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

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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.