

Responses of large mammals to climate change

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Most large terrestrial mammals, including the charismatic species so important for ecotourism, do not have the luxury of rapid micro-evolution or sufficient range shifts as strategies for adjusting to climate change. The rate of climate change is too fast for genetic adaptation to occur in mammals with longevities of decades, typical of large mammals, and landscape fragmentation and population by humans too widespread to allow spontaneous range shifts of large mammals, leaving only the expression of latent phenotypic plasticity to counter effects of climate change. The expression of phenotypic plasticity includes anatomical variation within the same species, changes in phenology, and employment of intrinsic physiological and behavioral capacity that can buffer an animal against the effects of climate change. Whether that buffer will be realized is unknown, because little is known about the efficacy of the expression of plasticity, particularly for large mammals. Future research in climate change biology requires measurement of physiological characteristics of many identified free-living individual animals for long periods, probably decades, to allow us to detect whether expression of phenotypic plasticity will be sufficient to cope with climate change.

Introduction

The 2013 Intergovernmental Panel on Climate Change synthesis report predicts an increase in global temperatures of between 1.5 °C and 4.5 °C during the 21st Century,¹ which will take us to the warmest global climate in more than two million years. Although the rate of the current warming episode probably does not exceed the normal background rate of climate change, continued warming over the next few decades will exceed the background rate of change by more than an order of magnitude.² The rate of future climate change will be unprecedented in the Earth's history.³ It probably will be that rate of climate change, rather than the eventual magnitude or duration of the episode, that will prove to be critical for biota.⁴ Indeed, the typical rate of niche evolution that has been observed in more than 500 species is about 10 000 times slower than the rate that will be required to keep track with climate change projections for 2100.⁵ Though worse is to come, it is delusional to envisage climate change only as a future challenge. Its biological consequences already are evident. Of the nearly 30 000 documented trends in physical systems and biological characteristics of plants and animals between 1970 and 2004, 90% have been in the direction consistent with environmental temperature increases.⁶

According to Huey et al.⁷ 'the vulnerability of a species to environmental change depends on the species' *exposure* and

sensitivity to environmental change, its *resilience* to perturbations and its potential to *adapt* to change'. Vulnerable species or animal populations have only three options when faced with climate change.⁸ First, they may shift their distribution range, to habitats where the climate is within the species' tolerance limits. Second, they may remain in a location but adjust to new climatic regimes either through a change in the genetic composition of a population or by phenotypic plasticity, which results in a different phenotype from an existing genotype via changes in epigenetic control of gene expression.⁹ Either of these outcomes may bring about changes in the timing of events (phenology), anatomical variation (e.g., color patterns, body shape and size), or changes in the behavior or physiology of a species, which could reduce the impact of climate change.¹⁰ Finally, if neither range shifts nor adjustment is possible, global or local extinction (extirpation) may result. Whatever options are realized, climate change will have a significant impact on biodiversity,^{11–14} and current conservation strategies, which attempt to conserve communities and ecosystems as they exist, will be unsustainable.^{15–18}

For many large mammals, especially those living in human-dominated landscapes, range shifts are unlikely options for coping with climate change. Because the research has not been done, we do not know whether large mammals can express sufficient genetic shifts or phenotypic plasticity to adjust to the current climate change event. We do know that large mammals are

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more likely to be adversely effected by climate change than their smaller counterparts.¹⁹ Here we review what we do know, and need to know, about the possible responses of large terrestrial mammals. We contextualize our discussion of large mammals within established principles of climate change biology.

Extinction

Global warming has been a common occurrence on Earth for the last 3.5 billion years. Modeling of the current episode predicts a temperature rise of the same order of magnitude as that evident at the end of the Permian, when mass volcanism increased global temperatures by 6 °C and resulted in the extinction of nearly 95% of species.²⁰ We cannot be sure that it was the warming that was responsible for all of those extinctions, but the fossil record is unequivocal that extinction and extirpation have been common outcomes for species facing past climate change events of comparable magnitude. A pivotal study by Thomas et al.²¹ predicted that, under mid-range climate change scenarios, a quarter of terrestrial plants and animals may be extinct by 2050. By extrapolating such predictions to a global scale, the authors predicted that well over one million species, among which will be many large terrestrial mammal species, could be threatened with extinction as a result of climate change. Their models predict that 45% of terrestrial species are likely to be committed to extinction by 2050 if their dispersal is limited.²¹

Among the large terrestrial mammals seemingly destined to become extinct are the charismatic species so important for ecotourism. Africa is rich in such species, and serves as an example of the future likely under climate change; 25–40% of a representative sample of 277 of its mammalian species is likely to be critically endangered or extinct by 2080.²² The charismatic species of South Africa are likely to be particularly vulnerable to climate change, as will be large mammals in human-dominated landscapes elsewhere, because the consequences of high human population density will prevent their dispersal. The extinction risk of South African mammals is estimated to be as high as 69% by 2050.²¹ Indeed, long-term population monitoring in the country's flagship Kruger National Park already has revealed declines in seven out of 11 ungulate species between 1977 and 1996.²³

Range Shifts

Although large mammals in fragmented, human-dominated habitats, like those prevailing in South Africa, will be precluded from shifting to a new habitat in response to current climate change, large mammals in more-pristine habitats such as bears in northern Canada, and smaller mammals everywhere, may be able to track suitable climates. In the temperate zone, for example, a 1 °C increase in mean annual temperature corresponds to a shift in isotherms of ~160 km in latitude or 160 m in elevation.^{24,25} Thus, biota that can do so, including mammals, are expected to follow the shifting climatic zones and move polewards in latitude and upwards in elevation.^{17,26} Numerous recent reports have documented shifts in the geographical distribution of extant biota (for reviews see refs. 24, 27, and 28). More than half of the species

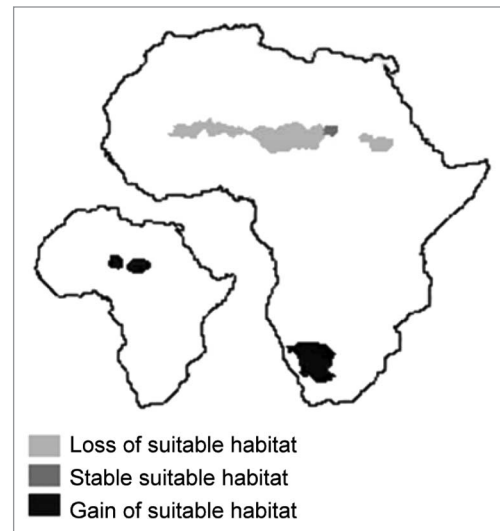


Figure 1. Small map: Observed current distribution of the scimitar-horned oryx (*Oryx dammah*). Large map: Predicted habitat distribution for the scimitar-horned oryx in 2050. Light gray indicates habitats that are presently climatically suitable but are predicted to be unsuitable in 2050. Moderate gray indicates habitats that are presently climatically suitable that are predicted to remain suitable in 2050. Dark gray indicates habitats that are presently climatically unsuitable that are predicted to be suitable by 2050 (adapted from Thuiller et al.²²).

examined have shifted their range into adjacent habitats between 1970 and 2000,²⁹ presumably in response to climate change. Observed range shifts averaged 11 m per decade upwards and nearly 17 km per decade polewards, with range shifts correlating positively with the rate of warming.²⁷ Global meta-analyses have revealed that 80% of range shifts have been consistent with climate change predictions.^{24,28,29} However, the recorded shifts include few, if any, large mammals.

Shifting range in response to climate change requires suitable new habitats to be accessible, and for the required traveling distances to be within the capacity of the species that is shifting range. The rapid rate of climate change will mean that nearly 10% of mammals in the western hemisphere will be unable to move fast enough to keep pace with projected climate changes.³⁰ A salutary example of unattainability of the required pace is the scimitar-horned oryx (*Oryx dammah*, Fig. 1). To track its suitable climate, this species would have had to move thousands of kilometers, from the Sahel to the Kalahari Desert, an impossible shift without human assistance.²² The species has become extinct in what was its current natural habitat in the last decade. In circumstances in which natural range shifts are not feasible, either as a result of unattainable traveling distances or loss of habitat connectivity, assisted colonization may provide a conservation option.^{31,32} Yet, moving species to areas where they do not currently occur is not without risk. The introduced species can carry disease, displace native species and thereby challenge ecosystem stability or alter the genetic structure of local populations. An in-depth knowledge of species' biology and accurate climate change predictions is required before assisted colonization can become a routine conservation option.^{33,34}

For assisted colonization to be a feasible conservation option for a species, we need an understanding of the fundamental niche (where species can occur) and realized niche (where species do occur), and the likely location of those niches in the future. Bioclimatic envelope, or niche-based, models are static models that correlate current species distributions with climate variables and project future distributions according to each species' "climatic envelope"³⁵⁻³⁷. Some models were developed sufficiently long ago for their predictions to be tested against actual observations, and they have proved their value. For example, in a meta-analysis of range shifts, latitudinal shifts matched the expected range shifts if a species were to track its bioclimatic envelope.²⁷ While of proven utility, the assumptions on which these models are based can be questioned regarding their ability to predict the potential impact of climate change.³⁸⁻⁴¹ Bioclimatic envelope models typically do not address stochastic events like local droughts and heat waves, which may impose the dominant climate stress on species in the future.^{42,43} They also do not address spatial variability. It is the microclimate experienced by an animal that has direct influence on an animal's thermal status.⁴⁴⁻⁴⁷ All thermal aspects of those microclimates need to be quantified before they can be incorporated into climate change models.⁷ Although they do not incorporate measures of evaporation, miniature black globe thermometers can be attached to large mammals to provide a quantitative measurement of heat loads of their microclimates.⁴⁸

Another shortfall of current bioclimatic envelope models is that they do not account for non-climatic influences on species' distributions, such as terrain and biotic interactions (but see ref. 49). Climate-induced species interactions are likely to have important consequences for future species distributions.^{50,51} For example, the climate-driven northward range expansion of the red fox (*Vulpes vulpes*) has been associated with a decrease in the distribution range of the arctic fox (*Alopex lagopus*) as a result of an increased interspecific competition.⁵² Since individual plant and animal species differ in their response to changing climatic conditions, species may shift their ranges independently of each other, resulting in changes in community structure and possibly in ecosystem disruption.^{26,53-55} For example, decreased rainfall altered the plant community and ultimately led to a decline in desert bighorn sheep (*Ovis canadensis nelsoni*) population in California.⁵⁶ These species interactions thus need to be incorporated into bioclimatic envelope models to better predict future species distributions,⁵⁷ which is the aim of a new scope of ecological research termed "global change ecology"⁵⁸.

We and others believe, however, that the major limitation of predictions derived from bioclimatic envelope models is the assumption that species lack sufficient phenotypic plasticity to adjust to climates beyond those in which they occur currently.⁵⁹ Models typically assume, for each species, that the realized niche is the fundamental niche: the species occupies today all habitats fulfilling the thermal conditions that it can tolerate, and it therefore cannot survive at a current habitat if conditions depart from those in which that species survives now. Yet, plasticity may allow animals to adjust to changing climatic conditions without changing their location. Some bioclimatic envelope models have

attempted to incorporate physiological factors to address the climatic tolerances of terrestrial ectotherms^{60,61} and mammals,^{62,63} but they require an understanding of species' physiological responses to climate,⁶⁴⁻⁶⁶ an understanding that we are far from having attained for most species. Although these physiologically-tuned models still have limitations, for example in not taking non-climatic factors into account, they are likely to be more robust than those bioclimatic envelope models that are based only on correlations between observed distributions and current climate variables.^{45,67,68}

Micro-Evolution

Future extinction risk is likely to be overestimated if species exhibit adaptive genotypic changes in response to environmental change. Evolutionary change often is considered too slow, given the rate of the climate change event, to allow genetic adaptation, but is likely to have accompanied range shifts in the past.^{3,4} A changing climate moves the so-called "fitness optimum" for different populations throughout the species range,^{3,4} making the fundamental niche flexible over time. Range shifts already are having genetic consequences in the current event. By mixing populations that are shifting, a range shift increases genetic variation, thereby increasing the population's chance of adapting to changing conditions. Northwards range shifts in the northern hemisphere, for example, may have the advantage of introducing genotypes that are better adapted to warmer conditions, thus promoting the adaptation of existing cooler-adapted populations to climate change.^{69,70} Conversely, range shifts also can decrease genetic variability that has occurred historically as a result of outbreeding of distinct populations. For example, climate change may result in genetic mixing among subspecies of the black bear, which could inhibit or even reverse sub-speciation.⁷¹

The genetic adaptation that will be required to survive climate change^{70,72} is not the slow process of speciation,^{3,73,74} but heritable shifts in allele frequencies in a population (without speciation) known as "micro-evolution". Micro-evolution already has occurred, in directions predicted by climate change,^{75,76} particularly for short-lived species with fast generation times (for examples, see refs. 77-82). Surprisingly, there have been shifts in genetic variability even in populations of the relatively long-lived Canadian lynx (*Lynx canadensis*) that have been associated with snow depth and winter precipitation.⁸³ It remains uncertain, though, whether micro-evolution can result in a change in the climate tolerance of any species sufficient to prevent extinction.⁸⁴

A morphological feature related to climate tolerance that is determined genetically is an animal's coat color. Analyses by Maloney et al.⁸⁵ support the view that progressive increases in ambient temperature explain the recent 20-y shift in the ratio of dark to light-colored Soay sheep on the archipelago of St Kilda, United Kingdom, contrary to the original explanation based on an association of coat color with body mass.^{86,87} The advantage enjoyed historically by dark-colored sheep in absorbing solar radiation better would carry less benefit in warmer environments. Similarly, there is thermoregulatory significance of pelt color for springbok (*Antidorcas marsupialis*), with black springbok

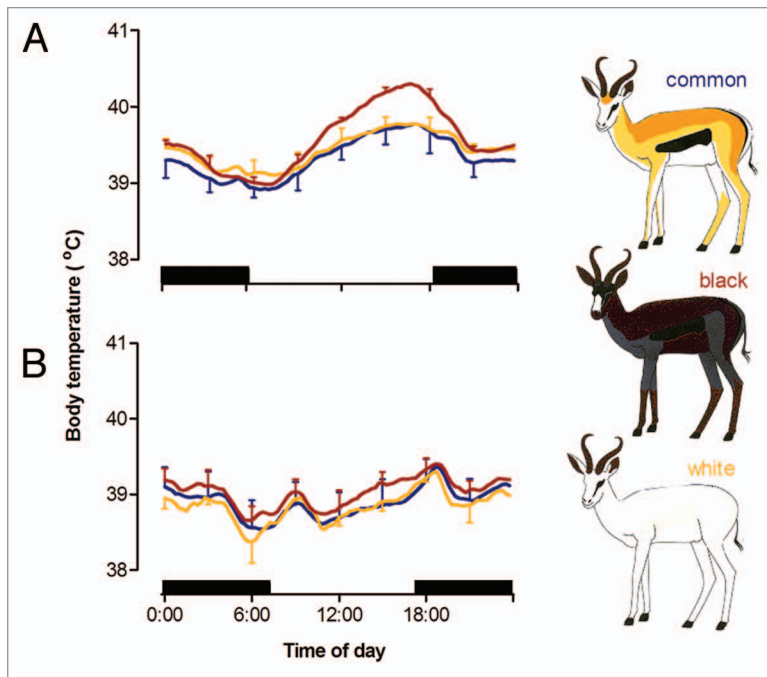


Figure 2. The pelt color variations of the black, common and white springbok. Nychthemeral rhythm of body temperature (mean \pm SD) for four black (red line), seven common (blue line) and four white (yellow line) springbok during a hot (A) and cold (B) season. Black bars represent night periods (adapted from Hetem et al.⁸⁸).

benefiting, compared with their white conspecifics, by being able to reduce metabolic costs in winter, as a result of increased absorption of solar radiation (Fig. 2B).⁸⁸ Increased absorption of solar radiation, however, may disadvantage the black springbok in the heat (Fig. 2A). As with the Soay sheep, we expect the black color morphs to decline as their habitats warm, if populations are left unmanaged.

Although coat color has a genetic basis amenable to micro-evolution in populations of mixed color morphs, and numerous studies have interpreted such anatomical changes as micro-evolutionary responses to climate change, the majority of studies have provided no evidence that the observed changes have a genetic basis.^{89,90} There is a general lack of evidence for or against genetic adaptations to climate change, resulting at least partially because molecular techniques remain inadequate to properly reveal how genetic sequences relate to ecologically important traits,^{91,92} an inadequacy that is hopefully temporary.⁹³ However, methods to quantify a genetic component of adjustment to climate change are likely to remain difficult to implement, especially in long-lived mammals.⁹⁴ To date, there have been only 12 studies published that have tested for the genetic basis of climate-related biological changes in mammals, and only one of these found evidence for a genetically-based response.⁹⁵ The most convincing example of micro-evolutionary response to climate change is a short-lived mammal, the North American red squirrel (*Tamiasciurus hudsonicus*), in Yukon from 1989 to 2001, a period over which mean lifetime parturition date advanced by six days per generation, associated with a mean spring temperature rise of

2 °C and a decrease in precipitation.⁹⁶ Réale et al.⁹⁷ calculated that 13% of the observed phenological changes in parturition date could be attributed to micro-evolution. However, since the investigators initially did not account for systematic environmental variation across years, even that 13% may be an overestimate of the role of genetic change.⁹⁸ Potentially, more than 60% of the observed changes in parturition date of the squirrel must be attributed to phenotypic plasticity.

Short-lived mammalian species, like the red squirrel, have the advantage of fast generation times, which may improve their chance of survival as each generation provides scope for micro-evolution.^{70,77,78,99,100} Conversely, large mammals with long generation times, and indeed those small mammal species, like bats, which have long generation times, are predicted to have less ability to respond genetically to any new selective pressures,¹⁰¹ making them more susceptible to extinction¹⁰² than are species with short generation times. The issue is compounded because large species have greater range requirements.¹⁰³ There are many species of mammals with longevities such that individuals alive now ought still to be alive in 2030, and a few species for which individuals alive now could be alive in 2100.⁸ Clearly, the survival of those individuals, and probably those species, cannot depend on genetic adaptation. Instead, for those that also cannot shift their ranges, survival is likely to be entirely dependent on sufficient phenotypic plasticity to buffer effects of climate change.

Phenotypic Plasticity

By definition, phenotypic plasticity is the process by which a single genotype gives rise to different phenotypes in different circumstances.¹⁰⁴⁻¹⁰⁶ The plasticity is known as an epigenetic effect. Phenotypic plasticity in animals exposed to a change in environment may involve acclimation, acclimatization, and learning¹⁰⁴ and can take place through phenology, developmental plasticity, physiological adjustments and behavioral flexibility.¹⁰⁷ Unlike genetic adaptation, phenotypic plasticity allows the animal itself, rather than its future lineage (except in the case of maternal effects; see below), to respond to environmental change.¹⁰⁸ The mechanism of plasticity can involve changes to the way that DNA is packaged in the nucleus and alters the probability of a particular gene being expressed.⁹ The best known mechanisms of epigenetics are DNA methylation, histone modification, and more recently it has become obvious that small non-coding RNA's have both transcriptional effects on gene expression and post-transcriptional effects that alter the fate of the RNA from gene transcription, prior to translation into RNA.⁹

Phenological changes

In addition to estimating the contribution of micro-evolution, the red squirrel study provided the first measurement of the role of phenotypic plasticity in climate-induced development of a functional trait,⁹⁷ but it was not the first to document changes in phenology, that is the timing of seasonal events, in response to

changing climatic conditions (see refs. 17,24,26,28,109). It still is the case that most known examples of phenotypic changes linked to climate change relate to phenology.⁹⁵ For example, in response to progressive environmental change over a 28-y period on the Isle of Rum, United Kingdom, red deer (*Cervus elaphus*) have displayed phenotypic plasticity in the phenological traits of estrus date, parturition date, antler cast and clean date and the start and end of the rut, with most of the variation being attributable to earlier plant growth.¹¹⁰

When phenological changes are observed, they often are taken as evidence that species are adjusting to changing environmental conditions in ways that help mitigate the effects of climate change. Yet the responses in nearly half of a set of studies reporting phenotypic changes in phenology, body mass, or litter size in mammals actually were associated with a decline in fitness.⁹⁵ For example, the advanced breeding of Chillingham cattle (*Bos primigenius taurus*) in response to warming led to more calves being born in winter, which resulted in an increase in calf mortality.¹¹¹ The responses in only one third of the studies qualified as adaptive phenotypic changes in phenology on the criterion that both the direction and the rate of change were appropriate.⁹⁵ Because species may show rates of phenological change different to those of other species on which they depend, asynchrony or a mistiming of key ecological events can result.^{17,112-114} For example, the calving date of caribou (*Rangifer tarandus*) on Greenland has been advancing more slowly, with warming, than has the onset of plant growth, creating a trophic mismatch and increasing calf mortality.¹¹⁵ Numerous studies have demonstrated the ecological and metabolic costs of such mistimed ecological events,^{112,116} which ultimately may lead to a decrease in biodiversity.

One possible cause of mismatch between phenological responses in connected species is the different environmental cues to which different species respond.¹¹⁷ Whereas most plants and insects respond to seasonal changes in temperature, most vertebrate species are more sensitive to changes in photoperiod, although, as was the case for red deer on Rum, better nutrition can also advance reproductive events.¹¹⁰ Thus, those vertebrates with a photoperiod-sensitive reproductive cycle that remain at their historic locations may face a mismatch between reproduction and food availability, while those dispersing latitudinally will have to adjust to an unfamiliar annual cycle of photoperiod in their new habitat.^{70,76} Those species that are unable to match the timing of key life-history events to the phenology of the species on which they depend will be forced to show plasticity in other life-history traits if they are to maintain their lifetime reproductive success. For example, flexibility in phenology of the Antarctic fur seal (*Arctocephalus gazelle*) is important in their highly variable thermal environment but is limited because of the long interval between conception and weaning of the pups. As their environment warms the female Antarctic fur seals appear to be adapting their life cycles by not breeding in years of low krill supply, thus increasing adult survival and fitness.¹¹⁸ Another species that is changing its life-history strategy in response to stochastic environmental conditions is the pronghorn (*Antilocapra americana*). Frequent severe weather events result in an increase in male mortality, which favors precocial maturation in male

pronghorn and may ultimately lead to a life-history strategy of faster development.¹¹⁹ Similarly, the Soay sheep mentioned above are also breeding at an earlier age as their climate warms, resulting in a general decrease in mean body size in that population.¹²⁰

Anatomical variation

Although the majority of reports of phenotypic responses to climate change, adaptive or not, relate to phenology, there are reports relating to other traits. A decline in body mass is considered the third universal response (after phenology and range shifts) to warming associated with climate change.¹²¹ The relationship between body mass and thermoregulation is complex. Relative to animals of larger body mass, animals of the same shape with lower body mass, for geometric reasons, have a higher surface area-to-mass ratio, and therefore have more difficulty preventing body heat loss in cold environments. That physical relationship is congruent with Bergmann's rule that predicts a positive correlation between the body mass of terrestrial endotherms and latitude, and, by inference, an inverse correlation between body mass and environmental temperature. With global warming, species with lower body mass would lose that disadvantage progressively, so a relative increase in proportion of smaller animals would be expected in a warmer world.¹⁸ There are some data supporting that expectation. As mentioned, over a 20-y period of progressive winter warming, the average body mass of the Soay sheep on St. Kilda has declined between -0.3% (senescents) and -0.8% (yearlings) of mean body mass per year. The proposed mechanism is that the milder winters resulted in less reliance on fat reserves, which in turn enables more of the small individuals to survive the winter.¹²⁰ However, a decline in body mass does not appear to be a universal response of mammals to climate change. Data from museum specimens collected during the last quarter of the twentieth century reveal that body size of otters (*Lutra lutra*) in Norway has increased, presumably as a result of increased food availability.¹²² Indeed, only 7% of recently-observed changes in mammalian body masses provide support for an advantage to smaller mammals.¹²³ Also, the physical principles outlined above have a reverse effect when ambient temperature exceeds body temperature, a situation which will become increasingly common with climate change. There the higher surface area-to-mass ratio increases environmental heat load. In those environments, thermal balance also will depend on the capacity for evaporative cooling, which may be unrelated to body mass. Despite a 4-fold difference in body mass between Arabian oryx (*Oryx leucoryx*) and Arabian sand gazelle (*Gazella subgutturosa marica*), both species showed an increased amplitude of body temperature rhythm (increased heterothermy) when they were exposed to the same extreme heat and aridity (Fig. 3).¹²⁴

Although understanding the physiological mechanisms is essential for predicting responses to climate change,^{70,113} a disproportional number (> 80%) of studies of phenotypic responses to climate change has focused on anatomical plasticity, with fewer studies on physiological and behavioral responses.¹²⁵ Such preponderance may reflect the ease of measurement of anatomical features like body mass. Gathering physiological and behavioral data, on the other hand, is labor-intensive and requires long periods of observation and monitoring. Given that natural selection

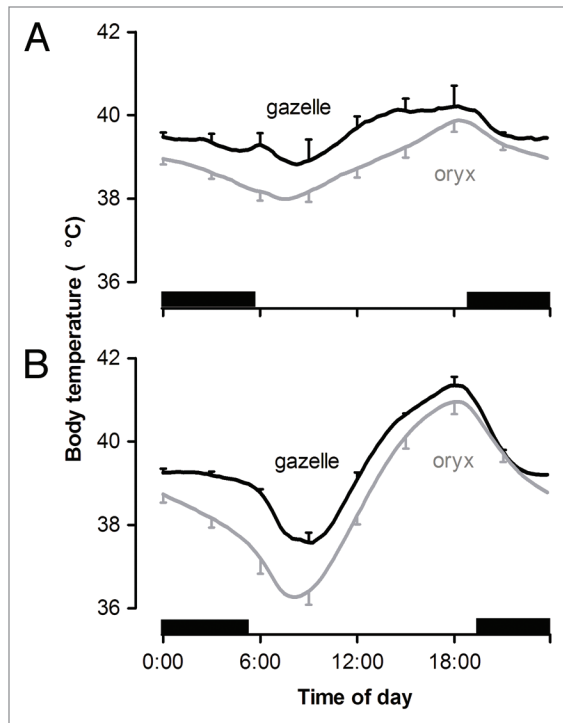


Figure 3. Nychthemeral rhythm of body temperature (mean \pm SD) for five free-living Arabian oryx (gray line) and four free-living Arabian sand gazelle (black line) during both the warm wet (A) and hot dry (B) periods. Black bars represent night periods (reprinted from Hetem et al.¹²⁴).

works primarily at the level of physiology and behavior,¹⁰⁰ it is concerning that we understand so little, for all mammals, about the direct links between physiology and vulnerability to climate change. We need to improve our understanding of the physiological and behavioral mechanisms that determine an animal's thermal tolerance and its capacity for acclimatization in order to better predict the impact of climate change on a particular species.^{54,126-128}

Physiological acclimatization

Though physiological mechanisms are responsible for the capacity of animals to adjust to new environments,¹²⁹ there are limits to the capacity of physiological systems to respond to changing environmental conditions, both because of limited environmental resources and because of biochemical and physical constraints. The physiological response of an organism therefore acts as a "filter" between a change in environmental conditions and fitness, which ultimately determines species persistence and ecosystem biodiversity.¹³⁰ To predict accurately the direct physiological effects of climate change on a species, we need, first, an understanding of the thermal physiological sensitivity of the species, including how close to its thermal limits, or "prescriptive zone"¹³¹, the species is living. Second, we need an understanding of the relationship between climate and the thermoregulation of the species, including the degree to which the species can adjust, or acclimatize.^{126,132,133} Because of the clearly-defined thermal niches which occur in the marine environment, most studies that have investigated the physiological principles underlying thermal limits and thermal sensitivity have focused on marine ectotherms

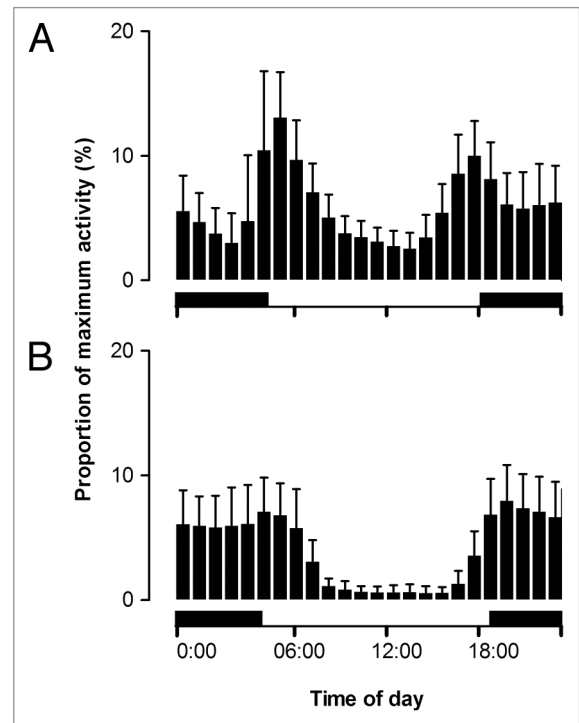


Figure 4. Nychthemeral rhythm of activity for five Arabian oryx during both the warm wet (A) and hot dry (B) periods. Oryx shifted from a continuous 24-h activity with crepuscular peaks during the warm wet period to nocturnal activity during the hot dry period. Activity counts are expressed as a percentage of maximum counts for that animal. Black bars represent night periods (adapted from Hetem et al.¹⁶⁹).

(for review see refs. 133 and 134). These studies have contributed substantially to our understanding of the key mechanisms of thermal adjustments and limitations, including finding that in those ectotherms thermal tolerance is limited by the capacity of circulatory and ventilatory tissues.¹³⁵ We are yet to establish how thermal sensitivity applies to acclimatization in endotherms, especially the large mammals, and how it applies might be substantially different to its application in ectotherms. In theory, endotherms may be more sensitive than ectotherms to rising ambient temperatures, because endothermy evolved during cold climatic conditions¹³⁵ and because enhanced organismic complexity often is accompanied by increased thermal sensitivity.¹³⁶

Generalist species, characterized by wide thermal tolerance windows but also with large geographic ranges and greater physiological plasticity, are less likely to be affected by climate change than are species that are physiologically specialized with respect to the thermal environment.^{113,137-139} Endotherms, as thermal specialists, then are likely to be particularly vulnerable to climate change.⁷ The width of the thermoneutral zone (TNZ) of endotherms, including large mammals, may provide a useful index of thermal specialization and has recently been used to assess the vulnerability of endotherms to climate change.¹⁴⁰ Tropical mammals display a narrower TNZ than do their arctic counterparts,¹⁴¹ primarily because of an elevated lower limit in tropical species. Mammalian species with narrow TNZ, such as tropical arboreal marsupials, indeed do appear to be more at risk from climate

change. For example, the white lemuroid possum (*Hemibelideus lemuroides*), a species endemic to the mountain forests of northern Queensland, risks extinction as a result of the recent 0.8 °C increase in ambient temperature there.¹⁴² Conversely, mammalian species with wide thermoneutral zones, such as the hibernating mammalian species in the Canadian Arctic region,^{143,144} are predicted by some researchers to show an increase in abundance and distribution in response to climate change. Yet, in a recent meta-analysis of responses of 81 mammalian species, hibernating species and those which display torpor were no less affected by climate change than were those which do not.¹⁹ Variation in the upper limit of tolerance seems to be more relevant in the context of climate change, yet such variation appears to be much less than that of the lower limit.⁷

As is the case with the white lemuroid possum, species that currently live in hot environments may be the most vulnerable to climate change, because they are already living close to their upper limits of thermal tolerance and have limited scope for further acclimatization.^{133,145} The Arabian oryx inhabiting the extreme environment of the Arabian Desert may be living at the edge of its physiological limits.^{146,147} In arid environments, the threat of increased ambient temperature is compounded, or even exceeded, by the threat of reduced water availability resulting from climate change.¹⁴⁸ Although many factors consequent upon the increase in temperatures and aridity with climate change may threaten survival at community and individual levels, other factors are irrelevant if individual animals cannot maintain homeostasis of body temperature and body fluids, as their habitats become hotter and drier. Desert-adapted artiodactyls have to trade off thermoregulation, osmoregulation, and energy acquisition.¹⁴⁹ In the Arabian oryx when conflict between regulatory systems occurs, priority is given to osmoregulation.¹⁴⁷ When water is scarce evaporative cooling is reduced (presumably to conserve body water) at the expense of homeothermy, resulting in higher core body temperature in hot conditions. Similarly, when energy supply is limited endotherms reduce metabolic heat production, resulting in lower core body temperature.¹⁵⁰ Though it may save water and/or energy, the resulting heterothermy increases the risk of mortality and morbidity if tissue temperatures depart from the tolerable range. Whether the heterothermy that has been observed in conditions of food and water shortage is a controlled thermoregulatory event that might serve as an adjustment to climate change, or whether it results from failure of homeothermy, remains debatable.^{147,151}

A second autonomic mechanism that the Arabian oryx used to conserve body water and facilitate homeostasis at high environmental heat loads was selective brain cooling.¹⁵² Mammals possessing a carotid rete employ selective brain cooling that reduces hypothalamic temperature. Because hypothalamic temperature provides the main drive for evaporative heat loss, the hypothalamic cooling conserves water by transferring heat loss to non-evaporative means.¹⁵³⁻¹⁵⁶ The evolution of the carotid rete is proposed to have promoted thermoregulatory flexibility and thus facilitated the invasion of arid zones by artiodactyls, which have a carotid rete, during the highly-seasonal post-Eocene period.¹⁵⁷ Plasticity in rete function may well provide an adjustment for

artiodactyls to cope with aridity and heat stress predicted to occur with climate change.^{151,158}

Maternal effects

Our discussion of physiological acclimatization in response to climate change relates to how function in an individual might change, potentially to its benefit, as it encounters climate change. That encounter might affect not just the animal itself, but also its offspring, through the phenomenon known as “maternal effects”: the conditions to which a female animal is exposed during her pregnancy can influence the life-history traits in her offspring.¹⁵⁹ These maternal effects involve epigenetic changes in the fetus and are controlled by hormones that regulate the expression of phenotypic variation in traits like body mass, growth and survival. Stress and reproductive hormone levels in free-living populations correlate with life-history traits and may provide useful biomarkers of how mammals might be adapting to climate change.¹⁶⁰

Numerous species of antelope in the northern hemisphere display plasticity in offspring birth mass in response to changing climatic conditions.⁵⁵ Although these maternal effects may promote the survival and enhance the reproductive success of the mother, such plasticity in birth mass has long-term consequences for the offspring. Like many morphological traits, body mass at birth is a “non-labile” trait as it is expressed only once in an individual’s lifetime.¹⁶¹ Most “non-labile” traits are traits that show plasticity only during development. However, such developmental plasticity can be adaptive only if the trends for changes in climatic conditions at the time of development remain similar throughout the offspring’s lifetimes.

Behavioral flexibility

Thermoregulatory behavior constitutes a set of rapid, extremely flexible, and precise mechanisms that can enhance an animal’s performance, and presumably its fitness, by incorporating both anatomical and physiological traits to optimize body temperature homeostasis.¹⁶²⁻¹⁶⁴ Behaviors that potentially reduce thermoregulatory costs include appropriate microclimate selection, postural adjustments and the restriction of daily activities to time periods when heat loads and water loss are lower.^{16,165} Since behavioral changes generally are less costly than are autonomic responses, behavioral adjustments are likely to be preferred.¹⁶⁶ However, to date, only two models, both in ectotherms,^{167,168} have evaluated the role of behavioral thermoregulation in buffering the impact of climate change revealing that behavioral flexibility will be important in species persistence. Whether such behavioral adjustments actually are occurring in mammals, with benefit, remains to be investigated.

At least theoretically, like ectotherms,¹⁶⁷ endotherms¹⁶⁹ should be able to buffer some of the additional thermal stress of climate change through appropriate thermoregulatory behavior. Terrestrial animals, because of their mobility and capacity for complex behaviors, can exploit the thermal mosaic of their habitat to select a preferred microclimate.^{162,163} Importantly, the available microclimates can differ substantially from the macroclimate used in many modeling exercises, provided there is sufficient thermal heterogeneity within a habitat.^{7,44,170} But a microhabitat selected for its thermal properties may have an increased risk of predation, parasites, competition, or a decreased availability of

resources, including energy, mates, food, or water.^{162,165,171} For example, in an arid high-elevation desert, the North American elk (*Cervus elaphus*), preferentially selected areas where their costs of thermoregulation were reduced, despite having limited access to high quality forage in such areas.¹⁷² In contrast, in a forest habitat the thermoregulatory costs of different habitats were less pronounced and elk selected areas on the basis of access to high quality forage, rather than lower thermoregulatory cost.¹⁷²

The interplay between competing homeostatic processes will become increasingly important under the thermal threat of climate change, and optimization of homeostasis increasingly difficult. The moose (*Alces alces*) provides an example of the potential costs associated with behavioral thermoregulation of a large mammal in the context of climate change. In the past 20 y, the moose population in Minnesota, USA, has halved and the population in the Isle Royale National Park, USA, has declined by 75%. Moose are particularly sensitive to heat and seek shelter when ambient temperatures exceed 14 °C.¹⁷³ Over the past 40 y, as the average summer temperature has increased by 2 °C, moose have forfeited valuable foraging time in preference for lethargy and microhabitat selection in the form of immersion in cool water. Forfeiting foraging has led to malnutrition and decreases fat reserves, which are essential for winter survival. Malnutrition also is likely to increase their risk of succumbing to parasites, disease and predation by wolves, all factors which are believed to have contributed to the recent decline in the moose population.¹⁷⁴ With further increases in summer temperatures predicted for the future, it seems likely that the moose will be extirpated from its historic southern range within the next 50 y. Recent warming already has resulted in populations of pika (*Ochotona princeps*) being extirpated from the lower elevations of their distribution range.¹⁷⁵ Pika stop foraging during the hottest part of the day, a behavior likely to result in decreased foraging time as ambient temperatures continue to increase.

Because of the increased exposure to high heat loads, those species that feed strictly by day are at increased risk of having their energy budgets constrained by increasing daytime temperatures,⁷ particularly if they are unable to compensate for reduced diurnal activity by increasing nocturnal activity. By increasing nocturnal activity, the usually-diurnal Arabian oryx was able to compensate completely when its diurnal activity was reduced as a result of shade-seeking in extreme daytime heat (Fig. 4).¹⁶⁹ The Arabian oryx were not prevented by natural predators from shifting freely between diurnal and nocturnal activity, but large mammals elsewhere will have an expensive trade-off to make because they may be exposed to a greater nocturnal predation pressure should they attempt to avoid high diurnal temperatures by becoming nocturnal. Nevertheless, species that show flexibility in their activity patterns are less likely to be affected adversely by climate change than are those species which are strictly diurnal, or even strictly nocturnal.¹⁹ If they are to survive climate change, large long-lived mammals will need to show flexibility in their behavioral repertoire, and not just behavior related to foraging.

Without a radical change in their behavior, the future survival of polar bears (*Ursus maritimus*) is considered bleak.¹⁰⁰ Over the past 28 y the number of polar bears in Hudson's Bay has

decreased, and those that remain are in poor body condition.¹⁷⁶ Polar bears are dependent heavily on Arctic spring ice, because that is where they discover the seals (on ice to give birth) that are their primary food source at this time.^{177,178} The Arctic ice is disappearing under the impact of global warming, and, if polar bears continue with their current lifestyle, the world population is likely to drop by two-thirds by 2050.¹⁷⁹ Polar bears may well survive if they have the capacity to make a major change in lifestyle (which the fossil record shows they have done previously), namely to abandon the ice, and their current food source, and to become land-based.¹⁷⁷ Another species forced to change its behavior and become land-based is the Pacific walrus (*Odobenus rosmarus divergens*). Walruses use sea ice as a breeding ground, as well as a resting platform between foraging dives, but the recent decline in Arctic sea ice has forced them to abandon the sea ice and haul out instead along the shores of Alaska and Russia.¹⁸⁰ Coastal haul outs often are associated with mortalities from trampling, exhaustion and the separation of calves from their mothers.¹⁸¹ Furthermore, there may be energetic costs as walruses are forced to spend more time at sea traveling between coastal haul out sites and offshore foraging areas than when offshore sea ice is available.¹⁸⁰ Unlike the walruses, which have to travel more, some humpback whales (*Megaptera novaeangliae*) are abandoning their migration habits and remaining in southeast Alaska throughout winter, seemingly in response to climate-induced increased availability of herring.¹⁸² Presumably the energetic cost of thermoregulation in the cold waters is offset by metabolic savings of not having to undertake one of the longest documented mammalian migrations, with food locally available.¹⁸³ The humpback whales will not be the only species for which migration patterns will be affected by climate change.¹⁸⁴

Future Research

Though we know so little about it, it will be on their physiological and behavioral plasticity that the future of large mammals, threatened by climate change, will depend. Plasticity of physiological and behavioral mechanisms allows the expression of latent talents, which can provide mammals with the capacity to adjust to new environments,^{129,185} and are fundamental to determining the consequences of climate change.^{127,130} Future research in climate change biology will require the measurement of physiological and behavioral characteristics of many identified individual mammals for long periods, probably decades.^{70,100} Since the responses to climate change are likely to be multifaceted responses to complex interrelated stresses, the approach will have to be that of field physiology,¹⁸⁶ namely the investigation of the mechanisms that an animal uses while going about its daily business in its natural habitat. The studies required fall within the sub-disciplines of conservation physiology^{129,130,187} and evolutionary physiology.¹⁸⁸ The growth of these sub-disciplines has resulted not just from the clear need for such an approach, but from the growing availability of suitable technology, such as the use of stable isotopes for field measurement of metabolic rate and water turnover,¹⁸⁹ and osmotic minipumps to deliver substances to¹⁹⁰ and equipment to sample blood from¹⁹¹ free-living animals.

The primary new technology, however, has been biotelemetry or biologging.^{187,192-194} Physiological variables such as body temperature, activity and energetic expenditure of terrestrial mammals now can be measured relatively easily in free-living animals. We need to make such sophisticated physiological measurements in individuals of several species inhabiting a variety of environments, measurements that would fall into the recently-defined field of macrophysiology, defined as “the investigation of variation in physiological traits over large geographical and temporal scales and the ecological implications of this variation”¹⁹⁵. Incorporating the resulting macrophysiological data into bioclimatic envelope models will allow us to better predict how species will respond to climate change. Knowing which species demonstrate sufficient physiological plasticity to cope with the consequences of climate change will allow for more informed decisions as to which species are particularly vulnerable to climate change.

About the Authors

In the face of climate change, large mammals will depend largely on their physiological phenotypic plasticity to survive, but there have been few appropriate studies of the physiological responses of free-living terrestrial mammals in their natural habitats. Performing such studies, in which they measure the effects of thermal stress and reduced water and food availability on behavioral patterns and physiological responses, is the main research focus of the authors. They have developed innovative techniques for long-term remote measurement of body temperature, locomotor activity, drinking patterns, thermoregulatory behavior and local microclimate around an animal, which they are using to investigate how free-living mammals, ranging in size from monkeys to elephants, respond to climate and habitat changes (Fig. 5).

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Figure 5. Photograph of the authors.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest are disclosed.

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