammals and birds less conducive to experimental evolutionary research than are many ectotherms. Although a few well-studied model species have been, and will continue to be, important in elucidating the mechanisms of adaptation, some research on adaptation will likely have to be conducted on populations exposed to natural selective pressures. Second, obvious ethical
considerations mean that it will be difficult (although not impossible) to gain substantial new insights into how endotherms respond to extremely high temperatures under controlled conditions. Thus, much of the research on extreme weather events may have to take advantage of natural events, making planning and experimental design difficult. Finally, the consideration of adaption and phenotypic plasticity is likely to increase complexity and therefore difficulty in writing, interpreting, and presenting models of responses by endotherms to climate change. Despite these difficulties, we believe the study of adaptive responses to a changing climate has important implications for both our understanding of the evolutionary processes governing thermoregulation in endotherms and of the conservation of our natural world.

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Adaptive thermoregulation in endotherms


