

Physiological Mechanisms in Coping with Climate Change*

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ABSTRACT

Although many studies have modeled the effects of climate change on future species distributions and extinctions, the theoretical approach most commonly used—climate envelope modeling—typically ignores the potential physiological capacity of animals to respond to climate change. We explore the consequences of the phenotypic plasticity available to animals, by examining physiological responses of free-living animals in their natural habitats and by applying integrative, mechanistic models of heat exchange in invertebrates and humans. Specifically, we explore how behavioral, autonomic, and morphological modifications such as nocturnal activity, selective brain cooling, and body color may potentially serve as buffers to the consequences of climate change. Although some species may adapt to climate change through phenotypic plasticity, there are significant limits to this strategy. Furthermore, predictions of the response of organisms to changes in climate can be erroneous when modeled at large scales using coarse spatial or temporal data. Environmental heterogeneity can provide habitats suitable for species even though large-scale changes in the climate might predict a species' extinction. A detailed understanding of physiology, combined with integrative biophysical

modeling and ecological manipulation, provides a powerful tool for predicting future ecological patterns and managing their consequences.

Introduction

An understanding of the physiological capacity of organisms to respond to climate change is essential if we wish to predict future species distributions and population dynamics and to implement successful conservation strategies (Wikelski and Cooke 2006; Chown and Gaston 2008; Williams et al. 2008). While bioclimatic envelope models provide a useful approximation of the potential impact of climate change on the distribution of species, they tend to assume that animals and plants can persist only in areas with an environment similar to the one they currently inhabit; that is, that future range boundaries can be predicted solely on correlations between environmental parameters and current range edges. Most bioclimatic envelope models thus do not explicitly consider biotic interactions between species or limitations to dispersal (Kearney 2006), and they assume that species lack sufficient plasticity to adapt to environments beyond those currently occupied (Jeschke and Strayer 2008). Organisms, however, can have the capacity to adapt to changing environmental conditions both by phenotypic plasticity within a life span and by microevolution over a few life spans. Bioclimatic envelope models may capture spatially explicit variation in physiology as a consequence of adaptation or microevolution, but they do not allow us to identify the processes that have been captured and that will therefore predict the future ability of the species to buffer the effects of climate change.

For a species, environmental changes can lead to at least four possible outcomes. Species may (1) become extinct or extirpated, (2) migrate or shift their current distribution range, (3) adapt to the changes through a change in the genetic composition of the population, or (4) employ phenotypic plasticity. To emigrate successfully requires the location and colonization of suitable new habitats, a challenging or impossible task for some species. Nevertheless, numerous recent reports have documented shifts in the geographical distribution of species, usually in the direction predicted by climate change models (Parmesan and Yohe 2003; Root et al. 2003). Genetic change and phenotypic plasticity are the outcomes that prevent local extinction. Although the rapid rate of climate change will prevent the evolution of adaptive heritable traits in long-lived species (with long generation times), there is evidence that microevolution—that is, heritable shifts in allele frequencies in a population (without speciation)—has occurred in response to climate warming (Bradshaw and Holzapfel 2006, 2008). Phe-

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notypic plasticity, however, is likely to represent the first response of individual organisms (Bradshaw and Holzapfel 2008) and is the only response available for long-lived species to be able to adapt to climate change. Phenotypic plasticity, defined as the process through which a genotype gives rise to different phenotypes under different conditions (Garland and Kelly 2006), includes phenology (changes in the timing of events), morphology (e.g., color patterns, body shape, and size), physiology, or behavior of a species. Adaptive changes in phenotype induced by climate change have been documented, for example, in the morphology and phenology of birds (Charmantier et al. 2008) and mammals (Réale et al. 2003; Linnen et al. 2009; Maloney et al. 2009; Ozgul et al. 2009). The extent to which changes in phenotype will enable animals to cope with climate change is unknown, but it will be limited. For the majority of species, and particularly the long-lived mammals (Wikelski and Cooke 2006; Mitchell et al. 2008), very little is known about their phenotypic plasticity. We illustrate that the ecological effects of climate change can be predicted only if we understand physiology at the level of the organism in its natural habitat. While some authors consider behavior to be distinct from physiology, we consider it to be a crucial element of the repertoire of physiological responses available to an animal. As framed by Williams and colleagues (2008), behavior and physiology contribute to both the resilience and the adaptive capacity of a species, ultimately influencing the vulnerability of a species to climate change. A mechanistic understanding of how organisms work, combined with knowledge of exposure to climate change, feedback between ecosystem processes, and the potential for adaptive management (Williams et al. 2008), is crucial if we are to act appropriately to conserve species.

Predicting Patterns of Stress in Space and Time

Several recent studies have explored the physiological plasticity of terrestrial and marine organisms by measuring and modeling the physiological responses of free-living organisms to changes in the local environment. A theme that has emerged from these studies is that biophysical models of heat exchange are important for predicting those axes of a species' fundamental niche (the environmental space occupied by a species) that are related to thermal stress. Specifically, biophysical modeling mechanistically integrates the factors that drive heat exchange between organisms and their environment, instead of simply correlating individual components of the environment, such as air temperature, with body temperature (Kearney and Porter 2009). This framework therefore permits an exploration of how changing climatic conditions are likely to affect patterns of species distributions even if the physiological vulnerability of organisms or populations changes over time or if vulnerability changes with location.

For example, Pearson et al. (2009) showed that intertidal algae are more sensitive to thermal stress at their southern range edge (Portugal) than at their poleward range edge (United Kingdom). This pattern occurred both because of differences in physiological sensitivity to temperature and because of sim-

ilarities in thermal regimes driven by the timing of low tide (Helmuth et al. 2006). Studies such as this one thus raise the question of whether the use of broad climate variables, such as air or water temperature, for determining range boundaries is sufficient (Kearney 2006). Wetthey and Woodin (2008) reconstructed sea surface temperature patterns over the past century along the coast of Europe and compared these data against observed shifts in the geographic distributions of barnacles and polychaetes. They found that changes in the distribution of barnacles appeared to be closely related to reproductive failures brought about by warmer winter temperatures. These trends generally resulted in a poleward shift but, importantly, there remained relict pockets at southern sites where cold upwelling occurred. The underlying distributional shifts in polychaetes were complex and appeared to be related to several underlying physiological drivers linked to either cold winters or cool summers. However, those underlying physiological mechanisms remain largely unexplored. In a similar study, Jones et al. (2009) studied the physiological vulnerability of intertidal mussels to both aerial and aquatic body temperatures and compared these results against historical reconstructions of temperature along the east coast of the United States. They found that mortality was driven by both low-tide (aerial) and high-tide (aquatic) temperatures and that the duration of exposure to water was a significant factor.

Understanding the interactions of organisms with their ambient environment at a niche level (Kearney 2006) is often key, because patterns of responses such as body temperature can be complex. By using model mussels containing temperature loggers placed in situ in the intertidal zone, Helmuth et al. (2006) measured geographic patterns of temperature that were relevant to physiological stress in these animals. Their results have shown that, instead of inhabiting a smooth temperature cline along a latitudinal gradient, these invertebrates experienced a thermal mosaic of "hot" and "cold" spots where local conditions of tide, cloud cover, and wave splash overrode the effect of the large-scale gradient in climate (Helmuth et al. 2006). Similarly, Holtmeier and Broll (2005) showed that the distribution of alpine trees was far more spatially and temporally complex than anticipated, due to the interactions of local weather and the history of human-mediated disturbance. For conservation purposes, these mismatches between predictions at the level of the organism/population and those generated from coarse weather and climate data are very important because the areas identified by specific physiological modeling identify "cool spots" that could serve as refuges for some species in a climate-changed future (Hoffman 2003). Ultimately, it is the microclimate and not the macroclimate that will directly influence an organism's thermal well-being (Williams et al. 2008; Helmuth 2009).

The ecological consequences of niche-level heterogeneity have also been well illustrated, with one model system involving a keystone marine predator (*Pisaster ochraceus*) and its prey (the mussel *Mytilus californianus*). While the body temperatures of predator and prey tracked each other at some sites, at other locations the body temperatures were uncoupled at short time-

scales (<6 h), with prey being markedly hotter than the predator (Broitman et al. 2008). Acute thermal stress increased the rate at which *Pisaster* consumed *Mytilus*, but chronic thermal stress decreased the rate of consumption (Pincebourde et al. 2008). Thus, the ecosystem outcome depends on a complex interaction between individual thermoregulation of species at different trophic levels and the timescale of environmental stressors.

The central thesis of these studies and of several recent reviews (Williams et al. 2008; Helmuth 2009) is that multiple abiotic and biotic stressors are likely to set the current and future range boundaries of species distributions and it is likely to be impossible to predict outcomes accurately without knowledge of how organisms interact with their environment and with other organisms. Moreover, current limiting factors may not be those that are most important in the future. For example, although only average environmental temperature increases are incorporated into most model predictions, it is likely that increases in weather extremes, such as droughts and heat waves, will impose critical stress in the future (Parmesan et al. 2000; Hallett et al. 2004). Indeed, increases in maximum rather than mean air temperatures in subtropical deserts, for example, are likely to increase substantially the frequency of catastrophic avian die-offs (McKechnie and Wolf 2010). Linking detailed physiological understanding with biophysical modeling and ecological manipulation emerges as a powerful tool for forecasting the impacts of future climate change (Kerr et al. 2007; Helmuth 2009; Kearney and Porter 2009).

Feedbacks between Behavior and Thermal Stress

In the face of climate change, keeping cool will become more of a priority for most marine and terrestrial ectotherms. As long as their behavior does not compromise life cycle, energy, and water requirements, exploiting complex microclimate mosaics will allow many ectotherms to buffer the effects of climate change (Huey and Tewksbury 2009; Kearney et al. 2009). For example, Pincebourde et al. (2009) showed that intertidal sea stars can behaviorally regulate their thermal inertia by increasing the rate of water uptake during high tide on hot days, a response that affords protection against extreme aerial temperatures during subsequent low tides. Mammals, as endothermic organisms with complex thermoregulatory behaviors, generally can occupy a fundamental niche with broader environmental variability than can ectotherms (Dormann et al. 2010). However, endotherms, like ectotherms, remain affected by temperature (Humphries et al. 2004), and endotherm activity and survival, particularly in species with narrow thermal tolerances (Pörtner and Farrell 2008), will also be influenced by rising ambient temperatures.

Indeed, Maloney and Forbes (2010) used integrative modeling for Perth, Australia, to show that the risk of heatstroke in humans during certain activities may increase by as much 20-fold by 2070. How susceptible individuals are, though, depends on the expression of plasticity in heat-loss capacity. The enhancement of the human sweat response during heat acclimatization is well documented; exposure of humans to hot

conditions on successive days induces an increase in sweat capacity (Nielsen et al. 1993). Other adaptations also ensue, including plasma volume expansion and decreased electrolyte content of sweat. A typical unacclimatized male, who can produce about 600 mL of sweat per hour, can double that output with heat acclimatization (Henane and Valatx 1973). Using an established model of human heat balance called the Man Model, or MANMO (Myrup and Morgan 1972) and a new model developed by themselves based on the kata thermometer, Maloney and Forbes modeled the effects of projected climate change on the body temperature of humans engaged in various activities. Using historical weather data for Perth and the 6°C increase in temperatures that is projected to occur by 2070 for that part of Australia (Commonwealth Scientific and Industrial Research Organisation 2001), they concluded that moderate exercise, such as 2 h walking on a golf course, will induce life-threatening rises in body temperature of unacclimatized individuals on 34–41 d per year in 2070 compared with 4–6 d per year at present. With acclimatization, heatstroke is likely to occur on only 1 d in 4 yr at present, but its occurrence will increase to between 5 and 6 d per year in 2070. Of greater economic concern is that unacclimatized humans will be unable to perform manual labor outdoors in Perth in 2070 without risking heatstroke on 68 to 71 d per year compared with 15 to 20 d per year with acclimatization. The important message to emerge from this modeling is the way in which phenotypic adaptation (in this case, heat acclimatization) can alter physiological tolerance (the risk of heat illness). Encouragingly, if the human population develops the full phenotypic potential of the sweat response, the impacts of climate change on outdoor activity will be greatly diminished. How widely the general principle, illustrated by the effect of heat acclimatization in humans, can be applied is at present unknown because the effect of acclimatization on heat-loss capacity is known for very few species. What is known is that bioclimatic envelope modeling does not capture any presently unexpressed plasticity.

How Phenotypically Plastic Are Natural Populations?

A major gap in our understanding of how climate change will affect natural populations is how much phenotypic plasticity contributes to the current realized niche of a species, because phenotypic plasticity in the natural setting has been studied in very few species. R. S. Hetem et al. (2010) proposed that animals inhabiting extreme environments are already living at the edge of their plasticity envelope. They showed that behavioral plasticity is an essential adaptation for wild free-living antelope exposed to the extreme heat and aridity of the Arabian desert. When conditions got hotter, Arabian oryx (*Oryx leucoryx*) shifted from a biphasic or crepuscular rhythm of activity to a more nocturnal rhythm, without reducing total 24-h activity. Other large herbivores also increase nocturnal activity in the face of high diurnal heat loads (Zervanos and Hadley 1973; Belovsky and Jordan 1978; Grenot 1992; Hayes and Krausman 1993; Berger et al. 1999; Dussault et al. 2004; Maloney et al. 2005), presumably allowing them to reduce evaporative water

loss. Because the reduction in diurnal activity was associated with high ambient temperatures and shade-seeking behavior, Hetem and colleagues suggested that activity scheduling changed in response to acute stressors rather than being a fixed seasonal response (R. S. Hetem, S. K. Maloney, L. C. Meyer, M. Shobrak, A. Fuller, and D. Mitchell, unpublished manuscript). If so, there is potential for rapid behavioral responses to a warming climate, without sacrificing foraging time. However, the current dependence of oryx on behavioral thermoregulation, combined with the loss of genetic variability as a result of a historical bottleneck (Marshall et al. 1999), may limit their capacity to adapt to further aridification. The Arabian oryx may already be at the edge of its physiological limits and, with future climate change predicted to increase summer temperatures in the southwest part of the Arabian Peninsula (Gitay et al. 1998), its behavioral plasticity may not be sufficient to ensure long-term survival.

Behavioral plasticity in oryx was also accompanied by apparent plasticity in autonomic thermoregulation. As demonstrated previously (Ostrowski et al. 2003), Arabian oryx displayed heterothermy, with higher maximum and lower minimum body temperatures in the hot periods than in warm periods. Hetem et al. (2010) showed that the implementation of heterothermy was not actually dependent on ambient temperature but rather on water availability, with oryx displaying a greater 24-h amplitude of body-temperature rhythm during warm, dry periods compared with during warm, wet periods. The low morning body temperatures, which occurred throughout the dry season, may reflect a reduced metabolic rate of desert ungulates in response to a reduction in water intake and a decline in food quality and availability during that dry season. Although it was argued originally that heterothermy provides an adaptive function, allowing large mammals to conserve body water by storing heat during the day, Hetem et al. (2010) proposed that heterothermy may reflect a failure of homeothermy as a result of a dehydration-induced hyperthermia combined with a starvation-induced hypothermia.

Another adaptation that may enhance plasticity in response to aridity that is available to oryx and other artiodactyls, as well as members of the cat family (Mitchell et al. 1987), is selective brain cooling. Selective brain cooling, the reduction of brain temperature below arterial blood temperature, was originally thought to protect the brain from thermal damage during heat stress. However, recent studies, mainly of free-living animals, have yielded data that are inconsistent with that concept (Mitchell et al. 2002). Rather, selective brain cooling appears to play a role in balancing thermoregulatory and osmoregulatory needs. By cooling the hypothalamus and, hence, the temperature sensors that drive evaporative heat loss, selective brain cooling inhibits evaporative heat loss and conserves body water (Kuhnen 1997; Fuller et al. 2007). Selective brain cooling therefore is likely to be particularly valuable to animals under concurrent heat stress and dehydration. Indeed, Fuller et al. (2008) argued that, as a water conservation mechanism, selective brain cooling may have been important for the past success of artiodactyls and that it also may offer a key adaptation for animals in a climate-changed future. Mitchell and

Lust (2008) also postulated that the success of artiodactyls relative to perissodactyls, and their occupancy of diverse habitats, might be attributable to the evolution of the carotid rete and the ability to exhibit selective brain cooling. Selective brain cooling, in those species that can implement it, may therefore permit habitat flexibility and provide an important preadaptation toward predicted climate change.

Another feature that sets mammals and birds apart from ectotherms is their pelage, that is, their fur and feathers. The insulation provided by this covering is crucial to the heat balance of these homeothermic classes, but it makes heat balance modeling more complex. Dawson and Maloney (2008) examined the role of fur and feathers in ameliorating climatic stresses. Their work shows that, at the interface between a homeotherm and its physical environment, pelage affects heat balance in ways other than simple insulation, particularly in complex environments with variable solar radiation and wind. Work on diurnally foraging large endotherms from the Australian arid zone—notably, several species of kangaroo (*Macropus* spp.) and the large ratite bird, the emu (*Dromaius novaehollandiae*)—showed that the heat load from radiation was not a simple function of insulation or color (Maloney and Dawson 1995; Dawson and Maloney 2004). The desert-inhabiting red kangaroo (*Macropus rufus*) is partially diurnally active (Watson and Dawson 1993), while the emu is fully diurnal and spends summer days feeding in the open. The high reflectivity and density of kangaroo fur has been regarded as an adaptive feature, because it provides a barrier to radiant heat inflow. Yet, emu feathers are black. There is some evidence that a dark pelage reduces energy costs in the cold if shortwave radiation is available (Hamilton and Heppner 1967; Heppner 1970; Dmi'el et al. 1980; Finch et al. 1980; Lustick et al. 1980), implying that radiant heat absorption becomes a significant component of heat balance. In the heat, a high radiant heat load would be undesirable and intuitively should limit an emu's diurnal activity. Resolution of this paradox lies in the complex association between penetration of shortwave radiation into the pelage (which depends on coat color, fiber density, and fiber diameter) and the insulation between the point of absorption and the skin.

The pelage surface of the red kangaroo absorbed half as much radiation as that of the emu, but the heat load at skin level was twice as high in the kangaroo as in the emu at low wind speeds (23% vs. 9% of incident load). The radiant heat load in both species decreased as wind speed increased, and at 10 m s⁻¹, the heat load was 11% in kangaroos but negligible in the emu. Although emu feathers absorbed more radiation, it was absorbed closer to the pelage surface and the feather layer (45 mm vs. 9 mm for the kangaroo fur) provided greater insulation against heat flow through the pelage to the skin. The result was that in the emu the absorbed heat was transferred mostly back to the environment. While multiple morphological and environmental factors affect heat flux into and out of organisms, Hetem et al. (2009) showed that the three color morphs of the springbok (*Antidorcas marsupialis*) exhibit differences in body temperature and activity that are consistent with differences in

solar heat load. Black springbok had a higher body temperature in summer but spent less time foraging in winter, leading to the suggestion that the energy costs of homeothermy were offset by radiant heat gain. Conversely, white springbok body temperatures were similar to those of the wild types in summer, but the animals had lower morning body temperatures in winter. As with the Arabian oryx, these lower temperatures may reflect negative energy balance. With less access to solar heat, the white springbok morph seems to have higher energy expenditure. Therefore, maintaining genetic diversity within a population, particularly diversity for a trait like pelage color that adapts individual animals to different thermal environments, may provide important plasticity for future climate change (Millien et al. 2006). There is already evidence that, over the past 30 yr as the climate has warmed, the proportion of dark-colored to light-colored Soay sheep has decreased on islands in the outer Hebrides (Maloney et al. 2009).

Predicting the Complex Effects of Climate Change on Organisms

Few studies have attempted to address how long-lived species, including humans, will respond to the stresses of climate change (Mitchell et al. 2008). Physiological phenotypic plasticity, which may include acclimatization, acclimation, and learning (Garland and Kelly 2006), is likely to be the only option available to these species. The studies required to identify mechanisms of physiological plasticity and predict future species distributions fall within the emerging discipline of conservation physiology, which aims to provide a detailed mechanistic basis for understanding conservation problems (Wikelski and Cooke 2006). Some models have attempted to incorporate physiological limitations to determine the climatic requirements of a diverse group of taxa, including insects (Crozier and Dwyer 2006; Musolin 2007), marine invertebrates (Pörtner et al. 2004; Osovitz and Hofmann 2007; Wethey and Woodin 2008), lizards (Kearney and Porter 2004), and mammals (Taulman and Robbins 1996; Johnston and Schmitz 1997; Humphries et al. 2002). Such models require an understanding of physiological responses to climate, which preferably should be obtained from long-term monitoring of free-living animals going about their daily business over large geographical domains. Such studies would fall into the field of macrophysiology, recently defined as “the investigation of variation in physiological traits over large geographical and temporal scales and the ecological implications of this variation” (Chown et al. 2004, p. 160).

The general theme of this article, and that of the session on which it is based, engenders hope that the plasticity of animals may allow some adaptation to changing environmental stressors. Such adaptation, at least initially, may ameliorate some of the worst predictions for the responses to climate change. However, such adaptation is likely to be limiting in scope, and consideration of its benefits thus risks the unintentional promotion of complacency in addressing or mitigating the potentially catastrophic effects of climate change. If species can and will adapt to the stressors imposed by climate change, through

the expression of both phenotypic plasticity and microevolution, why do we need to worry? We must worry because only some species will thrive—particularly pest and invasive species—and those that do might end up in quite different ecosystems. Such predicted ecosystem changes have led to a new field of ecological research termed “global change ecology” (Schlesinger 2006). For most biologists and many laypeople, any loss of current biological diversity is a tragedy. But even taking the extremely selfish attitude of the economic rationalist, we have to wonder whether those new ecosystems will supply the “ecosystem services” that large human populations require (Schröter et al. 2005). Indeed, in the face of both changing ecosystems and emergent pathogens (McMichael et al. 2006), one species that could become extinct as a consequence of its own actions is *Homo sapiens*.

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