

This article was downloaded by: [University of Sunderland]

On: 13 January 2015, At: 21:14

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Temperature

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ktmp20>

## Responses of large mammals to climate change

Robyn S Hetem<sup>a</sup>, Andrea Fuller<sup>a</sup>, Shane K Maloney<sup>ab</sup> & Duncan Mitchell<sup>ab</sup>

<sup>a</sup> Brain Function Research Group; School of Physiology; University of the Witwatersrand; Faculty of Health Science; Parktown, South Africa

<sup>b</sup> School of Anatomy, Physiology, and Human Biology; University of Western Australia; Crawley, Australia

Published online: 21 Jul 2014.



CrossMark

[Click for updates](#)

To cite this article: Robyn S Hetem, Andrea Fuller, Shane K Maloney & Duncan Mitchell (2014) Responses of large mammals to climate change, *Temperature*, 1:2, 115-127, DOI: [10.4161/temp.29651](https://doi.org/10.4161/temp.29651)

To link to this article: <http://dx.doi.org/10.4161/temp.29651>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Versions of published Taylor & Francis and Routledge Open articles and Taylor & Francis and Routledge Open Select articles posted to institutional or subject repositories or any other third-party website are without warranty from Taylor & Francis of any kind, either expressed or implied, including, but not limited to, warranties of merchantability, fitness for a particular purpose, or non-infringement. Any opinions and views expressed in this article are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor & Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

It is essential that you check the license status of any given Open and Open Select article to confirm conditions of access and use.

# Responses of large mammals to climate change

Robyn S Hetem<sup>1,\*</sup>, Andrea Fuller<sup>1</sup>, Shane K Maloney<sup>1,2</sup>, and Duncan Mitchell<sup>1,2</sup>

<sup>1</sup>Brain Function Research Group; School of Physiology; University of the Witwatersrand; Faculty of Health Science; Parktown, South Africa;

<sup>2</sup>School of Anatomy, Physiology, and Human Biology; University of Western Australia; Crawley, Australia

**Keywords:** climate change physiology, phenotypic plasticity, physiological acclimation, behavioral flexibility, range shift, microevolution, temperature

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,<sup>1</sup> 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.<sup>2</sup> The rate of future climate change will be unprecedented in the Earth's history.<sup>3</sup> 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.<sup>4</sup> 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.<sup>5</sup> 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.<sup>6</sup>

According to Huey et al.<sup>7</sup> '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.<sup>8</sup> 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.<sup>9</sup> 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.<sup>10</sup> 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,<sup>11–14</sup> and current conservation strategies, which attempt to conserve communities and ecosystems as they exist, will be unsustainable.<sup>15–18</sup>

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

\*Correspondence to: Robyn S Hetem; Email: robyn.hetem@wits.ac.za

Submitted: 06/16/2014; Revised: 7/15/2014; Accepted: 07/19/2014; Published Online: 07/21/2014  
<http://dx.doi.org/10.4161/temp.29651>

more likely to be adversely effected by climate change than their smaller counterparts.<sup>19</sup> 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.

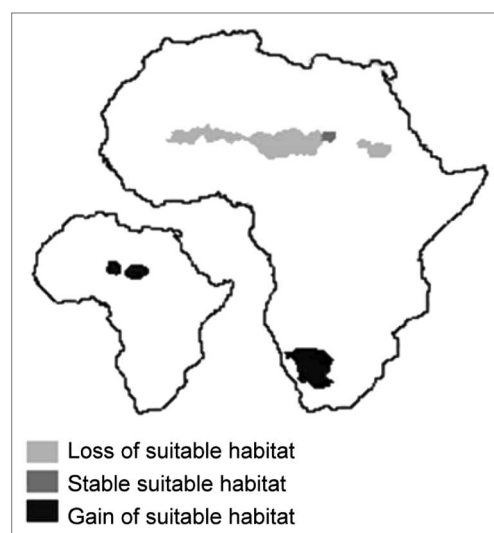
## Extinction

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.<sup>20</sup> 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.<sup>21</sup> 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.<sup>21</sup>

Among the large terrestrial mammals seemingly destined to become extinct are the charismatic species so important for eco-tourism. 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.<sup>22</sup> 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.<sup>21</sup> 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.<sup>23</sup>

## 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.<sup>24,25</sup> 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.<sup>17,26</sup> 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.<sup>22</sup>).

examined have shifted their range into adjacent habitats between 1970 and 2000,<sup>29</sup> 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.<sup>27</sup> Global meta-analyses have revealed that 80% of range shifts have been consistent with climate change predictions.<sup>24,28,29</sup> 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.<sup>30</sup> 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.<sup>22</sup> 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.<sup>31,32</sup> 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.<sup>33,34</sup>

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"<sup>35-37</sup>. 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.<sup>27</sup> 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.<sup>38-41</sup> 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.<sup>42,43</sup> 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.<sup>44-47</sup> All thermal aspects of those microclimates need to be quantified before they can be incorporated into climate change models.<sup>7</sup> 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.<sup>48</sup>

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.<sup>50,51</sup> 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.<sup>52</sup> 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.<sup>26,53-55</sup> For example, decreased rainfall altered the plant community and ultimately led to a decline in desert bighorn sheep (*Ovis canadensis nelsoni*) population in California.<sup>56</sup> These species interactions thus need to be incorporated into bioclimatic envelope models to better predict future species distributions,<sup>57</sup> which is the aim of a new scope of ecological research termed "global change ecology"<sup>58</sup>.

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.<sup>59</sup> 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<sup>60,61</sup> and mammals,<sup>62,63</sup> but they require an understanding of species' physiological responses to climate,<sup>64-66</sup> 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.<sup>45,67,68</sup>

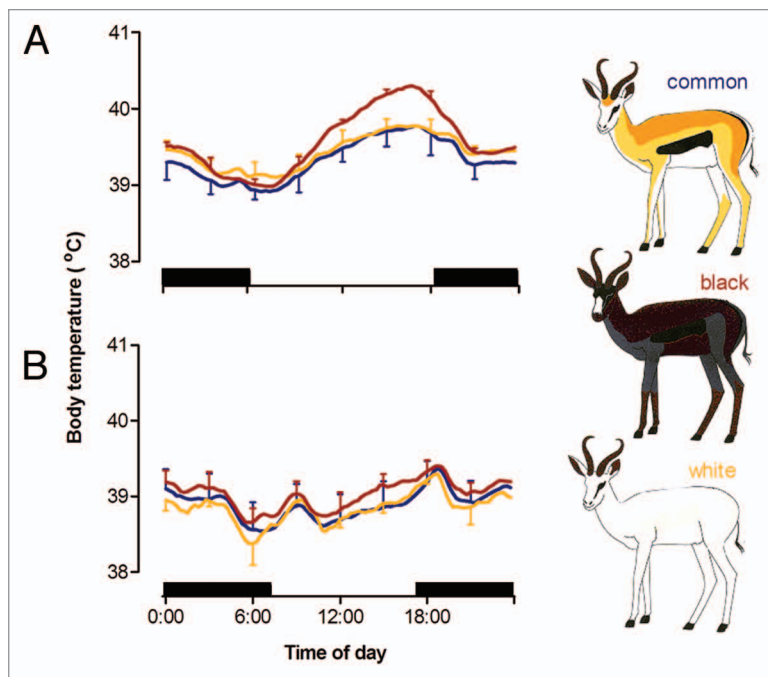
## Micro-Evolution

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.<sup>3,4</sup> A changing climate moves the so-called "fitness optimum" for different populations throughout the species range,<sup>3,4</sup> 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.<sup>69,70</sup> 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.<sup>71</sup>

The genetic adaptation that will be required to survive climate change<sup>70,72</sup> is not the slow process of speciation,<sup>3,73,74</sup> 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,<sup>75,76</sup> 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.<sup>83</sup> It remains uncertain, though, whether micro-evolution can result in a change in the climate tolerance of any species sufficient to prevent extinction.<sup>84</sup>

A morphological feature related to climate tolerance that is determined genetically is an animal's coat color. Analyses by Maloney et al.<sup>85</sup> 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.<sup>86,87</sup> 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.<sup>88</sup>).

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).<sup>88</sup> 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.<sup>89,90</sup> 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,<sup>91,92</sup> an inadequacy that is hopefully temporary.<sup>93</sup> However, methods to quantify a genetic component of adjustment to climate change are likely to remain difficult to implement, especially in long-lived mammals.<sup>94</sup> 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.<sup>95</sup> 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.<sup>96</sup> Réale et al.<sup>97</sup> 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.<sup>98</sup> 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.<sup>70,77,78,99,100</sup> 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,<sup>101</sup> making them more susceptible to extinction<sup>102</sup> than are species with short generation times. The issue is compounded because large species have greater range requirements.<sup>103</sup> 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.<sup>8</sup> 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.<sup>104-106</sup> The plasticity is known as an epigenetic effect. Phenotypic plasticity in animals exposed to a change in environment may involve acclimation, acclimatization, and learning<sup>104</sup> and can take place through phenology, developmental plasticity, physiological adjustments and behavioral flexibility.<sup>107</sup> 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.<sup>108</sup> 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.<sup>9</sup> 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.<sup>9</sup>

### 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,<sup>97</sup> 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.<sup>95</sup> 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.<sup>110</sup>

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.<sup>95</sup> 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.<sup>111</sup> 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.<sup>95</sup> 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.<sup>17,112-114</sup> 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.<sup>115</sup> Numerous studies have demonstrated the ecological and metabolic costs of such mistimed ecological events,<sup>112,116</sup> which ultimately may lead to a decrease in biodiversity.

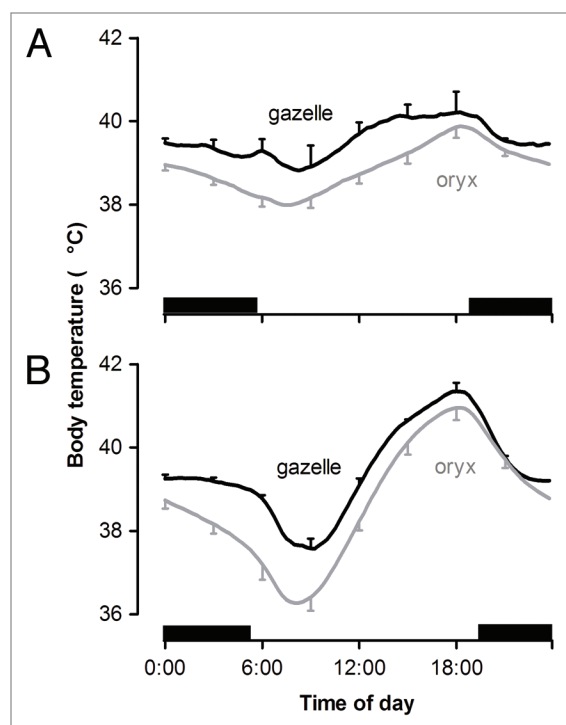
One possible cause of mismatch between phenological responses in connected species is the different environmental cues to which different species respond.<sup>117</sup> Whereas most plants and insects respond to seasonal changes in temperature, most vertebrate species are more sensitive to changes in photoperiod, although, as was the case for red deer on Rum, better nutrition can also advance reproductive events.<sup>110</sup> 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.<sup>70,76</sup> 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.<sup>118</sup> 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.<sup>119</sup> 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.<sup>120</sup>

### 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.<sup>121</sup> 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.<sup>18</sup> 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.<sup>120</sup> 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.<sup>122</sup> Indeed, only 7% of recently-observed changes in mammalian body masses provide support for an advantage to smaller mammals.<sup>123</sup> 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).<sup>124</sup>

Although understanding the physiological mechanisms is essential for predicting responses to climate change,<sup>70,113</sup> 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.<sup>125</sup> 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

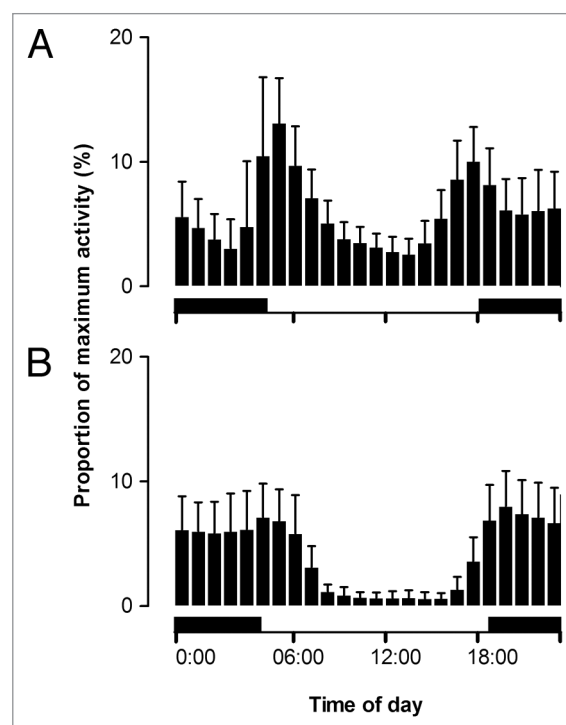


**Figure 3.** Nychthemeral rhythm of body temperature (mean  $\pm$  SD) for five free-living Arabian oryx (gray line) and four free-living Arabian sand gazelle (black line) during both the warm wet (A) and hot dry (B) periods. Black bars represent night periods (reprinted from Hetem et al.<sup>124</sup>).

works primarily at the level of physiology and behavior,<sup>100</sup> 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.<sup>54,126-128</sup>

#### Physiological acclimatization

Though physiological mechanisms are responsible for the capacity of animals to adjust to new environments,<sup>129</sup> 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.<sup>130</sup> 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"<sup>131</sup>, 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.<sup>126,132,133</sup> 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.<sup>169</sup>).

(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.<sup>135</sup> 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 conditions<sup>135</sup> and because enhanced organismic complexity often is accompanied by increased thermal sensitivity.<sup>136</sup>

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.<sup>113,137-139</sup> Endotherms, as thermal specialists, then are likely to be particularly vulnerable to climate change.<sup>7</sup> 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.<sup>140</sup> Tropical mammals display a narrower TNZ than do their arctic counterparts,<sup>141</sup> 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.<sup>142</sup> Conversely, mammalian species with wide thermoneutral zones, such as the hibernating mammalian species in the Canadian Arctic region,<sup>143,144</sup> 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.<sup>19</sup> 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.<sup>7</sup>

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.<sup>133,145</sup> The Arabian oryx inhabiting the extreme environment of the Arabian Desert may be living at the edge of its physiological limits.<sup>146,147</sup> 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.<sup>148</sup> 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.<sup>149</sup> In the Arabian oryx when conflict between regulatory systems occurs, priority is given to osmoregulation.<sup>147</sup> 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.<sup>150</sup> 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.<sup>147,151</sup>

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.<sup>152</sup> 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.<sup>153-156</sup> 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.<sup>157</sup> Plasticity in rete function may well provide an adjustment for

artiodactyls to cope with aridity and heat stress predicted to occur with climate change.<sup>151,158</sup>

### 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.<sup>159</sup> 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.<sup>160</sup>

Numerous species of antelope in the northern hemisphere display plasticity in offspring birth mass in response to changing climatic conditions.<sup>55</sup> 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.<sup>161</sup> 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.<sup>162-164</sup> 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.<sup>16,165</sup> Since behavioral changes generally are less costly than are autonomic responses, behavioral adjustments are likely to be preferred.<sup>166</sup> However, to date, only two models, both in ectotherms,<sup>167,168</sup> 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,<sup>167</sup> endotherms<sup>169</sup> 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.<sup>162,163</sup> Importantly, the available microclimates can differ substantially from the macroclimate used in many modeling exercises, provided there is sufficient thermal heterogeneity within a habitat.<sup>7,44,170</sup> 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.<sup>162,165,171</sup> 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.<sup>172</sup> 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.<sup>172</sup>

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.<sup>173</sup> 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.<sup>174</sup> 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.<sup>175</sup> 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,<sup>7</sup> 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).<sup>169</sup> 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.<sup>19</sup> 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.<sup>100</sup> 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.<sup>176</sup> 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.<sup>177,178</sup> 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.<sup>179</sup> 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.<sup>177</sup> 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.<sup>180</sup> Coastal haul outs often are associated with mortalities from trampling, exhaustion and the separation of calves from their mothers.<sup>181</sup> 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.<sup>180</sup> 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.<sup>182</sup> 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.<sup>183</sup> The humpback whales will not be the only species for which migration patterns will be affected by climate change.<sup>184</sup>

## 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,<sup>129,185</sup> and are fundamental to determining the consequences of climate change.<sup>127,130</sup> 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.<sup>70,100</sup> 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,<sup>186</sup> 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<sup>129,130,187</sup> and evolutionary physiology.<sup>188</sup> 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,<sup>189</sup> and osmotic minipumps to deliver substances to<sup>190</sup> and equipment to sample blood from<sup>191</sup> free-living animals.

The primary new technology, however, has been biotelemetry or biologging.<sup>187,192-194</sup> 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”<sup>195</sup>. 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).

### References

1. Stocker TF, Qin D, Plattner G-K, Alexander LV, Allen SK, Bindoff NL, Bréon F-M, Church JA, Cubasch U, Emori S, et al. Technical summary. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, eds. *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA.: Cambridge University Press, 2013.
2. Barnosky AD, Hadly EA, Bell CJ. Mammalian response to global warming on varied temporal scales. *J Mammal* 2003; 84:354-68; [http://dx.doi.org/10.1644/1545-1542\(2003\)084<0354:MRTGW>2.0.CO;2](http://dx.doi.org/10.1644/1545-1542(2003)084<0354:MRTGW>2.0.CO;2)
3. Davis MB, Shaw RG. Range shifts and adaptive responses to Quaternary climate change. *Science* 2001; 292:673-9; PMID:11326089; <http://dx.doi.org/10.1126/science.292.5517.673>
4. Davis MB, Shaw RG, Etterson JR. Evolutionary responses to changing climate. *Ecology* 2005; 86:1704-14
5. Quintero I, Wiens JJ. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecol Lett* 2013; 16:1095-103; PMID:23800223; <http://dx.doi.org/10.1111/ele.12144>
6. Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL, Estrella N, Seguin B, et al. Attributing physical and biological impacts to anthropogenic climate change. *Nature* 2008; 453:353-7; PMID:18480817; <http://dx.doi.org/10.1038/nature06937>
7. Huey RB, Kearney MR, Krockenberger A, Holtum JA, Jess M, Williams SE. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos Trans R Soc Lond B Biol Sci* 2012; 367:1665-79; PMID:22566674; <http://dx.doi.org/10.1098/rstb.2012.0005>
8. Mitchell D, Fuller A, Hetem RS, Maloney SK. Climate change physiology: the challenge of the decades. In: Morris S, Vosloo A, eds. *4th Comparative Physiology Biochemistry Meeting in Africa. Maasai Mara Game Reserve, Kenya: Medimond Publishing S.r.l., Via Maserati 5, 40128 Bologna, Italy, 2008:383-94.*
9. Goldberg AD, Allis CD, Bernstein E. Epigenetics: a landscape takes shape. *Cell* 2007; 128:635-8; PMID:17320500
10. Fuller A, Dawson T, Helmuth B, Hetem RS, Mitchell D, Maloney SK. Physiological mechanisms in coping with climate change. *Physiol Biochem Zool* 2010; 83:713-20; PMID:20578846; <http://dx.doi.org/10.1086/652242>
11. Malcolm JR, Markham A. Global warming and terrestrial biodiversity decline. *World Wildlife Fund Climate Change Campaign*. Washington, USA, 2000:33.
12. Sala OE, Chapin FS 3<sup>rd</sup>, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, et al. Global biodiversity scenarios for the year 2100. *Science* 2000; 287:1770-4; PMID:10710299; <http://dx.doi.org/10.1126/science.287.5459.1770>
13. Lovejoy TE, Hannah L. *Climate change and biodiversity*. New Haven, CT: Yale University Press, 2005.
14. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. Impacts of climate change on the future of biodiversity. *Ecol Lett* 2012; •••; <http://dx.doi.org/10.1111/j.1461-0248.2011.01736.x>; PMID:22257223
15. Hannah L, Midgley GF, Lovejoy T, Bond WJ, Bush M, Lovett JC, Scott D, Woodward FI. Conservation of biodiversity in a changing climate. *Conserv Biol* 2002; 16:264-8; <http://dx.doi.org/10.1046/j.1523-1739.2002.00465.x>
16. Hannah L, Midgley GF, Millar D. Climate change-integrated conservation strategies. *Glob Ecol Biogeogr* 2002; 11:485-95; <http://dx.doi.org/10.1046/j.1466-822X.2002.00306.x>
17. Hughes I. Biological consequences of global warming: is the signal already apparent? *Trends Ecol Evol* 2000; 15:56-61; PMID:10652556; [http://dx.doi.org/10.1016/S0169-5347\(99\)01764-4](http://dx.doi.org/10.1016/S0169-5347(99)01764-4)
18. Millien V, Lyons SK, Olson L, Smith FA, Wilson AB, Yom-Tov Y. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol Lett* 2006; 9:853-69; PMID:16796576; <http://dx.doi.org/10.1111/j.1461-0248.2006.00928.x>



**Figure 5.** Photograph of the authors.

### Disclosure of Potential Conflicts of Interest

No potential conflicts of interest are disclosed.

### Acknowledgments

We thank the South African National Research Foundation (NRF), the Oppenheimer Memorial Trust, the Carnegie Corporation of New York, the global change SysTem for Analysis, Research and Training (START), the University of the Witwatersrand, and the Australian Research Council for financial support. We thank Dr Leith Meyer and the Central Animal Services of the University of the Witwatersrand for providing veterinary expertise in our field studies, and the managers and owners of numerous field sites for allowing us access to their facilities, and providing invaluable support.

19. McCain CM, King SRB. Body size and activity times mediate mammalian responses to climate change. *Glob Change Biol* 2014; 20:1760-9; PMID:24449019; <http://dx.doi.org/10.1111/gcb.12499>
20. Benton MJ, Twitchett RJ. How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol Evol* 2003; 18:358-65; [http://dx.doi.org/10.1016/S0169-5347\(03\)00093-4](http://dx.doi.org/10.1016/S0169-5347(03)00093-4)
21. Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, De Siqueira MF, Grainger A, Hannah L, et al. Extinction risk from climate change. *Nature* 2004; 427:145-8; PMID:14712274
22. Thuiller W, Broennimann O, Hughes G, Alkemade JRM, Midgley GF, Corsi F. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Glob Change Biol* 2006; 12:424-9; <http://dx.doi.org/10.1111/j.1365-2486.2006.01115.x>
23. Ogutu JO, Owen-Smith N. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecol Lett* 2003; 6:412-9; <http://dx.doi.org/10.1046/j.1461-0248.2003.00447.x>
24. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 2003; 421:37-42; PMID:12511946; <http://dx.doi.org/10.1038/nature01286>
25. Thuiller W. Biodiversity: climate change and the ecologist. *Nature* 2007; 448:550-2; PMID:17671497; <http://dx.doi.org/10.1038/448550a>
26. Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F. Ecological responses to recent climate change. *Nature* 2002; 416:389-95; PMID:11919621; <http://dx.doi.org/10.1038/416389a>
27. Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. Rapid range shifts of species associated with high levels of climate warming. *Science* 2011; 333:1024-6; PMID:21852500; <http://dx.doi.org/10.1126/science.1206432>
28. Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. Fingerprints of global warming on wild animals and plants. *Nature* 2003; 421:57-60; PMID:12511952; <http://dx.doi.org/10.1038/nature01333>
29. Thomas CD. Climate, climate change and range boundaries. *Divers Distrib* 2010; 16:488-95; <http://dx.doi.org/10.1111/j.1472-4642.2010.00642.x>
30. Schloss CA, Nuñez TA, Lawler JJ. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc R Soc Lond B Biol Sci* 2014;doi/10.1073/pnas.1116791109.
31. Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD. Ecology. Assisted colonization and rapid climate change. *Science* 2008; 321:345-6; PMID:18635780; <http://dx.doi.org/10.1126/science.1157897>
32. Hunter ML Jr. Climate change and moving species: furthering the debate on assisted colonization. *Conserv Biol* 2007; 21:1356-8; PMID:17883502; <http://dx.doi.org/10.1111/j.1523-1739.2007.00780.x>
33. Davidson I, Simkanin C. Skeptical of assisted colonization. *Science* 2008; 322:1048-9, author reply 1049-50; PMID:19008427; <http://dx.doi.org/10.1126/science.322.5904.1048b>
34. Loss SR, Terwilliger LA, Peterson AC. Assisted colonization: Integrating conservation strategies in the face of climate change. *Biol Conserv* 2011; 144:92-100; <http://dx.doi.org/10.1016/j.biocon.2010.11.016>
35. Austin M. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol Modell* 2007; 200:1-19; <http://dx.doi.org/10.1016/j.ecolmodel.2006.07.005>
36. Huntley B, Green RE, Collingham YC, Hill JK, Willis SG, Bartlein PJ, Cramer W, Hagemeyer WJM, Thomas CJ. The performance of models relating species geographical distributions to climate is independent of trophic level. *Ecol Lett* 2004; 7:417-26; <http://dx.doi.org/10.1111/j.1461-0248.2004.00598.x>
37. Peterson AT. Predicting the geography of species' invasions via ecological niche modeling. *Q Rev Biol* 2003; 78:419-33; PMID:14737826; <http://dx.doi.org/10.1086/378926>
38. Heikkinen RK, Luoto M, Araujo MB, Virkkala R, Thuiller W, Sykes MT. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog Phys Geogr* 2006; 30:751-77; <http://dx.doi.org/10.1177/03091333060071957>
39. Luoto M, Pöyry J, Heikkinen RK, Saarinen K. Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Glob Ecol Biogeogr* 2005; 14:575-84; <http://dx.doi.org/10.1111/j.1466-822X.2005.00186.x>
40. Pearson RG, Dawson TP. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob Ecol Biogeogr* 2003; 12:361-71; <http://dx.doi.org/10.1046/j.1466-822X.2003.00042.x>
41. Thuiller W. Patterns and uncertainties of species' range shifts under climate change. *Glob Change Biol* 2004; 10:2020-7; <http://dx.doi.org/10.1111/j.1365-2486.2004.00859.x>
42. Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* 2004; 430:71-5; PMID:15229599; <http://dx.doi.org/10.1038/nature02708>
43. Parmesan C, Root TL, Willig MR. Impacts of extreme weather and climate on terrestrial biota. *Bull Am Meteorol Soc* 2000; 81:443-50; [http://dx.doi.org/10.1175/1520-0477\(2000\)081<0443:IOEWAC>2.3.CO;2](http://dx.doi.org/10.1175/1520-0477(2000)081<0443:IOEWAC>2.3.CO;2)
44. Helmut B, Broitman BR, Blanchette CA, Gilman S, Halpin P, Harley CDG, O'Donnell MJ, Hofmann GE, Menge B, Strickland D. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol Monogr* 2006; 76:461-79; [http://dx.doi.org/10.1890/0012-9615\(2006\)076\[0461:MPOTSI\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2)
45. Hodkinson ID. Species response to global environmental change or why ecophysiological models are important: a reply to Davis et al. *J Anim Ecol* 1999; 68:1259-62; <http://dx.doi.org/10.1046/j.1365-2656.1999.00372.x>
46. Porter WP, Budaraju S, Stewart WE, Ramankutty N. Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. *Am Zool* 2000; 40:597-630; [http://dx.doi.org/10.1668/0003-1569\(2000\)040\[0597:CCEOBA\]2.0.CO;2](http://dx.doi.org/10.1668/0003-1569(2000)040[0597:CCEOBA]2.0.CO;2)
47. Porter WP, Sabo JL, Tracy CR, Reichman OJ, Ramankutty N. Physiology on a landscape scale: plant-animal interactions. *Integr Comp Biol* 2002; 42:431-53; PMID:21708738; <http://dx.doi.org/10.1093/icb/42.3.431>
48. Hetem RS, Maloney SK, Fuller A, Meyer LCR, Mitchell D. Validation of a biotelemetric technique, using ambulatory miniature black globe thermometers, to quantify thermoregulatory behaviour in ungulates. *J Exp Zool A Ecol Genet Physiol* 2007; 307:342-56; PMID:17480034; <http://dx.doi.org/10.1002/jez.389>
49. Urban MC, Tewksbury JJ, Sheldon KS. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proc Biol Sci* 2012; 279:2072-80; PMID:22217718; <http://dx.doi.org/10.1098/rspb.2011.2367>
50. Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 1998; 391:783-6; PMID:9486646; <http://dx.doi.org/10.1038/35842>
51. Mustin K, Sutherland WJ, Gill JA. The complexity of predicting climate-induced ecological impacts. *Clim Res* 2007; 35:165-75; <http://dx.doi.org/10.3354/cr00723>
52. Hersteinsson P, MacDonald DW. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos* 1992; 64:505-15; <http://dx.doi.org/10.2307/3545168>
53. Schneider SH, Root TL. Ecological implications of climate change will include surprises. *Biodivers Conserv* 1996; 5:1109-19; <http://dx.doi.org/10.1007/BF00052720>
54. McCarty JP. Ecological consequences of recent climate change. *Conserv Biol* 2001; 15:320-31; <http://dx.doi.org/10.1046/j.1523-1739.2001.015002320.x>
55. Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan K-S, Lima M. Ecological effects of climate fluctuations. *Science* 2002; 297:1292-6; PMID:12193777; <http://dx.doi.org/10.1126/science.1071281>
56. Epps CW, McCullough DR, Wehausen JD, Bleich VC, L. Reche J. Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conserv Biol* 2004; 18:102-13; <http://dx.doi.org/10.1111/j.1523-1739.2004.00023.x>
57. Guisan A, Thuiller W. Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 2005; 8:993-1009; <http://dx.doi.org/10.1111/j.1461-0248.2005.00792.x>
58. Schlesinger WH. Global change ecology. *Trends Ecol Evol* 2006; 21:348-51; PMID:16769436; <http://dx.doi.org/10.1016/j.tree.2006.03.004>
59. Levinsky I, Skov F, Svenning J-C, Rahbek C. Potential impacts of climate change on the distributions and diversity patterns of European mammals. *Biodivers Conserv* 2007; 16:3803-16; <http://dx.doi.org/10.1007/s10531-007-9181-7>
60. Kearney M, Porter WP. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 2004; 85:3119-31; <http://dx.doi.org/10.1890/03-0820>
61. Pörtner HO. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* 2001; 88:137-46; PMID:11480701; <http://dx.doi.org/10.1007/s001140100216>
62. Johnston K, Schmitz O. Wildlife and climate change: assessing the sensitivity of selected species to simulated doubling of atmospheric CO<sub>2</sub>. *Glob Change Biol* 1997; 3:531-44; <http://dx.doi.org/10.1046/j.1365-2486.1997.00093.x>
63. Taulman JF, Robbins LW. Recent range expansion and distributional limits of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. *J Biogeogr* 1996; 23:635-48; <http://dx.doi.org/10.1111/j.1365-2699.1996.tb00024.x>
64. Franklin J. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Prog Phys Geogr* 1995; 19:474-99; <http://dx.doi.org/10.1177/030913339501900403>
65. Guisan A, Zimmermann NE. Predictive habitat distribution models in ecology. *Ecol Modell* 2000; 135:147-86; [http://dx.doi.org/10.1016/S0304-3800\(00\)00354-9](http://dx.doi.org/10.1016/S0304-3800(00)00354-9)
66. Mack RN. Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biol Conserv* 1996; 78:107-21; [http://dx.doi.org/10.1016/0006-3207\(96\)00021-3](http://dx.doi.org/10.1016/0006-3207(96)00021-3)
67. Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM. A global biome model based on plant physiology and dominance, soil properties and climate. *J Biogeogr* 1992; 19:117-34; <http://dx.doi.org/10.2307/2845499>



68. Sykes MT, Prentice IC. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. *Clim Change* 1996; 34:161-77; <http://dx.doi.org/10.1007/BF00224628>
69. Garant D, Forde SE, Hendry AP. The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct Ecol* 2007; 21:434-43; <http://dx.doi.org/10.1111/j.1365-2435.2006.01228.x>
70. Visser ME. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc Biol Sci* 2008; 275:649-59; PMID:18211875; <http://dx.doi.org/10.1098/rspb.2007.0997>
71. Kerr J, Packer L. The impact of climate change on mammal diversity in Canada. *Environ Monit Assess* 1998; 49:263-70; <http://dx.doi.org/10.1023/A:1005846910199>
72. Rice KJ, Emery NC. Managing microevolution: restoration in the face of global change. *Front Ecol Environ* 2003; 1:469-78; [http://dx.doi.org/10.1890/1540-9295\(2003\)001\[0469:MMRITF\]2.0.CO;2](http://dx.doi.org/10.1890/1540-9295(2003)001[0469:MMRITF]2.0.CO;2)
73. Bradshaw AD, McNeilly T. Evolutionary response to global climatic change. *Ann Bot (Lond)* 1991; 67:5-14
74. Huntley B. Limitations on adaptation: evolutionary response to climatic change? *Heredity (Edinb)* 2007; 98:247-8; PMID:17406660; <http://dx.doi.org/10.1038/sj.hdy.6800972>
75. Bradshaw WE, Holzapfel CM. Climate change. Evolutionary response to rapid climate change. *Science* 2006; 312:1477-8; PMID:16763134; <http://dx.doi.org/10.1126/science.1127000>
76. Bradshaw WE, Holzapfel CM. Genetic response to rapid climate change: it's seasonal timing that matters. *Mol Ecol* 2008; 17:157-66; PMID:17850269; <http://dx.doi.org/10.1111/j.1365-294X.2007.03509.x>
77. Hendry AP, Kinnison MT. Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution* 1999; 53:1637-53; <http://dx.doi.org/10.2307/2640428>
78. Kinnison MT, Hendry AP. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 2001; 112-113:145-64; PMID:11838763; <http://dx.doi.org/10.1023/A:1013375419520>
79. Reznick DN, Ghalambor CK. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 2001; 112-113:183-98; PMID:11838765; <http://dx.doi.org/10.1023/A:1013352109042>
80. Rodríguez-Trelles F, Rodríguez MA. Rapid micro-evolution and loss of chromosomal diversity in *Drosophila* in response to climate warming. *Evol Ecol* 1998; 12:829-38; <http://dx.doi.org/10.1023/A:1006546616462>
81. Thompson JN. Rapid evolution as an ecological process. *Trends Ecol Evol* 1998; 13:329-32; PMID:21238328; [http://dx.doi.org/10.1016/S0169-5347\(98\)01378-0](http://dx.doi.org/10.1016/S0169-5347(98)01378-0)
82. Yoshida T, Jones LE, Ellner SP, Fussmann GF, Hairston NG Jr. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* 2003; 424:303-6; PMID:12867979; <http://dx.doi.org/10.1038/nature01767>
83. Row JR, Wilson PJ, Gomez C, Koen EL, Bowman J, Thornton D, Murray DL. The subtle role of climate change on population genetic structure in Canada lynx. *Glob Chang Biol* 2014; 20:2076-86; <http://dx.doi.org/10.1111/gcb.12526>; PMID:24415466
84. Parmesan C. Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Syst* 2006; 37:637-69; <http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110100>
85. Maloney SK, Fuller A, Mitchell D. Climate change: is the dark Soay sheep endangered? *Biol Lett* 2009; 5:826-9; PMID:19625302; <http://dx.doi.org/10.1098/rsbl.2009.0424>
86. Clutton-Brock TH, Wilson K, Stevenson IR. Density-dependent selection on horn phenotype in Soay sheep. *Philos Trans R Soc Lond B Biol Sci* 1997; 352:839-50; PMID:9279899; <http://dx.doi.org/10.1098/rstb.1997.0064>
87. Gratten J, Wilson AJ, McRae AF, Beraldi D, Visscher PM, Pemberton JM, Slate J. A localized negative genetic correlation constrains microevolution of coat color in wild sheep. *Science* 2008; 319:318-20; PMID:18202287; <http://dx.doi.org/10.1126/science.1151182>
88. Hetem RS, de Witt BA, Fick LG, Fuller A, Kerley GI, Meyer LC, Mitchell D, Maloney SK. Body temperature, thermoregulatory behaviour and pelt characteristics of three colour morphs of springbok (*Antidorcas marsupialis*). *Comp Biochem Physiol A Mol Integr Physiol* 2009; 152:379-88; PMID:19056508; <http://dx.doi.org/10.1016/j.cbpa.2008.11.011>
89. Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J. Bergmann's rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. *Proc Natl Acad Sci U S A* 2008; 105:13492-6; PMID:18757740; <http://dx.doi.org/10.1073/pnas.0800999105>
90. Wolf M, Friggens M, Salazar-Bravo J. Does weather shape rodents? Climate related changes in morphology of two heteromyid species. *Naturwissenschaften* 2009; 96:93-101; PMID:18843477; <http://dx.doi.org/10.1007/s00114-008-0456-y>
91. Gienapp P, Teplitsky C, Alho JS, Mills JA, Merilä J. Climate change and evolution: disentangling environmental and genetic responses. *Mol Ecol* 2008; 17:167-78; PMID:18173499; <http://dx.doi.org/10.1111/j.1365-294X.2007.03413.x>
92. Holt RD. The microevolutionary consequences of climate change. *Trends Ecol Evol* 1990; 5:311-5; PMID:21232381; [http://dx.doi.org/10.1016/0169-5347\(90\)90088-U](http://dx.doi.org/10.1016/0169-5347(90)90088-U)
93. Franks SJ, Hoffmann AA. Genetics of climate change adaptation. *Annu Rev Genet* 2012; 46:185-208; PMID:22934640; <http://dx.doi.org/10.1146/annurev-genet-110711-155511>
94. Merilä J, Hendry AP. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol Appl* 2014; 7:1-14; PMID:24454544; <http://dx.doi.org/10.1111/eva.12137>
95. Boutin S, Lane JE. Climate change and mammals: evolutionary versus plastic responses. *Evol Appl* 2014; 7:29-41; PMID:24454546; <http://dx.doi.org/10.1111/eva.12121>
96. Réale D, Berteaux D, McAdam AG, Boutin S. Lifetime selection on heritable life-history traits in a natural population of red squirrels. *Evolution* 2003; 57:2416-23; PMID:14628929; <http://dx.doi.org/10.1111/j.0014-3820.2003.tb00253.x>
97. Réale D, McAdam AG, Boutin S, Berteaux D. Genetic and plastic responses of a northern mammal to climate change. *Proc Biol Sci* 2003; 270:591-6; PMID:12769458; <http://dx.doi.org/10.1098/rspb.2002.2224>
98. Postma E. Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. *J Evol Biol* 2006; 19:309-20; PMID:16599906; <http://dx.doi.org/10.1111/j.1420-9101.2005.01007.x>
99. Hendry AP, Kinnison MT. An introduction to microevolution: rate, pattern, process. *Genetica* 2001; 112-113:1-8; PMID:11838760; <http://dx.doi.org/10.1023/A:1013368628607>
100. Berteaux D, Réale D, McAdam AG, Boutin S. Keeping pace with fast climate change: can arctic life count on evolution? *Integr Comp Biol* 2004; 44:140-51; PMID:21680494; <http://dx.doi.org/10.1093/icb/44.2.140>
101. Rosenheim JA, Tabashnik BE. Influence of generation time on the rate of response to selection. *Am Nat* 1991; 137:527-41; <http://dx.doi.org/10.1086/285181>
102. Gomulkiewicz R, Holt RD. When does evolution by natural selection prevent extinction? *Evolution* 1995; 49:201-7; <http://dx.doi.org/10.2307/2410305>
103. Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A. Multiple causes of high extinction risk in large mammal species. *Science* 2005; 309:1239-41; PMID:16037416; <http://dx.doi.org/10.1126/science.1116030>
104. Garland T Jr., Kelly SA. Phenotypic plasticity and experimental evolution. *J Exp Biol* 2006; 209:2344-61; PMID:16731811; <http://dx.doi.org/10.1242/jeb.02244>
105. Pigliucci M. Evolution of phenotypic plasticity: where are we going now? *Trends Ecol Evol* 2005; 20:481-6; PMID:16701424; <http://dx.doi.org/10.1016/j.tree.2005.06.001>
106. Via S, Gomulkiewicz R, De Jong G, Scheiner SM, Schlichting CD, Van Tienderen PH. Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol Evol* 1995; 10:212-7; PMID:21237012; [http://dx.doi.org/10.1016/S0169-5347\(00\)89061-8](http://dx.doi.org/10.1016/S0169-5347(00)89061-8)
107. Fitzpatrick BM. Underappreciated consequences of phenotypic plasticity for ecological speciation. *Int J Ecol* 2012. Article ID 2012; 256017:12
108. Donnelly A, Caffarra A, Kelleher CT, O'Neill BF, Diskin E, Pletsers A, Proctor H, Stirnemann R, O'Halloran J, Peñuelas J, et al. Surviving in a warmer world: environmental and genetic responses. *Clim Res* 2012; 53:245-62; <http://dx.doi.org/10.3354/cr01102>
109. Harrington R, Woiwod I, Sparks T. Climate change and trophic interactions. *Trends Ecol Evol* 1999; 14:146-50; PMID:10322520; [http://dx.doi.org/10.1016/S0169-5347\(99\)01604-3](http://dx.doi.org/10.1016/S0169-5347(99)01604-3)
110. Moyes K, Nussey DH, Clements MN, Guinness FE, Morris A, Morris S, Pemberton JM, Kruuk LEB, Clutton-Brock TH. Advancing breeding phenology in response to environmental change in a wild red deer population. *Glob Change Biol* 2011; 17:2455-69; <http://dx.doi.org/10.1111/j.1365-2486.2010.02382.x>
111. Burthe S, Butler A, Searle KR, Hall SJ, Thackeray SJ, Wanless S. Demographic consequences of increased winter births in a large seasonally breeding mammal (*Bos taurus*) in response to climate change. *J Anim Ecol* 2011; 80:1134-44; PMID:21668894; <http://dx.doi.org/10.1111/j.1365-2656.2011.01865.x>
112. Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 2001; 291:2598-600; PMID:11283370; <http://dx.doi.org/10.1126/science.1057487>
113. Visser ME, Both C. Shifts in phenology due to global climate change: the need for a yardstick. *Proc Biol Sci* 2005; 272:2561-9; PMID:16321776; <http://dx.doi.org/10.1098/rspb.2005.3356>
114. Visser ME, Both C, Lambrechts MM. Global climate change leads to mistimed avian reproduction. *Adv Ecol Res* 2004; 35:89-110; [http://dx.doi.org/10.1016/S0065-2504\(04\)35005-1](http://dx.doi.org/10.1016/S0065-2504(04)35005-1)
115. Post E, Forchhammer MC. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philos Trans R Soc Lond B Biol Sci* 2008; 363:2369-75; PMID:18006410; <http://dx.doi.org/10.1098/rstb.2007.2207>
116. Stenseth NC, Mysterud A. Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. *Proc Natl Acad Sci U S A* 2002; 99:13379-81; PMID:12370424; <http://dx.doi.org/10.1073/pnas.212519399>



117. Voigt W, Perner J, Davis AJ, Eggers T, Schumacher J, Bährmann R, Fabian Br, Heinrich W, Köhler G, Licher D, et al. Trophic levels are differentially sensitive to climate. *Ecology* 2003; 84:2444; <http://dx.doi.org/10.1890/02-0266>
118. Forcada J, Trathan PN, Murphy EJ. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Glob Change Biol* 2008; 14:2473-88
119. Mitchell CD, Maher CR. Horn growth in male pronghorns *Antilocapra americana*: selection for precocial maturation in stochastic environments. *Acta Theriol (Warsz)* 2006; 51:405-9; <http://dx.doi.org/10.1007/BF03195187>
120. Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science* 2009; 325:464-7; PMID:19574350; <http://dx.doi.org/10.1126/science.1173668>
121. Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. Declining body size: a third universal response to warming? *Trends Ecol Evol* 2011; 26:285-91; PMID:21470708; <http://dx.doi.org/10.1016/j.tree.2011.03.005>
122. Yom-Tov Y, Heggberget TM, Wiig O, Yom-Tov S. Body size changes among otters, *Lutra lutra*, in Norway: the possible effects of food availability and global warming. *Oecologia* 2006; 150:155-60; PMID:16868759; <http://dx.doi.org/10.1007/s00442-006-0499-8>
123. Teplitsky C, Millien V. Climate warming and Bergmann's rule through time: is there any evidence? *Evol Appl* 2014; 7:156-68; PMID:24454554; <http://dx.doi.org/10.1111/eva.12129>
124. Hetem RS, Strauss WM, Fick LG, Maloney SK, Meyer LC, Shobrak M, Fuller A, Mitchell D. Does size matter? Comparison of body temperature and activity of free-living Arabian oryx (*Oryx leucoryx*) and the smaller Arabian sand gazelle (*Gazella subgutturosa marica*) in the Saudi desert. *J Comp Physiol B* 2012; 182:437-49; PMID:22001971; <http://dx.doi.org/10.1007/s00360-011-0620-0>
125. Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P, Beerli P. The strength of phenotypic selection in natural populations. *Am Nat* 2001; 157:245-61; PMID:18707288; <http://dx.doi.org/10.1086/319193>
126. Stillman JH. Acclimation capacity underlies susceptibility to climate change. *Science* 2003; 301:65; PMID:12843385; <http://dx.doi.org/10.1126/science.1083073>
127. Helmuth B, Kingsolver JG, Carrington E. Biophysics, physiological ecology, and climate change: does mechanism matter? *Annu Rev Physiol* 2005; 67:177-201; PMID:15709956; <http://dx.doi.org/10.1146/annurev.physiol.67.040403.105027>
128. Calosi P, Bilton DT, Spicer JJ. Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biol Lett* 2008; 4:99-102; PMID:17986429; <http://dx.doi.org/10.1098/rsbl.2007.0408>
129. Carey C. How physiological methods and concepts can be useful in conservation biology. *Integr Comp Biol* 2005; 45:4-11; PMID:21676738; <http://dx.doi.org/10.1093/icb/45.1.4>
130. Seebacher F, Franklin CE. Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Philos Trans R Soc Lond B Biol Sci* 2012; 367:1607-14; PMID:22566670; <http://dx.doi.org/10.1098/rstb.2012.0036>
131. Kenney WL, DeGroot DW, Alexander Holowatz L. Extremes of human heat tolerance: life at the precipice of thermoregulatory failure. *J Therm Biol* 2004; 29:479-85
132. Gilman SE, Wetthey DS, Helmuth B. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proc Natl Acad Sci U S A* 2006; 103:9560-5; PMID:16763050; <http://dx.doi.org/10.1073/pnas.0510992103>
133. Somero GN. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J Exp Biol* 2010; 213:912-20; PMID:20190116; <http://dx.doi.org/10.1242/jeb.037473>
134. Pörtner HO, Farrell AP. Physiology and climate change: studies of physiological mechanisms are needed to predict climate effects on ecosystems at species and community levels. *Science* 2008; 322:690-2; PMID:18974339; <http://dx.doi.org/10.1126/science.1163156>
135. Pörtner HO. Climate variability and the energetic pathways of evolution: the origin of endothermy in mammals and birds. *Physiol Biochem Zool* 2004; 77:959-81; PMID:15674770; <http://dx.doi.org/10.1086/423742>
136. Pörtner HO. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp Biochem Physiol A Mol Integr Physiol* 2002; 132:739-61; PMID:12095860; [http://dx.doi.org/10.1016/S1095-6433\(02\)00045-4](http://dx.doi.org/10.1016/S1095-6433(02)00045-4)
137. Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, et al. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob Change Biol* 2002; 8:1-16; <http://dx.doi.org/10.1046/j.1365-2486.2002.00451.x>
138. Potts R. Evolution and climate variability. *Science* 1996; 273:922-3; <http://dx.doi.org/10.1126/science.273.5277.922>
139. Codron D, Brink JS, Rossouw L, Clauss M. The evolution of ecological specialization in southern African ungulates: competition- or physical environmental turnover? *Oikos* 2008; 117:344-53; <http://dx.doi.org/10.1111/j.2007.0030-1299.16387.x>
140. Khaliq I, Hof C, Prinzinger R, Bohning-Gaese K, Pfenninger M. Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc R Soc Lond B Biol Sci* 2014; 281:20141097; <http://dx.doi.org/10.1098/rspb.2014.1097>
141. Scholander PF, Hock R, Walters V, Johnson F, Irving L. Heat regulation in some arctic and tropical mammals and birds. *Biol Bull* 1950; 99:237-58; PMID:14791422; <http://dx.doi.org/10.2307/1538741>
142. Isaac JL, Vanderwal J, Williams SE, Johnson CN. Resistance and resilience: quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates. *Divers Distrib* 2009; 15:280-8; <http://dx.doi.org/10.1111/j.1472-4642.2008.00531.x>
143. Humphries MM, Thomas DW, Speakman JR. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 2002; 418:313-6; PMID:12124621; <http://dx.doi.org/10.1038/nature00828>
144. Humphries MM, Umbanhowar J, McCann KS. Bioenergetic prediction of climate change impacts on northern mammals. *Integr Comp Biol* 2004; 44:152-62; PMID:21680495; <http://dx.doi.org/10.1093/icb/44.2.152>
145. Tewksbury JJ, Huey RB, Deutsch CA. Ecology. Putting the heat on tropical animals. *Science* 2008; 320:1296-7; PMID:18535231; <http://dx.doi.org/10.1126/science.1159328>
146. Ostrowski S, Williams JB, Ismael K. Heterothermy and the water economy of free-living Arabian oryx (*Oryx leucoryx*). *J Exp Biol* 2003; 206:1471-8; PMID:12654886; <http://dx.doi.org/10.1242/jeb.00275>
147. Hetem RS, Strauss WM, Fick LG, Maloney SK, Meyer LC, Shobrak M, Fuller A, Mitchell D. Variation in the daily rhythm of body temperature of free-living Arabian oryx (*Oryx leucoryx*): does water limitation drive heterothermy? *J Comp Physiol B* 2010; 180:1111-9; PMID:20502901; <http://dx.doi.org/10.1007/s00360-010-0480-z>
148. Gitay H, Noble IR, Pilifosova O, Alijani B, Safriel UN. Middle East and arid Asia. In: Watson RT, Zinyowera MC, Moss RH, II IPCCWG, eds. *The Regional Impacts of Climate Change: An Assessment of Vulnerability*. Cambridge, UK: Cambridge University Press, 1998:233-50.
149. Cain JW, Krausman PR, Rosenstock SS, Turner JC. Mechanisms of thermoregulation and water balance in desert ungulates. *Wildl Soc Bull* 2006; 34:570-81; [http://dx.doi.org/10.2193/0091-7648\(2006\)34\[570:MOTAWB\]2.0.CO;2](http://dx.doi.org/10.2193/0091-7648(2006)34[570:MOTAWB]2.0.CO;2)
150. Maloney SK, Meyer LCR, Blache D, Fuller A. Energy intake and the circadian rhythm of core body temperature in sheep. *Physiol Rep* 2013; 1:n/a-n/a.
151. Fuller A, Hetem RS, Maloney SK, Mitchell D. Adaptation to heat and water shortage in large, arid-zone mammals. *Physiology (Bethesda)* 2014; 29:159-67; PMID:24789980; <http://dx.doi.org/10.1152/physiol.00049.2013>
152. Hetem RS, Strauss WM, Fick LG, Maloney SK, Meyer LC, Fuller A, Shobrak M, Mitchell D. Selective brain cooling in Arabian oryx (*Oryx leucoryx*): a physiological mechanism for coping with aridity? *J Exp Biol* 2012; 215:3917-24; PMID:22899527; <http://dx.doi.org/10.1242/jeb.074666>
153. Jessen C. Brain cooling: an economy mode of temperature regulation in artiodactyls. *News Physiol Sci* 1998; 13:281-6; PMID:11390804
154. Jessen C. Selective brain cooling in mammals and birds. *Jpn J Physiol* 2001; 51:291-301; PMID:11492953
155. Kuhnen G. Selective brain cooling reduces respiratory water loss during heat stress. *Comp Biochem Physiol A Physiol* 1997; 118:891-5.
156. Mitchell D, Maloney SK, Jessen C, Laburn HP, Kamerman PR, Mitchell G, Fuller A. Adaptive heterothermy and selective brain cooling in arid-zone mammals. *Comp Biochem Physiol B Biochem Mol Biol* 2002; 131:571-85; PMID:11923074; [http://dx.doi.org/10.1016/S1096-4959\(02\)00012-X](http://dx.doi.org/10.1016/S1096-4959(02)00012-X)
157. Mitchell G, Lust A. The carotid rete and artiodactyl success. *Biol Lett* 2008; 4:415-8; PMID:18426746; <http://dx.doi.org/10.1098/rsbl.2008.0138>
158. Fuller A, Hetem RS, Meyer LCR, Mitchell D, Maloney SK. Selective brain cooling: a physiological mechanism for coping with aridity? In: Morris S, Vosloo A, eds. *4th Comparative Physiology Biochemistry Meeting in Africa. Maasai Mara Game Reserve, Kenya: Medimond Publishing S.r.l., Via Maserati 5, 40128 Bologna, Italy, 2008:375-82.*
159. Bernardo J. Maternal effects in animal ecology. *Am Zool* 1996; 36:83-105
160. Meylan S, Miles DB, Clobert J. Hormonally mediated maternal effects, individual strategy and global change. *Philos Trans R Soc Lond B Biol Sci* 2012; 367:1647-64; PMID:22566673; <http://dx.doi.org/10.1098/rstb.2012.0020>
161. Nussey DH, Wilson AJ, Brommer JE. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J Evol Biol* 2007; 20:831-44; PMID:17465894; <http://dx.doi.org/10.1111/j.1420-9101.2007.01300.x>
162. Bartholomew G. The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. In: Hughes G, ed. *Symposia of the Society of Experimental Biology vol 18: Homeostasis and Feedback Mechanisms*. Cambridge: Cambridge University Press, 1964:7-29.

163. Bartholomew G. Interspecific comparison as a tool for ecological physiologists. In: Feder M, Bennett A, Burggren W, Huey R, eds. *New Directions in Ecological Physiology*. Cambridge: Cambridge University Press, 1987:11-37.
164. Huey RB, Hertz PE, Sinervo B. Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am Nat* 2003; 161:357-66; PMID:12699218; <http://dx.doi.org/10.1086/346135>
165. Huey R. Physiological consequences of habitat selection. *Am Nat* 1991; 137:S91-112; <http://dx.doi.org/10.1086/285141>
166. Huey RB, Tewksbury JJ. Can behavior douse the fire of climate warming? *Proc Natl Acad Sci U S A* 2009; 106:3647-8; PMID:19276126; <http://dx.doi.org/10.1073/pnas.0900934106>
167. Kearney M, Shine R, Porter WP. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proc Natl Acad Sci U S A* 2009; 106:3835-40; PMID:19234117; <http://dx.doi.org/10.1073/pnas.0808913106>
168. Mitchell NJ, Kearney MR, Nelson NJ, Porter WP. Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? *Proc Biol Sci* 2008; 275:2185-93; PMID:18595840; <http://dx.doi.org/10.1098/rspb.2008.0438>
169. Hetem RS, Strauss WM, Fick LG, Maloney SK, Meyer LCR, Shobrak M, Fuller A, Mitchell D. Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis? *Zoology (Jena)* 2012; 115:411-6; PMID:23036437; <http://dx.doi.org/10.1016/j.zool.2012.04.005>
170. Suggitt AJ, Gillingham PK, Hill JK, Huntley B, Kunin WE, Roy DB, Thomas CD. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* 2011; 120:1-8; <http://dx.doi.org/10.1111/j.1600-0706.2010.18270.x>
171. Bakken G. Measurement and application of operative and standard operative temperatures in ecology. *Am Zool* 1992; 32:194-216
172. Long RA, Bowyer RT, Porter WP, Mathewson P, Monteith KL, Kie JG. Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecol Monogr* 2013; <http://dx.doi.org/10.1890/13-1273.1>
173. Dussault C, Ouellet JP, Courtois R, Huot J, Breton L, Larochelle J. Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* 2004; 11:321-8
174. Murray DL, Cox EW, Ballard WB, Whitlaw HA, Lenarz MS, Custer TW, Barnett T, Fuller TK. Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildl Monogr* 2006; 166:1-30; [http://dx.doi.org/10.2193/0084-0173\(2006\)166\[1:PNDACI\]2.0.CO;2](http://dx.doi.org/10.2193/0084-0173(2006)166[1:PNDACI]2.0.CO;2)
175. Beever EA, Brussard PF, Berger J. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *J Mammal* 2003; 84:37-54; [http://dx.doi.org/10.1644/1545-1542\(2003\)084<0037:POAEAI>2.0.CO;2](http://dx.doi.org/10.1644/1545-1542(2003)084<0037:POAEAI>2.0.CO;2)
176. Stirling I, Derocher AE. Effects of climate warming on polar bears: a review of the evidence. *Glob Change Biol* 2012; 18:2694-706; PMID:24501049; <http://dx.doi.org/10.1111/j.1365-2486.2012.02753.x>
177. Derocher AE, Lunn NJ, Stirling I. Polar bears in a warming climate. *Integr Comp Biol* 2004; 44:163-76; PMID:21680496; <http://dx.doi.org/10.1093/icb/44.2.163>
178. Stirling I, Parkinson CI. Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. *Arctic* 2006; 59:261-75
179. Amstrup SC, Marcot BG, Douglas DC. Forecasting the range-wide status of polar bears at selected times in the 21st century. In: Myers MD, ed. *US Geological Survey Science Strategy to support US Fish and Wildlife Service polar bear listing decision*. Reston, Virginia, 2007.
180. Jay CV, Fischbach AS, Kochnev AA. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Mar Ecol Prog Ser* 2012; 468:1-13; <http://dx.doi.org/10.3354/meps10057>
181. Fischbach AS, Monson DH, Jay CV. Enumeration of Pacific walrus carcasses on beaches of the Chukchi Sea in Alaska following a mortality event, September 2009. *U.S. Geological Survey Open-File Report* 2009-1291, 2009:10.
182. Moore SE, Huntington HP. Arctic marine mammals and climate change: impacts and resilience. *Ecol Appl* 2008; 18(Suppl):s157-65; PMID:18494369; <http://dx.doi.org/10.1890/06-0571.1>
183. Rasmussen K, Palacios DM, Calambokidis J, Saborío MT, Dalla Rosa L, Secchi ER, Steiger GH, Allen JM, Stone GS. Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biol Lett* 2007; 3:302-5; PMID:17412669; <http://dx.doi.org/10.1098/rsbl.2007.0067>
184. Robinson RA, Learmonth JA, Hutson AM, Macleod CD, Sparks TH, Leech DI, Pierce GJ, Rehfish MM, Crick HQP. Climate change and migratory species. In: CR0302 ARfDRC, ed. *BTO Research Report 414*. British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, 2005.
185. Feder ME, Block BA. On the future of animal physiological ecology. *Funct Ecol* 1991; 5:136-44; <http://dx.doi.org/10.2307/2389251>
186. Costa DP, Sinervo B. Field physiology: physiological insights from animals in nature. *Annu Rev Physiol* 2004; 66:209-38; PMID:14977402; <http://dx.doi.org/10.1146/annurev.physiol.66.032102.114245>
187. Wikelski M, Cooke SJ. Conservation physiology. *Trends Ecol Evol* 2006; 21:38-46; PMID:16701468; <http://dx.doi.org/10.1016/j.tree.2005.10.018>
188. Feder ME, Bennett AF, Huey RB. Evolutionary physiology. *Annu Rev Ecol Syst* 2000; 31:315-41; <http://dx.doi.org/10.1146/annurev.ecolsys.31.1.315>
189. Tomlinson S, Arnall SG, Munn A, Bradshaw SD, Maloney SK, Dixon KW, Didham RK. Applications and implications of ecological energetics. *Trends Ecol Evol* 2014; 29:280-90; PMID:24725438; <http://dx.doi.org/10.1016/j.tree.2014.03.003>
190. Goldstein DL, Pinshow B. Taking physiology to the field: using physiological approaches to answer questions about animals in their environments. *Physiol Biochem Zool* 2006; 79:237-41; PMID:16555183; <http://dx.doi.org/10.1086/4999995>
191. Hattigh J, Ganhao MF, Kruger FJ, De Vos V, Kay GW. Remote controlled sampling of cattle and buffalo blood. *Comp Biochem Physiol A Physiol* 1988; 89:231-5.
192. Andrews RD. Instrumentation for the remote monitoring of physiological and behavioral variables. *J Appl Physiol* (1985) 1998; 85:1974-81; PMID:9804606
193. Block BA. Physiological ecology in the 21st century: advancements in biologging science. *Integr Comp Biol* 2005; 45:305-20; PMID:21676774; <http://dx.doi.org/10.1093/icb/45.2.305>
194. Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ. Biotelemetry: a mechanistic approach to ecology. *Trends Ecol Evol* 2004; 19:334-43; PMID:16701280
195. Chown SL, Gaston KJ. Macrophysiology for a changing world. *Proc Biol Sci* 2008; 275:1469-78; PMID:18397867; <http://dx.doi.org/10.1098/rspb.2008.0137>