Declining body size: a third universal response to warming?

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A recently documented correlate of anthropogenic climate change involves reductions in body size, the nature and scale of the pattern leading to suggestions of a third universal response to climate warming. Because body size affects thermoregulation and energetics, changing body size has implications for resilience in the face of climate change. A review of recent studies shows heterogeneity in the magnitude and direction of size responses, exposing a need for large-scale phylogenetically controlled comparative analyses of temporal size change. Integrative analyses of museum data combined with new theoretical models of size-dependent thermoregulatory and metabolic responses will increase both understanding of the underlying mechanisms and physiological consequences of size shifts and, therefore, the ability to predict the sensitivities of species to climate change.

Body size reductions: is the signal clear and what does it matter?

A recently documented correlate of rising temperatures associated with anthropogenic climate change involves reductions in the body size of many organisms. This phenomenon is being reported from a growing number of species on multiple continents and appears to apply to both endotherms and ectotherms, in both terrestrial and aquatic environments (Table 1). The geographic pattern and phylogenetic scale of findings to date suggest a broad-scale physiological response to some major environmental change over the past 50–100 years. This has led to the suggestion that body-size reduction is a third universal response to global warming [1], alongside changes in the phenology [2] and distributions [3] of species.

Changes in body size have important implications for the thermal biology and energetics of endotherms and ectotherms. This is because body size directly affects energy and water requirements for thermoregulation [4–6], energy and mass acquisition and utilization rates [7] and life-history characteristics [8,9]. Changing body size will, therefore, have implications for resilience in the face of climate change. Here, we examine the relationship between body size and physiological sensitivity to climate warming, and the implications for selection and the persistence of organisms. We discuss: (i) evidence that body-size reductions are indeed a universal response to climate change; (ii) progress in understanding of the underlying mechanisms; and (iii) the potential for integrating historical data with metabolic theory and biophysical ecology to identify the physiological and life-history consequences of size change.

The pattern and extent of body-size change

Variation in body size is a well-studied phenomenon in animal biology and there are strong theoretical frameworks for interpreting patterns of size differentiation [8,9]. Bergmann's rule, the best-known ecogeographic rule in biology, describes a positive relationship between body size and latitude, smaller individuals being found at lower latitudes where climates are generally warmer [10] (Box 1). This clinal size pattern also applies to many ectotherm species, although the original endothermic thermoregulatory explanations for the rule do not apply. A general temperature–size rule has been proposed to explain the pattern in ectotherms in the context of development reaction norms for size [11,12] (Box 1), but the causes of size patterns remain hotly debated [7,13–15]. Size shifts in response to temperature can include morphological change over contemporary and geological timescales, and can apply to species as well as to populations and communities [16]. This consistency in size patterns associated with latitude and temperature gives rise to the prediction that current climate warming will lead to shifts in entire latitudinal clines in body size. Thus far, this has been tested in only a few bird species [17].

In addition to ambient temperature, body size and body temperature interact to affect metabolic rate and a range of ecological and demographic life-history traits [8,9]. Heterogeneity in both the magnitude and direction of body-size responses within and between studies, including increasing body size (e.g. [18,19]), is therefore not surprising (Table 1). Studies of single species at individual locations or over short geographic distances are likely to reflect localized effects on body size, and such studies constitute much of the evidence for size reductions as a correlate of

Table 1. Summary of studies undertaken since 2000 investigating body-size change in the context of recent climate warming

Order	Species (n)	Study period	Region[a]	Body-size response[b]	Suggested cause and/ or key finding	Refs
Endotherms						
Passeriformes, Galliformes and Falconiformes	61	Since 1797	Europe[2]	Variable	Competition for resources; island rule	[58]
Passeriformes	5	1950–1999	Europe[2]	4/5 decreased	Unknown	[69]
	14	–	Europe	Variable	Food or predation	[70]
	12	1972–2006	Europe[1]	Variable	Most show plastic response to temperature; genetic response(s) are also suggested	[21]
	102	1961–2006	North America[1]	Mostly decreased	Plastic and/or genetic response to temperature	[22]
	8	1860–2001	Australia[3]	4/8 decreased	Shift in latitudinal size cline might suggest a genetic cause; nutritional cause unlikely	[17]
	1	1985–2005	Europe[1]	Increased	Linked to changing water flow	[71]
	1	1989–2003	Europe[1]	Increased	No correlation with temperature; possibly with food availability	[72]
Charadriiformes	1	1958–2004	New Zealand[1]	Decreased	Possibly food availability	[20]
Falconiformes	1	1854–1998	Europe[2]	Decreased	Change in diet	[73]
Galliformes	1	Since ca 1950	Middle East[2]	No change	Heat conservation mechanism may not underlie latitudinal size variation	[74]
Anseriformes	1	1954–1971	Europe[1]	Decreased	Small individuals moving to escape colder northern winters	[75]
Carnivora	22	1900–1987	Europe and North America[2]	Mostly none, but variable at population level	Temporal size change unaffected by food, temperature or body mass	[76]
	1	1858–1999	Europe[2]	Decreased	Temperature via food availability or Bergmann's rule	[77]
	2	1949–1998	North America[2]	Increased	Food availability	[78]
	2	1862–2000	Europe[2]	Increased	Change in diet	[79]
	5	1948–2000	Middle East[2]	4/5 increased	Food availability and diet	[80]
	1	1969–1986	Europe[2]	Increased	Food availability	[81]
	1	1953–2000	North America[2]	Decreased	Food availability or competition for food	[82]
	1	1982–2006	North America[1]	Decreased	Nutritional limitation via reduction of sea-ice habitat	[83]
Artiodactyla	1	1986–2006	Europe[1]	Decreased	Multiple effects of temperature including those on food; plasticity of response	[18]
Rodentia	1	1976–2008	North America[1]	Increased	Plastic not genetic response to temperature, including density-dependent response to food availability	[30]
	1	1989–1996	North America[1]	No change	Abundance, not size related to climate	[84]
	2	1920–1989	Asia[1]	Increased	Food availability and diet	[85]
	25	1892–2001	Central, South and North America; and Asia[2]	General decrease	Climate change or human population density	[86]
Soricomorpha	1	1950–2003	North America[2]	Increased	Food availability	[87]
Lagomorpha, Carnivora, Rodentia, Erinaceomorpha, Soricomorpha	25	1800–1972	Europe[2]	Variable	Food availability	[88]
Ectotherms						
Squamata	1	1984–2001	Europe[2]	Increased	Correlated with temperature in first year of life	[89]
	1	1905, 2000	South America[3]	Increased	Temperature effect on foraging	[90]
Various in Osteichthyes, Calanoida, phytoplankton and bacteria	>16	1979–2007	North Sea and Europe	Decreased	Related to temperature	[1]
Various in Osteichthyes	53	1970–2008	Northwest Atlantic	Widespread decrease	Harvesting and trophic restructuring	[34]
Various in Osteichthyes and Chondrichthyes	30	1911–2007	Europe	Widespread decrease	Harvesting and sea temperature	[91]

[a]Study undertaken at: 1, single site; 2, multiple sites, 3, across range of species.

[b]Measures of body size are body mass or structural size.

Box 1. Bergmann's rule and the temperature size rule

Bergmann's rule is the tendency for mean body size to decrease with decreasing latitude [10]. The original explanation for the pattern involved endothermic thermoregulation and geometric arguments about heat loss [10]. Smaller bodies have proportionally larger surface areas and thinner boundary layers, enabling them to dump heat convectively more effectively (as long as the air temperature is below skin temperature) [4,5,10]. This is advantageous in warmer climates. Latitudinal clines in size are widely cited as evidence for genetic adaptation to local climate, and this interpretation is supported by a recent phylogenetically controlled examination of geographic patterns of avian body size [68].

Latitudinal clines in body size are also exhibited by a range of ectotherms [11]. In contrast to endotherms, ectotherms do not generate sufficient metabolic heat to elevate their body temperature significantly; therefore, endothermic heat dissipation mechanisms do not apply [11,12]. Instead, ectotherms rely on microclimatic variation in their environment to maintain thermal homeostasis for metabolic processes. The temperature–size rule was proposed to explain clinal size patterns in ectotherms and describes phenotypic plasticity responses to temperature, in which species usually reach a smaller size at higher development temperatures, potentially through thermal sensitivity of growth rates and cell size [12].

global warming (Table 1). Although essential for examining mechanisms of size change, localized studies are less useful for defining broad-scale patterns. Larger scale phylogenetically controlled comparative analyses of temporal size change are needed to pinpoint the geographic, ecological and life-history correlates of this phenomenon across taxa. Until such information is available, it might be premature to suggest that body-size declines are the universal response to climate change suggested by some authors [1].

Natural history collections are fast gaining recognition as rich sources of historical data for examining intraspecific shifts in size because they contain long time-series useful for detecting broad-scale patterns of change that can be correlated with temperature [20]. Their use can be complemented with shorter term but more detailed morphological data from fixed monitoring sites, to test explicitly whether body size has been tracking temperature *per se*, or other types of environmental change, such as rainfall or food availability [21–23]. This approach provides unprecedented opportunities to establish whether body-size declines are indeed universal across taxa and ecological guilds, or are specific to particular taxa and ecological circumstances, and whether the change in body size relates specifically to temperature versus other environmental change.

The ultimate causes of size change: nature or nurture?

The mechanisms underlying historical body-size reductions have been difficult to isolate. The debate over size reductions has tended to focus on whether size shifts either represent evolved genetic responses to climate warming or constitute phenotypic plasticity in response to temperature or other concomitant changes in the environment [24]. This is an important issue because the likelihood that species can respond fast enough to climate change will ultimately depend on whether their response is genetic or plastic [24–27]. Although plasticity can evolve under selection, it is unlikely to provide long-term solutions to continued directional change, and this is significant in the

context of rapid environmental change such as global warming [25,28].

Direct evidence for evolutionary (genetic) responses to global warming is rare [24]. No study has found evidence for microevolution driving body-size shifts in the context of current warming, although there is evidence for genetic change underlying other responses to climate change (e.g. phenology of breeding and migration) [24,28–30]. Documenting genetic change requires testing for changes in allele frequencies in genes functionally linked to traits or quantitative genetics approaches to estimate trait heritability [29,30]. Both approaches have limited application because they require long-term data sets, which are available for relatively few species.

Testing for changes in genes that encode body size is impractical because the relevant genes are still unknown for most species. Indeed, multiple genes are likely to be involved in many cases, adding to the difficulty of the task, at least with current molecular techniques. A more fruitful approach might be to test for temporal changes in genetic polymorphisms in temperature-related traits that are linked to fitness (e.g. heat resistance and desiccation), as has been shown in *Drosophila melanogaster* in eastern Australia [31]. In this case, a latitudinal cline in allele frequencies associated with heat resistance shifted over a 20-year period. This study provides some of the best evidence to date for genetic adaptation to climate warming and led the authors to suggest that genetic markers that vary across environmental gradients will be useful in detecting and monitoring adaptation to climate change in natural populations [31]. At present, however, this approach is limited to a few invertebrate species where the genotypes are well known (e.g. *Drosophila* species [28,29]), and all have relatively short generation times, which makes it difficult to generalize across taxa. Nevertheless, rapid technological advances might make monitoring genetic adaptation a feasible option in the future [29].

A second approach to testing for genetic change in body size involves quantitative genetics and the use of an animal model. Recent studies of red-billed gulls (*Larus novaehollandiae*) and soay sheep (*Ovis aries*) found no evidence for genetic change underlying climate-related shifts in size over the past 20–40 years and concluded that phenotypic plasticity was more likely to be involved [21,32]. Despite this lack of evidence, adaptation is known to underlie other types of climate-driven size shifts in vertebrates over a similar time frame. Rapid adaptive evolution of body size (wing length) and bill morphology in response to drought has been convincingly demonstrated in a Galapagos finch species, *Geospiza fortis* [33]. This suggests that genetic change should be detectable in the time frame of current climate warming, at least where hard selection is involved. Given the limitations of detecting genetic change using these approaches, we suggest that further exploration of the proximate processes underlying body-size shifts, together with the physiological consequences of size change in the context of current climate warming, is of immediate importance.

The proximate causes of size change

In addition to ambient temperature, one probable proximate cause of changing body size is a change in the

availability or quality of food that, in turn, affects nutrition, and this has been implicated as a mechanism in the majority of the studies to date (Table 1). Changes in nutrition could result from changing temperature, for example via changes in the length of growing season [18,32] or via changes in temperature-dependent activity budgets that constrain feeding [34]. Alternatively, size change might be the result factors affecting nutrition independent of temperature, for example via changing food availability resulting from habitat loss and fragmentation, changing land use and agricultural practices [35]. The selective harvesting and removal of top predators might also lead to changes in available prey via trophic restructuring of body size and biomass [36]. In reality, these processes might act simultaneously [16].

Despite the potential importance of nutrition as a driver of body-size shifts, few studies have examined whether, and to what extent, changes in nutrition underlie the recent size declines. One group of organisms that allows a direct test of the hypothesis that nutrition or other stresses associated with environmental change contribute to size change is birds. Not only are extended (>100 years) time series available in the form of extensive, high-quality museum collections, but birds, particularly their feathers, provide an exceptionally informative window onto environmental conditions at the time of sampling [37,38]. For example, examination of museum collections showed that color morph frequencies of an owl species have changed over time in response to ongoing climate change [39]. Owing to a detailed understanding of the mechanisms underlying qualities of feathers (e.g. [40]), combined with several recent analytical advances [41–46], it is now possible to derive estimates of nutrition, stress, diet and size in a single individual (see below) to an extent not possible in other groups of animals. Sampling multiple individuals across sites and over time would enable examination of stressors singly and in combination.

The most useful measure of environmental impact might be via highly condition-dependent traits, as these represent the sum of stresses on the animal [47].The color of plumage might be particularly informative. The best evidence for environmental determination of plumage color exists for carotenoid-based colors [48,49]. Carotenoids are fixed within feathers, and plumage color (reflectance) remains sufficiently stable over time in museum specimens [37]. Birds cannot synthesize carotenoids and their presence in plumage is ultimately determined by habitat quality, specifically through the type and amount of food available [49,50]. Carotenoid-based feather coloration can thus be used as a proxy for habitat quality [50,51]. Recently developed statistical methods allow inter- and intraspecific comparisons of color quality [41–43]. Changes in coloration can be correlated with feather growth rates using ptilochronology [38], a simple, effective technique that provides an index of condition and the availability of nutrients during the period of feather growth. This could be augmented by stable isotope analysis of feather samples: nutritional stress has been shown to alter stable isotope ratios in tissue samples, [46] and isotopic variation in feathers can be used to determine geographic variation in quality of the molt diet [52]. Furthermore, the avian

stress hormone, corticosterone, can also be quantified in feathers. There is now abundant evidence that stress from changed ecological conditions can reduce growth, survival, reproductive output and resistance to disease [53] and corticosterone is released in response to stressors of various sorts and is linked to fitness [53,54]. Feather corticosterone is thus a reliable integrated measure of stress and is stable in museum skins [44,45].

Integrating measures of stress hormones, nutritional condition via feather growth rates, and diet and habitat quality inferred from plumage coloration and possible stable isotope ratios have the potential to provide, for the first time, a much-needed historical perspective on the nature and timing of stressors associated with body-size change, using birds as a model system. Although birds could be trail-blazers in this regard, this approach could be extended to other groups. For example the otoliths of fish can provide estimates of age, growth rate and related stress [55]. Such broad-scale comparative studies should detect patterns of body-size variation that can be correlated with environmental variables to evaluate the potential of biotic factors (e.g. nutrition) and traditional abiotic factors (temperature and precipitation) as mechanisms driving size change. They also provide metrics for use in energy- and mass-budget modeling to provide insight into the mechanistic links between environmental variation and body size.

Modeling the links between size, temperature and nutrition

Theoretical developments in biophysical ecology and metabolic theory provide new opportunities to understand the physiological consequences and underlying mechanisms of body-size change in the context of changing thermal and nutritional environments. Metabolic theories [7,56] enable an understanding of how resource availability and temperature interact to affect body size both through plastic responses and selective shifts [57]. In combination with insights from comparative analyses of body-size change, they can result in the generation of explicit hypotheses to test specific causes and consequences of size change.

Body size is strongly tied to heat exchange and, thus, body temperature, and biophysical models provide a mechanistic basis for linking body size to climatic and nutritional change [58,59]. Such models apply the physics of heat and mass (water) transfer to predict the thermal state of organisms [58,60]. For ectotherms, this enables predictions of body temperature in a given environment, with changes in size relating to foraging opportunities, life-history timing and nutrition. For example, [60] used a biophysical model to predict thermally suitable activity windows for lizards exhibiting size clines and argued that body-size increases relate to positive selection pressure for delayed maturation in cool environments.

For homeothermic endotherms, by contrast, the quantity of energy or water expended to maintain a constant body temperature is a function of the thermal environment. For endotherms, size (together with shape and insulation) has a strong influence on the position of the 'thermoneutral zone' (TNZ; i.e. the environmental conditions where no excess energy or water is required to maintain thermal

homeostasis [5]). Biophysical models can quantify how changes in size affect water and energy expenditure and the consequent implications for survival in a given environment [5,60,61]. For example, Porter and Kearney considered a medium-sized (1–5 kg) mammal and showed that if selection acted to maximize time within the TNZ, smaller body sizes would be favored at low latitudes [5].

Conclusions

Understanding the mechanistic links between body size and environmental heterogeneity (e.g. climate and nutrition) will identify key traits that shape the potential of a species to respond to climate change and provide insights into thermal tolerances, information that is currently lacking for most species (e.g. [58]). Knowledge of the mechanistic links between body size and environmental variability will also greatly improve the ability to predict the responses of species to future climate warming, and use of body-size metrics for this purpose confers some advantages over other modeling approaches. Precision in quantifying the magnitude of both the response to climate change (size change) and the proposed stressor (temperature or nutrition) has an important influence on model results, particularly in identifying the degree of risk posed to a species and its physiological capacity to resist the threat [62]. It is an inherent lack of precision in quantifying responses to climate change (e.g. the use of species occurrence along environmental gradients in species distribution models) and the lack of an underpinning ecological theory that hampers interpretation and the predictive power of other approaches [63].

Recent reports of mass die-offs of endotherms [6,64] and ectotherms [65] in response to heat waves add urgency to the development of a better understanding of heat, energy and water balance in the context of body size. A recent model of avian water requirements as a function of body
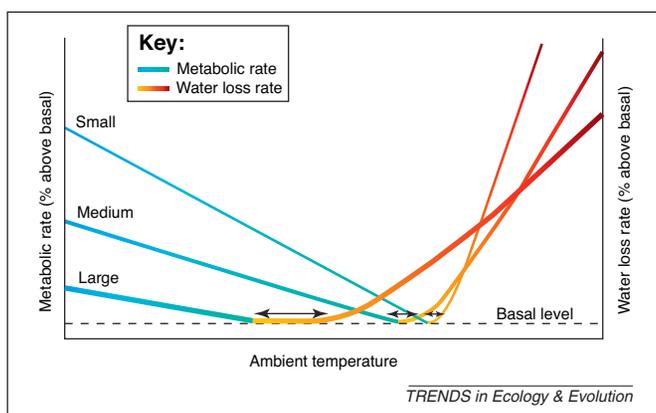
Figure 1. Heat-transfer theory [5,57,59] and empirical data [6] enable prediction of how the energy and water requirements of endotherms should change with environmental temperature and body size (small, medium or large). For any given size, metabolic rate (in blue) declines as temperature increases until the basal metabolic rate is reached. Above a threshold temperature, water-loss rate (in orange) increases. The range of ambient temperatures in between, where energy and water requirements are at basal levels, is known as the TNZ (thermoneutral zone). As body size increases (thicker lines), the TNZ becomes broader and shifts to cooler environments; thus the long-term energy and water requirements of larger individuals are minimized in cooler environments. Although the upper boundary of the TNZ of larger individuals occurs at lower ambient temperatures, smaller individuals lose water proportionally faster above this threshold and, hence, dehydrate faster under extreme heat.
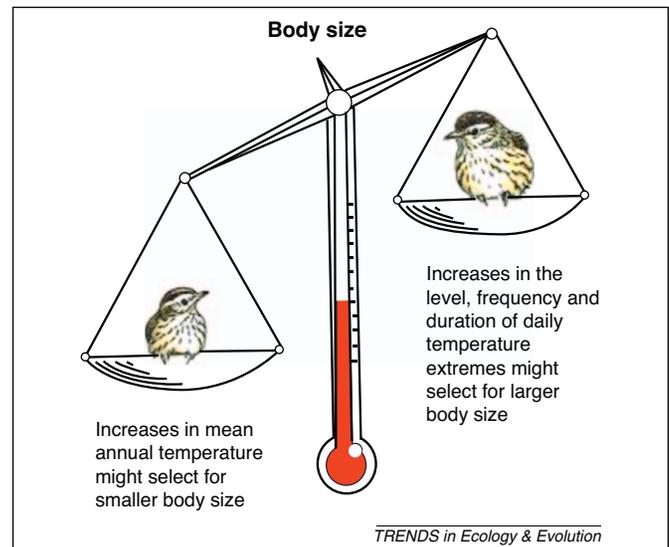
Figure 2. The predicted effects of ambient temperature on the direction of selection for small versus large body size in the context of anthropogenic climate change. The increased surface area:volume ratios and thinner boundary layers of smaller terrestrial endotherms increases potential rates of heat loss to cooler air [10]. However, smaller individuals might be more vulnerable to dehydration and overheating under short-term exposure to extreme high temperatures [6]. Thus, we predict that the direction of selection on body size will swing depending on the nature of temperature change: a gradual increase in mean temperature will exert sustained selective pressure for small size if water budgets are limiting, but occasional exposures to sufficiently high daily temperatures will periodically reverse the direction of selection on size.

size [6] highlights the potential of extreme climatic events to shape selection (reviewed in [66]). Rates of evaporative water loss increased disproportionately with decreasing body mass on extremely hot days, with smaller bodied desert bird species most vulnerable to acute dehydration and mortality [6]. This implies that the selective advantages of smaller size under a gradual rise in mean temperature might become disadvantageous under short-term exposure to temperature extremes, as demonstrated in other contexts [33] (Figure 1). Accordingly, the direction of selection on body size is predicted to swing depending on the nature and extent of temperature change (Figure 2) and could, in part, account for heterogeneity in the direction of body-size responses to global warming recorded to date (Table 1). Biophysical models provide a much-needed means of exploring the mechanistic basis of selection on size in the face of extreme events versus gradual warming, under different environmental conditions. Given that the frequency and intensity of extreme temperature events is predicted to increase [67], investigating the effect of temperature and nutrition on body size is an urgent priority and novel approaches to make the most of available historical data will provide an essential contribution.

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