REVIEW AND SYNTHESIS

Ecotypic variation in the context of global climate change: revisiting the rules

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Abstract

Patterns of ecotypic variation constitute some of the few 'rules' known to modern biology. Here, we examine several well-known ecogeographical rules, especially those pertaining to body size in contemporary, historical and fossil taxa. We review the evidence showing that rules of geographical variation in response to variation in the local environment can also apply to morphological changes through time in response to climate change. These rules hold at various time scales, ranging from contemporary to geological time scales. Patterns of body size variation in response to climate change at the individual species level may also be detected at the community level. The patterns underlying ecotypic variation are complex and highly context-dependent, reducing the 'predictive-power' of ecogeographical rules. This is especially true when considering the increasing impact of human activities on the environment. Nonetheless, ecogeographical rules may help interpret the likely influences of anthropogenic climate change on ecosystems. Global climate change has already influenced the body size of several contemporary species, and will likely have an even greater impact on animal communities in the future. For this reason, we highlight and emphasise the importance of museum specimens and the continued need for documenting the earth's biological diversity.

INTRODUCTION

"The present more or less unstable condition of the circumstances surrounding organic beings, together with the known mutations of climate our planet has undergone in past geological ages, points clearly to the agency of physical conditions as one of the chief factors in the evolution of new forms of life" (Allen 1877, p. 139).

Climate change is nothing new to the Earth system. At various times throughout the 3.5 billion years (Ba) history of life on our planet, major shifts in climate may have led to the entire reorganizations of biota (Sepkoski 1998). For example, global warming by 6 °C due to mass volcanism may have been the driving factor behind the end Permian mass extinction, where perhaps as many as 95% of all species perished (Benton & Twitchett 2003). Unlike these earlier events, however, contemporary changes in climate are accentuated by anthropogenic inputs and may be occurring at a greatly accelerated pace (Houghton *et al.* 2001; Jones *et al.* 2001). The past 30 years have been the warmest of the last millennium, and temperature increases have been

the greatest – *c.* 0.6 °C – during the 20th century (Houghton *et al.* 2001). Current estimates suggest that warming of 1.4–5.8 °C is likely over the next 100 years (Houghton *et al.* 2001). Recent studies agree that the rate of climate change may be even more critical than its magnitude and duration (Davis *et al.* 2005). In light of the increased rate of global warming, we urgently require a clear understanding of the potential impacts of these expected climate changes on living organisms.

The impacts of climate change on living organisms are already detectable at many levels, from alterations in the phenology of individuals to physiological, ecological and microevolutionary changes in individuals, populations and communities (Hughes 2000; Davis & Shaw 2001; McCarty 2001; Stenseth *et al.* 2002; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003). There is accumulating evidence of the detectable results of climate change on a wide spectrum of organisms, including plants, insects, fishes, reptiles, amphibians and mammals (reviewed in Parmesan & Yohe 2003; Root *et al.* 2003).

As might be expected, the response of organisms to environmental change is complex and highly context-dependent, and is shaped by both their physical and biological environments. The biotic response of species to their changing environment may involve modifications to their physiology, phenology, morphology and distribution (Hughes 2000), and can be categorized into three main classes: (i) shifts in the species' range to track the shifting climate; (ii) persistence *in situ* and local adaptation through phenotypical and/or phenological changes; and (iii) local extirpation and at a larger scale, extinction (Fig. 1; McCarty 2001; Walther *et al.* 2002, 2005; Davis *et al.* 2005). A combination of these responses may be observed across the range of a given species: migration towards the poles at higher latitudes, morphological and ecological adaptation in the centre of the range and extinction (range contraction) at lower latitudes of the species range (Davis & Shaw 2001). For mammals, however, the change in distribution
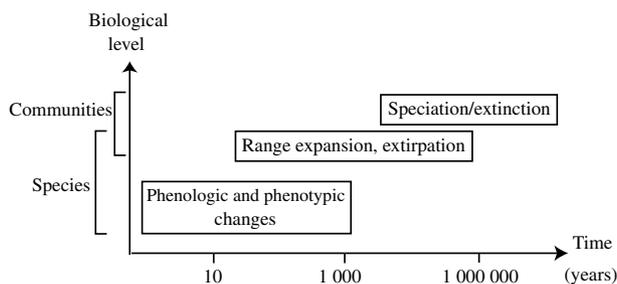
is rarely a simple shift to higher latitudes, and the direction and extent of the range shifts may vary across species (FAUNMAP Working Group 1996; Lyons 2003). In addition to the spatial scale, the temporal scale is also critical when documenting species' responses to climate change, and varied responses can be observed with increasing time intervals (Barnosky *et al.* 2003) (Fig. 1).

The challenge of accelerated climate warming in the next few decades combined with human-induced habitat deterioration (McCarty 2001) highlights the importance of adaptation in response to future climate change. Here, we review the evidence from contemporary, historical and evolutionary studies to estimate the power of ecogeographical rules in interpreting likely patterns of organismal responses to climate change.

VARIATION AT THE SPECIES LEVEL

Variation in space: ecogeographical rules

"Ecogeographical rules … are purely empirical generalizations describing parallelism between morphological variation and physiogeographical features." (Mayr 1956, p. 105).

There are a several well-established ecogeographical rules in animals, reflecting their adaptation to local conditions (Mayr 1956). The widespread existence of these patterns by itself may be evidence for a species' capacity to adapt to fluctuating environmental conditions. Ecogeographical rules have been abundantly validated by studies of many species of mammals, birds, other vertebrates, and even some invertebrates. Roughly, there are three main patterns of geographical phenotypic differentiation between populations within a species: (i) variation in colour; (ii) variation in the size of appendages; and (iii) variation in body size (Allen 1877). All these rules were originally formulated for endothermic vertebrates and thermal regulation was believed to be the chief explanation for their existence (Gloger 1833; Bergmann 1847; Allen 1877).

According to Gloger's rule, individuals that live in warm and humid areas are darker in colour than those living in cold and dry areas (Gloger 1833). The underlying mechanism for Gloger's rule is that individuals with more cryptic colouration are under reduced predation pressure. Gloger's rule also relates to thermoregulation: individuals with darker pigmentation are found in the tropics, while individuals with lighter pigmentation predominate towards the poles. This rule was first observed in birds but also applies to mammals, and maybe some insects. A classic example is provided by the hares which have white fur in the northern latitudes (*Lepus arcticus*) and a darker, brown fur in temperate habitats (*Lepus alleni*).

Figure 1 Temporal scales of biological responses to climate change. Phenotypical and phenological changes occur at the smaller time scales, from a few years up to several 100 years. Shifts in species distributions and extinctions are detectable at larger time scales.

According to Allen's rule, appendages size is reduced in cold climates (Allen 1877). Allen's rule is based on the simple reasoning that the less surface area an organism has relative to its body mass, the more thermally efficient it will be (e.g. the less heat it will lose). One way to reduce heat loss is through the reduction of appendages such as ears, tails, bills or limbs (Scholander 1955). This ecogeographical rule has been found within and across various species of mammals and birds (Allen 1877). For example, relative ear size increases in the fox from the artic fox (*Alopex lagopus*), the red fox (*Vulpes vulpes*) to the desert fox (*Fennecus zerda*).

Additional rules of geographical variation have been described during the last century but have been less studied (Rensch 1938). Briefly, they are the 'hair-rule' (mammals have longer and thicker hairs in colder areas), the 'rule of the shape of the wing' (birds have more slender and pointed wings in colder areas), the 'egg-rule' in birds and the 'rule of the litter-size' in mammals (increased clutch or litter size in colder areas).

In this review, we concentrate on the most widely studied pattern of ecotypic variation, the geographical differentiation in body size. Geographical variation often involves a complex combination of traits. Of these, body size is probably the single most obvious and important character. Most physiological and life history traits are known to scale with size, including lifespan, metabolic rate, fasting endurance, rate of development, fecundity, interspecific relations, and numerous other morphological, physiological, behavioural and ecological factors (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Moreover, body size is relatively easy to characterise, even for fossil species, which facilitates comparisons across a wide range of taxa (Damuth & MacFadden 1990; Alroy 1998).

An impressive majority of studies of geographical variation in body size have been carried out on mammals (Fig. 1, Appendix 1). There are much more data available for mammal species than for any other group of animal, and our review therefore concentrates on body size variation in this taxon.

Variation in body size and Bergmann's rule

The most well-known ecogeographical trend is the tendency of individuals within the geographical range of a species to be larger in body size under colder climatic conditions (Rensch 1938; Mayr 1956). This trend is named after Carl Bergmann (1847), who is generally credited with the idea that the heat loss of an organism is proportional to its surface-to-volume ratio (but see Rameaux & Sarrus 1838). There is a selective advantage to a higher body surface-to-volume ratio in warm areas, and conversely, to the reduced heat loss that accompanies a lowered surface-to-volume ratio in higher latitude and colder climates (e.g. Mayr 1956). Bergmann's rule was originally formulated to describe body

size variation among species within a given genus (Bergmann 1847), but there are many examples of an extension of Bergmann's rule describing latitudinal variation of body size among individuals within species. Environmental temperature is highly correlated with latitude and a positive relation between latitude and body size has been widely documented among endotherms including mammals and birds, as well as ectotherms such as amphibians, reptiles, some fishes and invertebrates (Appendix 1A). Bergmann's rule holds for most – between 62% and 83% – of vertebrate species, with the exception of squamates and fishes, where fewer than 30% of species conform to Bergmann's rule (Fig. 2). Although latitude is not an environmental factor, it has frequently been used as a proxy for ambient temperature and other environmental factors (Hawkins & Diniz-Filho 2004). In the past this was justified by lack of direct climate measurements, but presently such data are available for most part of the world, and we predict that in the future the use of latitude as a proxy for temperature will be less common.

Because environmental/ambient temperature can have direct effects on the ecology and physiology of organisms, Bergmann's rule is often interpreted as a direct response to temperature (Birch 1957; Brown & Lee 1969; Dawson 1992). However, a thermal explanation for the existence of Bergmann's rule has been questioned by several researchers. Scholander (1955), for example, argued that vascular control and fur insulation are more efficient at heat dissipation and conservation than are changes in body size. Factors correlated with body size such as basal metabolic rate, cost of transport, dominance in a community, success in mating, size and type of food, and competition may also be the actual targets of selection (McNab 1971; Calder 1984; Schmidt-Nielsen 1984). It may also be that environmental factors correlated with ambient temperature are responsible
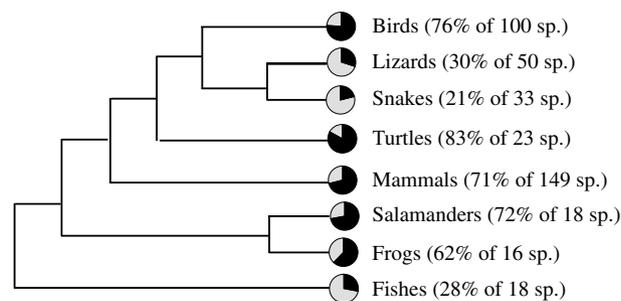
Figure 2 The extent of Bergmann's rule among vertebrates. A significant positive relation between body size and latitude has been found in a majority of the vertebrate species examined; data from the most recent reviews on Bergmann's rule (Appendix 1); black filling, agrees with Bergmann's rule; grey filling, disagrees with Bergmann's rule.

for observed trends in body size. James (1970), for example, suggested that body size varied in response to a combination of climatic factors, specifically the interactions of moisture and temperature. This hypothesis was supported by a study on body size variation among North America bobcats (*Lynx rufus*) (Wigginton & Dobson 1999). Similarly, moisture apparently influences wing and skull size of the bat *Eptesicus fuscus* more than temperature, perhaps because of the need to conserve water in hot and dry environments (Burnett 1983). A study of body-size variation in five species of Australian mammals demonstrated that both moisture index and precipitation were often better correlated with body size than temperature (Yom-Tov & Nix 1986). Still others suggested that body size is better correlated with primary plant productivity or food availability (Rosenzweig 1968). Lastly, Bergmann's rule also applies to some ectotherms, and factors other than thermal regulation are likely better explanations of body size gradients in these species. Clearly, the debate over the factors influencing the body size of organisms has not been settled.

The interpretation of correlations between body size, latitude, temperature and precipitation is difficult, because these environmental factors often covary. One way to deal with this problem is to use information theory-derived indices (such as the Akaike information criterion; Johnson & Omland 2004). Another way to tease apart the effects of several climatic factors is to test them simultaneously, and to assume that the relative effect of each factor represents its effect on body size itself (Yom-Tov & Nix 1986; Ashton 2001). However, the relative effect of the factors used in the analysis depends to some extent on the order of entering them into the analysis. This problem was recently tackled by Yom-Tov & Geffen (2006) who studied body size trends in 20 species of mammals inhabiting Israel and Sinai. The authors used a conservative approach by entering precipitation as the last factor into a sequential regression and found that for several species precipitation explained as much of the variation in body size as did temperature. Other species in the area were more influenced by summer temperature. They concluded that in areas where rain is a limiting factor for primary production (as it is in arid and semi-arid regions), primary productivity may have an important effect on mammalian body size. This was evident from the considerable proportion of the variability in body size explained by rain, as well as by the positive relationships between average minimum January temperature and body size in four of the six species influenced by rain (low ambient temperature inhibits plant growth and primary production). Different ecological factors may be responsible for generating Bergmannian size patterns, even in very closely related species (Angilletta & Dunham 2003). Clearly, the underlying causes for ecogeographical variation involve a number of interrelated variables.

Variation in body size and the island rule

Populations that evolve on islands often provide valuable examples of body size evolution. The reduced species diversity on islands results in a total reorganization of interspecific interactions within island communities, and island species are generally subjected to reduced predation and interspecific competition. Also, because islands are clearly delimited in space, changes in the environment may be easier to track on islands than on the mainland; islands therefore represent natural replicated experiments to ecologists and paleontologists. Among insular mammals, there is a general tendency for small mammals to evolve towards larger size and larger species towards smaller size (Foster 1964; Van Valen 1973; Lomolino 1985, 2005). This tendency has come to be known as the island rule (Van Valen 1973). For example, the trend of increased body size ('gigantism') has been documented in numerous island taxa of rodent, bird and reptile such as the giant tortoises of the Galapagos and the Caribbean anoles (Appendix 1D). As with Bergmann's rule, the island rule has exceptions. For instance, based on an extensive survey of museum collections, Meiri *et al.* (2005) showed that there was no consistent pattern of body size evolution among carnivores on islands. The pattern of body size variation in island snakes is also less consistent and appears to be dependent on prey availability (Appendix 1D).

The strength of the island effect on body size evolution is usually presumed to be inversely proportional to the size of the island (Heaney 1978) and positively related to the degree of isolation from the mainland source of the island population (Foster 1964). Various selective forces are thought to explain the size evolution in island mammals, including the absence of predators and/or competitors or resource limitations (Sondaar 1977; Heaney 1978; Damuth 1993; Dayan & Simberloff 1998).

Recently, Millien & Damuth (2004) and Millien (2004) studied the combined effects of both climate warming *and* isolation on the body size evolution in the two Japanese field mice, *Apodemus speciosus* and *Apodemus argenteus*, over the Quaternary. The authors studied over 350 specimens stored in the collections of the National Science Museum in Tokyo. They found that *Apodemus speciosus* conforms today to both Bergmanns's rule (larger size at higher latitude) and the island rule (larger size on smaller islands) (Fig. 3). The fossil record suggests that, overall, climate warming has been the main driving factor of body size evolution in this species, but the effect of temperature change has been attenuated on the smaller islands, in accordance with the island rule. Interestingly, the small Japanese field mouse, *Apodemus argenteus*, does not conform to Bergmann's rule and the effect of isolation on body size evolution is much weaker in this species
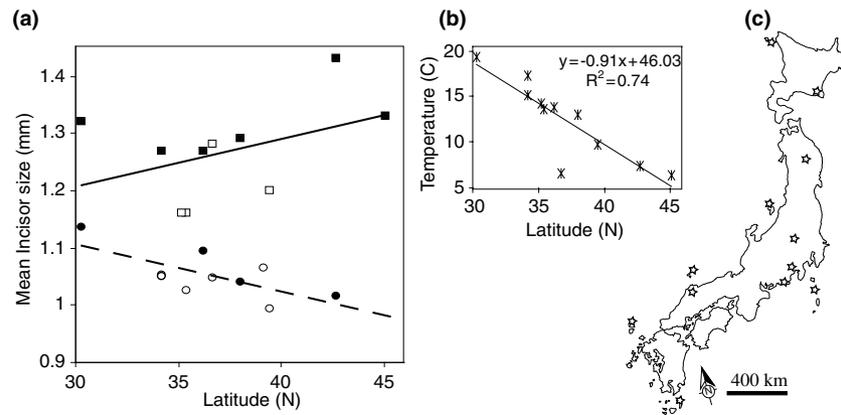
Figure 3 (a) Geographical variation in the antero-posterior diameter of the lower incisor in the two Japanase field mice, *Apodemus speciosus* (squares) and *Apodemus argenteus* (circles); open symbols represent populations on the large island of Honshu, filled symbols represent those on the smaller islands. As predicted from Bergmann's rule, there is an increase in size with latitude in *Apodemus speciosus* (size = $0.008 \times$ latitude + 0.95; $n = 206$; $P < 0.0002$), whereas this trend is reversed in *Apodemus argenteus* (size = $-0.005 \times$ latitude + 1.21; $n = 151$; $P < 0.03$). In both species, at a given latitude, individuals are usually larger on the smaller islands than on Honshu, conforming to the island rule; (b) there is a significant decrease in temperature with increasing latitude in Japan; (c) a map of the Japanese archipelago with the sample localities.

than in *Apodemus speciosus* (Fig.3). The variation in size in the two species at both spatial and temporal scales, while being driven by climate change and isolation, may also be strongly influenced by interspecific competition, especially on the smaller islands (Millien-Parra & Loreau 2000).

For both Bergmann's rule and the island rule, the causal nature of the link between the environment and the adaptive response in terms of body size change is far from clear. In the former, the variation in body size can be correlated with ambient temperature or any latitudinal-related factor, while in the latter, body size can be correlated with island area and isolation. Moreover, as with any correlational approach, there is still a possibility that factors of the environment other than the one(s) chosen would provide a better explanation of the observed trends. These other factors should be investigated at both ecological and historical levels.

Bergmann's rule and the island rule emphasize the importance of both climate and environment in generating patterns of geographical variation, and it is reasonable to assume that these geographical trends *also occurred in the past*. The prevalence of ecogeographical rules across a broad taxonomic range indicates that many species have the potential to adapt to environmental change, which is critical within the current context of climate warming (Davis *et al.* 2005). To estimate the potential biological and ecological responses to future climate changes, we review the evidence for the adaptation of species to past climate fluctuations at several temporal scales.

Variation in time: from recent times to the fossil record

"...fossil records can provide tests of evolutionary hypotheses, enhancing understanding of the evolutionary consequences of climate change" (Davis *et al.* 2005, p. 1704).

Barnosky *et al.* (2003) proposed that in mammals morphological changes (together with minor changes in species distribution) constitute the first response of species to climate change (Fig. 1); they also suggested that morphological changes are detectable on a 100-year scale. There are several examples of rapid changes in species morphology or behaviour that have been associated with environmental changes in historical time (Kinnison & Hendry 2001; Hairston *et al.* 2005). For example, within a few decades, the direction of evolution in body size and beak morphology changed several times in two species of Darwin's finches on the Galapagos island of Daphne Major following drought events on the island (Grant & Grant 2002). Similarly, the convergence of geographical clines in recently introduced and ancestral populations suggests an adaptive response of the introduced population to its new environmental conditions (Yom-Tov *et al.* 1986; Huey *et al.* 2000). In the following sections, we will review the evidence for changes in morphology that have been related to environmental fluctuations at successive increasing time intervals, from a few decades up to several million years.

Evolutionary size changes following species introduction

Recent introductions of species provide convincing cases of patterns of geographical variation that may in part be a direct response to local environmental conditions. For example, there is a significant geographical pattern of body size increase with latitude in New Zealand in the house sparrow (*Passer domesticus*), which was introduced from Europe between 1862 and 1871. The 110 introduced individuals were all from a single region in England and were released at only five localities in New Zealand. The latitudinal trend seen today took only 100 years to establish, and it has been attributed to adaptation to local environmental factors (Baker 1980).

Introductions of mammals also provide compelling evidence in support of the role of environmental conditions on body size. In its native Australian range, the brushtail possum (*Trichosurus vulpecula*) exhibits a body size trend that conforms to Bergmann's rule. After 1837, there were several introductions of this species from Southeastern Australia (where possums are the largest and have thick fur) to New Zealand. Today, the brushtail possum is distributed throughout New Zealand, and within several decades and less than 50 generations, body size variation in New Zealand populations converged on that observed in Australia, as expected from Bergmann's rule (Yom-Tov *et al.* 1986). Yom-Tov *et al.* (1999) examined the effects of latitude, island size and competition on skull size of three species of rats (*Rattus rattus*, *Rattus norvegicus* and *Rattus exulans*) that have been introduced to 71 Pacific and New Zealand islands and found that skull size of *R. exulans* conforms to Bergmann's rule and is inversely correlated with island size. For *R. exulans* and *R. rattus*, skull size is inversely correlated with the number of other rodent species on the same islands, suggesting that interspecific competition affected body size in these species. European rabbits (*Oryctolagus cuniculus*) introduced to Australia have also adapted to different climatic regions through changes in body proportions after little more than a century; individuals inhabiting arid and warm region were found to have relatively larger ears (conforming to Allen's rule) and to be relatively heavier (a trend opposed to Bergmann's rule) than in cooler, more humid regions (Williams & Moore 1989). Similarly, Simberloff *et al.* (2000) showed that males of the small Indian mongoose (*Herpestes javanicus*) have increased in size on all islands where this species was introduced approximately a century ago.

Body size gradients may also develop extremely rapidly in introduced ectothermic species. A decade after its introduction, there was no wing length cline in the North American populations of the fruit fly, *Drosophila subobscura*. However, after two decades, Huey *et al.* (2000) documented such a latitudinal trend, convergent with the ancestral European one. In contrast to these examples of convergent evolution in ancestral and introduced species, the introduction of the pumpkinseed sunfish (*Lepomis gibbosus*) from North America to Europe in the late 19th century has led to divergent patterns of body size variation in native and introduced populations (Copp *et al.* 2004). While body size variation in the native North American range of the species fits a converse Bergmann size gradient, European populations of *Lepomis gibbosus* conform to Bergmann's rule. As European sunfish are also significantly smaller than those from North America, Copp *et al.* (2004) suggest that limited food resources across the introduced range may have a stronger influence on body size variation than temperature differences associated with latitude. Despite some exceptions, there is often a parallel in geographical variation between the ancestral form and the newly introduced species, supporting the importance of the impact of the environment on species morphology.

Evolutionary size changes related to historical climate change

The historical record of local and regional climate allows an examination of adaptation to climate warming over the past century. For example, work in central New Mexico has documented a significant response of rodents to climate warming over the past decade. By examining hundreds of museum specimens archived at the Museum of Southwestern Biology, Smith *et al.* (1998) demonstrated that the average body size of woodrat populations (*Neotoma albigula*) at the Sevilleta long-term ecological research station, New Mexico, had decreased by *c.* 15% over this period (Fig. 4). This was apparently due to smaller individuals successfully overwintering because of warmer winter temperatures, coupled with smaller size also being favoured in the warmer summers (Smith *et al.* 1998). Similarly, four of the five passerine bird species studied by Yom-Tov (2001) decreased in body size during the second-half of the 20th century in Israel. Body size decreases have also been observed among several species of British passerines studied continuously during the last three decades in England (Yom-Tov *et al.* 2006).

Global warming may also affect animals in the opposite way. Increased temperature, especially during the winter, enables animals to divert energy from maintenance to growth. Furthermore, elevated temperature may increase the length of the growing season, thus increasing primary production and consequently food availability. Individuals may in turn increase in body size, thus producing a trend contrary to Bergmann's rule. For instance, recent increases in body size have been observed in the Japanese large field mouse *Apodemus speciosus* (Yom-Tov & Yom-Tov 2004) and the masked shrew *Sorex cinereus* in Alaska (Fig. 5; Yom-Tov & Yom-Tov 2005). In both cases the observed trends were attributed indirectly to global warming: elevated autumn and winter temperatures affected food availability, thus enabling these species to utilize the extra energy available for growth.
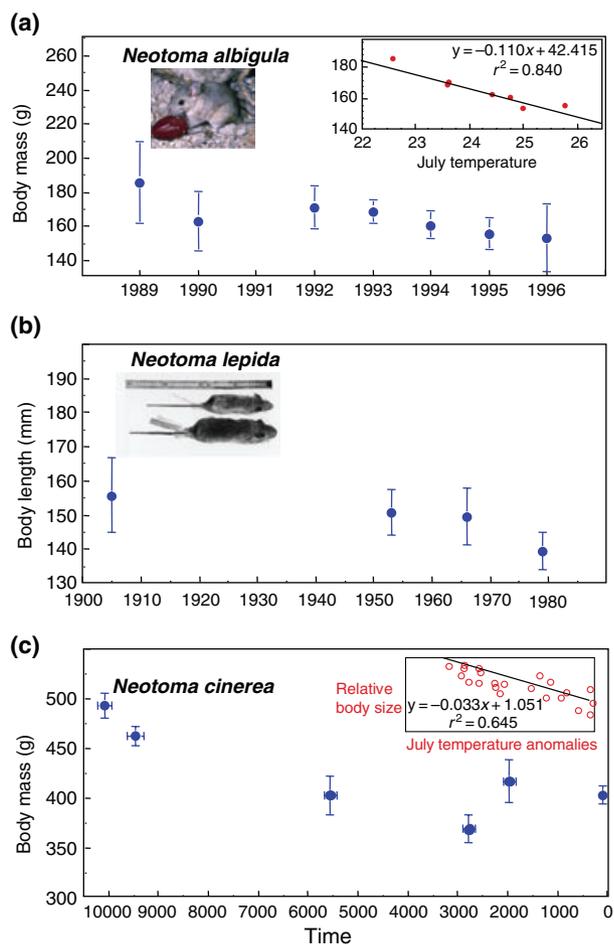
Figure 4 Body mass and body length variation over time in woodrat species. (a) Size changes over a decadal scale in *Neotoma albigula*; inset shows the significant decrease in body size with mean July temperature in this species; (b) size change over centennial scale in *Neotoma lepida*; (c) size change in *Neotoma cinerea* over the last 10 000 years; inset shows the significant decrease in body size with mean July temperature in this species. In all cases, size changes occurred according to Bergmann's rule.

Other recent increases in body size, mainly among carnivoran mammals, have been attributed to increased food availability due to human activity. An increase in prey availability for harbour porpoises (*Phocoena phocoena*) (presumably due to hunting pressure and a decrease in population density) resulted in an increase in body length of calves as well as earlier sexual maturity of females (Read & Gaskin 1990). In many countries, anthropogenic factors are responsible for an appreciable increase in food availability for predators over the past century. The significant rise in human living standards has generally been coupled with an increase in the amount and nutritional quality of garbage. Increases in skull size (which is highly correlated with body size) among red foxes (*Vulpes vulpes*)

and Eurasian badgers (*Meles meles*) in Denmark (Yom-Tov *et al.* 2003) and in body length among four species of carnivores in Israel (Yom-Tov 2003) during the second half of the 20th century have been attributed to an improved diet due to greater availability of garbage, road kills and changes in agricultural practices.

Species surviving in fragmented landscapes are also confronted with a modified environment characterized by a reduced area and an increased isolation relative to their undisturbed habitat. These new environmental conditions parallel those seen in true island habitats and one may suspect that phenotypic changes in response to fragmentation are similar to changes in island species. Accordingly, Schmidt & Jensen (2003) demonstrated that body size changes have occurred in 25 Danish mammal species over the last two centuries. The authors showed that body size changes in these species are in accordance with the island rule and are attributed to anthropogenic habitat fragmentation in Denmark. The same authors recently observed a similar 'island pattern' in the evolution of body size in Danish bird species over the same period of time (Schmidt & Jensen 2005). It seems thus that habitat fragmentation has a direct effect on body size evolution. More importantly, habitat loss and fragmentation may increase species susceptibility to climate change by limiting their chance of migrating to track climate variations (Thomas *et al.* 2004). However, as both climate change and fragmentation may affect body size evolution in a similar way (e.g. increased size in fragmented landscape and in colder climates for small mammals), their relative effects on body size evolution are difficult to tease apart.

We have focussed here on the correlation between morphological changes and local environmental variables such as temperature, precipitation or food availability. However, given the current context of global climate change, it may be more relevant to concentrate on larger scale patterns of variation over evolutionary time scales (Stenseth *et al.* 2002), as some ecological processes may paradoxically be better predicted by large-scale global climate indices than by local weather parameters (Hallett *et al.* 2004). To better understand long-term ecological and evolutionary changes in response to climate warming, scientists have turned to the past. Examination of the responses of organisms to changes occurring over geological time allows us to include climatic fluctuations of greater magnitude than those observed over the past few decades.

Evolutionary changes in the fossil record
Increasingly, scientists interested in the effects of anthropogenic warming have turned to the fossil record. The Plio-Pleistocene is of particular interest, as this was a period of repeated climatic fluctuations, many of which may have occurred rapidly. Greenland ice core records, for example,
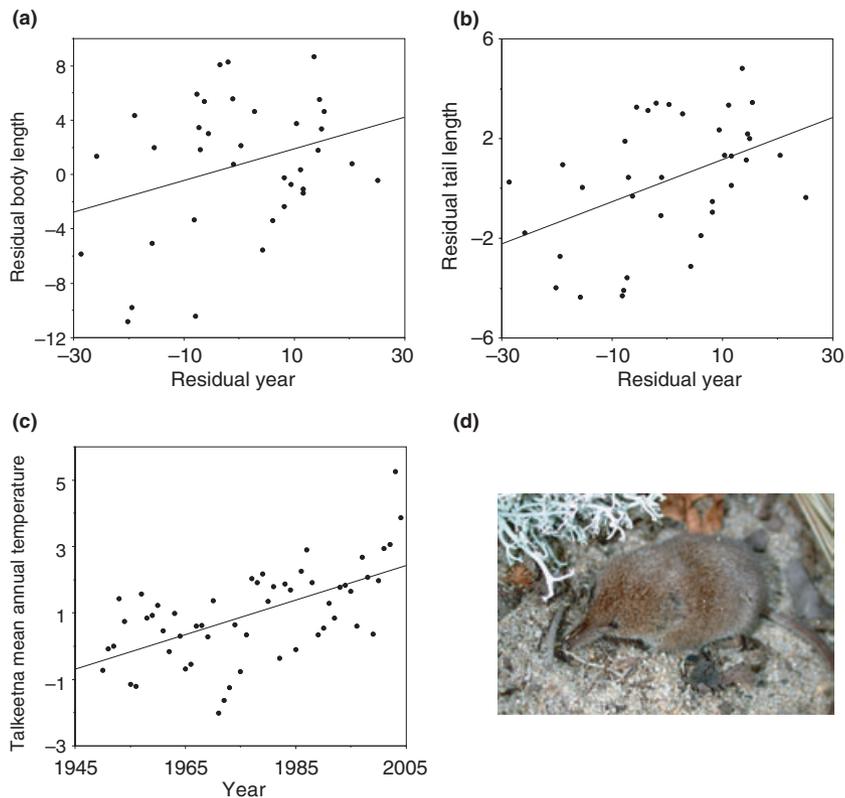
Figure 5 The relationship between: (a) residual body length; (b) residual tail length (annual mean values, corrected for latitude, longitude and sinus month of collection, where May = 1) and year of collection (corrected for mean annual temperature at Talkeetna 62.30 N 150.10 W, Alaska, a site close to the distribution centre of our data) of masked shrews (*Sorex cinereus*) in Alaska; The increase in body length and tail length is significant ($-2\sum \ln P = 15.544$; $P < 0.005$); (c) mean ambient temperature at Talkeetna significantly increased ($P < 0.0001$) by 2.8 °C during the study period (1950–2004); (d) *Sorex cinereus* (photo courtesy of Phil Myers and the Animal Diversity Web, University of Michigan Museum of Zoology).

suggest at least 20 abrupt warming events during the last glacial period (Dansgaard *et al.* 1993). More regional records such as high-resolution lake sediment cores and dendroclimatic reconstructions also suggest substantial oscillations in both temperature and hydrology (Biondi *et al.* 1999; Benson *et al.* 2002). These large shifts in both regional and global temperature fluctuations undoubtedly exerted substantial selection pressures on organisms (Grayson 2000). By investigating the responses of organisms to the climatic fluctuations of the late Quaternary, we may be able to more accurately characterize the likely responses to anthropogenic climate forcing. The past few thousand years are arguably the best proxy we have for understanding the effects of anthropogenic climate change (Houghton *et al.* 2001).

Several recent studies have documented that Bergmann's rule applies to temporal responses over the Pleistocene; animals became smaller during the warmer conditions of the middle and late Holocene, and were larger during the cooler conditions of the full glacial, the Little Ice Age and the Younger Dryas (Smith *et al.* 1995; Smith & Betancourt 1998, 2003). Size changes in Quaternary mammal species have often been attributed to the climate change occurring during this period (Appendix 1B).

In many ways, woodrats (*Neotoma*) are the poster children for Bergmann's rule. This is because, despite the fact that they often live in hot deserts, woodrat (*Neotoma*)

species lack specialized adaptations to heat and their body size appears to be profoundly sensitive to environmental temperature (Brown & Lee 1969; Smith & Betancourt 2006). Not only do contemporary species within the genus conform to Bergmann's rule, but individual populations within species also display robust relationships with temperature (Smith *et al.* 1995; Smith & Betancourt 1998, 2003, 2006). In this instance, physiological constraints may be important; both maximum and minimum environmental temperatures have also been demonstrated to scale inversely with body mass as does lethal temperature (Smith *et al.* 1995). Moreover, studies examining populations over both historical and millennial time scales demonstrate that woodrats adapt to climate change by altering body size (Fig. 4; Smith *et al.* 1995, 1998; Smith & Betancourt 1998, 2003, 2006). The response is robust and in the direction predicted by Bergmann's rule; woodrats are larger during cold intervals, and smaller during warmer episodes. These patterns are remarkably concordant across the species range, reflecting common environmental conditions over the late Pleistocene (Smith & Betancourt 2006). Responses to temperature are more complicated at range boundaries, where animals are at the limits of their thermal tolerances (Smith & Betancourt 2003). In these areas, populations at high elevation sites demonstrate a typical Bergmann's rule

response to temperature, while populations located at low elevation sites display a different response at various times over the Holocene. During colder episodes, they adapt by increases in body size, in accordance with Bergmann's rule. During warmer conditions, however, such as those of the Altithermal during the mid-Holocene, local populations are extirpated (Smith & Betancourt 2003). These sites are only repopulated when environmental conditions become more moderate. In deeper time, morphological changes in the fossil record have also often been attributed to changes in the environment in Miocene mammals (Appendix 1C). Bergmann's rule was recently proposed as a mechanism for the size increase in deep-sea ostracods over the past 40 million years (Hunt & Roy 2006). In this study, the authors suggested that Bergmann's rule and Cope's rule (the tendency for organisms in evolving lineages of size increase over geological time) are related patterns, both reflecting the influence of environmental temperature changes.

There are many striking examples of evolutionary size change in island mammals that parallel those seen today. The dwarfing of large mammals on islands is remarkably well illustrated by Pleistocene mammals (Appendix 1E). For example, the Quaternary Sicilian elephant (*Elephas falconeri*) reached a height of less than 1 m – a quarter of the size of its mainland ancestor (Palombo 2003), and its body mass was estimated at 100 kg – 150 times less than its mainland relative (Roth 1992). A very striking example of the island rule has recently been discovered in the case of the dwarfed Pleistocene hominins of Flores island in Indonesia (Brown *et al.* 2004; Morwood *et al.* 2005; but see Barham 2004). The 1-m high *Homo floresiensis* coexisted with pygmy elephants (*Stegodon*) and Komodo dragons and is assumed to have evolved from an isolated ancestral population of *Homo erectus* during the Quaternary. Conversely, a trend towards gigantism of island rodents has been observed in numerous fossil species (Appendix 1E). For instance, Millien & Jaeger (2001) estimated a size increase of 200% in the giant endemic murid rodent *Microtia* from a paleoisland in Southern Italy.

While it appears that many species follow Bergmann's rule and the island rule across space and time, there is also some evidence for contrary geographical or evolutionary responses. The existence of conflicting patterns of body size variation with geography in closely related species also highlights the importance of ecology in the establishment of body size gradients (Millien-Parra & Loreau 2000; Ashton 2001; Angilletta & Dunham 2003). Ashton (2001) identified significant variation in body size in two sister taxa of rattlesnake (*Crotoalus viridis* and *Crotoalus oreganus*). While *C. viridis* exhibited body size variation consistent with Bergmann's rule, *C. oreganus* showed the opposite pattern, with body size variation consistent with a converse

Bergmann's rule. Similarly, the two Japanese field mice (*Apodemus speciosus* and *Apodemus argenteus*) show opposite latitudinal trends in body size (Millien & Damuth 2004; Millien 2004) (Fig. 3). Different and even sometimes reversed responses to similar climatic variation in space and time *within* species have also often been documented (Dayan *et al.* 1991).

VARIATION AT THE COMMUNITY LEVEL

"…data are needed not just for one species, but for all the organisms within a community" (Davis 1990, p. 269).

The varied responses of species or populations to global climate change can be explained by locally unique manifestations of global climate change, depending upon the geographical areas (Barnosky 2001). However, factors operating at the community level (predation and competition/character displacement) may be stronger than climate forcing or at least have some effects interacting with climatic factors (Brown *et al.* 1997; Stenseth *et al.* 2002). In fact, many studies have proposed that biotic factors are more important than environmental effects in driving evolution of species and communities (see review in Barnosky 2001). Darwin himself, based on examples on acclimatization of domestic animals and plants, was convinced that "species in nature are closely limited in their ranges by the competition of other organic beings quite as much as, or more than, by adaptation to particular climates" (Darwin 1859, p. 180). It may also be that the environment is more important at the poleward limit of a species' range, whereas biotic interactions predominate in the more equatorial portions of a species' range (Davis & Shaw 2001). The strength of interspecific interactions may also depend upon the environmental gradient (Holt 1990). One way to characterize species' interactions within a community is to study the properties of the log-transformed body size distribution of species that make the community. In this context, the body size structure of fossil mammal communities as a whole – as opposed to the body size of a single species – has been linked to paleoenvironmental changes (Legendre 1989; Montuire 1999; Croft 2001). At large spatial and temporal scales, community level body size distributions seem to have a consistent response to climate change (Lyons *et al.* 2003), although the ultimate drivers of body size patterns are still debated. Brown & Nicoletto (1991) argued that body size distributions of North American mammal communities tend to be relatively uniform (but see Marquet & Cofre 1999; Bakker & Kelt 2000), whereas at the continental scale, body size distributions are right-skewed and unimodal. The proximate cause for the differences in distribution shape with spatial scale is thought to be turnover in the identity of species in the modal body size class of *c.* 100 g across

communities. Moreover, Smith *et al.* (2004) documented multimodality in modern continental body size distributions on North America, South America, Australia and Africa, but with significant differences in the shapes of the distributions for all continents. Africa was the only continent that had a distinctly bimodal body size distribution. When the extinct late Pleistocene mammals were included, the distributions were bimodal on all continents except Australia (Lyons *et al.* 2004). Indeed, the late Pleistocene continental distributions of North and South America were significantly different from the modern distributions documented by Smith *et al.* (2004), but not significantly different from the late Pleistocene of Africa (Lyons *et al.* 2004). Accordingly, examination of body size distributions for mammals in North America across the Cenozoic indicates that bimodality has been the norm since *c.* 40 million years ago (Alroy 1998, 2003).

Such consistent, robust patterns in continental body size distributions for Cenozoic mammals suggest that body size plays an important role in the evolution of mammalian biotas through time. The uniform body size distributions found at the community level in North America also indicate that body size may play an important role in community assembly. If so, we would predict consistent body size distributions at the community level across time. Lyons *et al.* (2003) compiled species lists and body sizes for 328 mammal assemblages across the last 40 000 years and evaluated the shapes of the resulting body size distributions. Mean, median, skew and kurtosis values for fossil assemblages were compared with shape statistics describing 80 modern assemblages for North America. The descriptive statistics of the shapes of most fossil assemblages (>60%) fell within the range of values for the modern assemblages, suggesting that body size is indeed an inherent component of communities. Because of the limits of the fossil record, some of the variation in the shapes of paleocommunity body size distributions is likely due to errors in body size estimation of fossil species, and taphonomic biases. However, the different shapes of local community distributions found in forest vs. open habitats in South America (Bakker & Kelt 2000) suggest that some of the variation is also due to local and regional climate changes (Lyons *et al.* 2003). If so, we should expect changes in the shapes of local body size distributions as climate changes in the future. Overall, these results suggest that changes at the community and continental scales as a result of climate warming may have some predictability, despite the individualistic response of constituent species.

The evolving role of museum collections in climate change studies

"Old dead rats are valuable" (Diamond 1990, p. 334).

The critical but often underacknowledged role museum collections play in studies of ecotypic variation warrants final mention here. The relevance of museum specimens to disciplines outside of taxonomy and systematics (e.g. ecology and paleoecology) is undeniable, if not always obvious (see reviews in Suarez & Tsutsui 2004; Winker 2004). For example, over two-thirds ($\geq$ 65) of the 92 studies surveyed by Ashton *et al.* (2000) in their literature review of Bergmann's rule in mammals relied, at least in part, on museum specimens and their associated data. Collectively, these studies represent well over *fifty thousand* examined specimens archived in various natural history collections throughout the world (L. Olson, unpubl. data), all of which remain available for repeated or expanded investigations. Similarly, most of the studies detailed in this paper would not have been possible if it were not for the efforts of countless collectors, preparators, collection managers, and curators, as well as the availability of resources associated with the collection and preservation of these irreplaceable records of the past. Many contemporary species are very well represented in museum collections with records spanning the last several centuries. In an era of diminishing support for museum collections (e.g. Stokstad 2003), the proliferation of collection-based studies investigating the effects of environmental change on biological diversity at all levels will (hopefully) be looked back on as a timely renaissance. Museum specimens have been likened to "canaries in the coal mine" (Winker 2004) in this regard, and the expense associated with their maintenance and growth is trivial when compared with the potential costs of their absence (Suarez & Tsutsui 2004). As the studies reviewed here demonstrate all too clearly, the need for continued collecting efforts should perhaps be more appropriately viewed as an obligation if we are to continue to rigorously and responsibly document the changes we are causing. Not only have "old dead rats" and other museum specimens *always* been valuable, their value increases with the passage of time, the development of new analytical techniques, and the emergence of questions associated with our changing earth.

CONCLUSION

Even though the pattern of climate change over long periods of time is complex, some parallels can still be drawn between changes in species morphology and global climate change. An encouraging lesson from the fossil record is that species have the capacity to evolve in the face of environmental change. However, the extent and rate of current climatic trends may be unprecedented (Hughes 2000; Houghton *et al.* 2001, but see Biondi *et al.* 1999), and we may discover that some species will soon reach their limit to adaptation (Holt 1990). This limit is in theory set by

the amount of genetic variability of individuals within populations, and little is known about the extent of genetic variability and the 'evolvability' (or evolutionary potential) of most species. More importantly, the rate of evolution at the population level of a morphological character such as body size is the most critical during periods of rapid climate change as in the Quaternary or as predicted for the next decades; species have to evolve quickly enough to adapt to their new environmental conditions and track the rapidly changing climate.

For many species, it may be difficult to predict the effect of climate change on morphology. For a few species (e.g. woodrats), much is known about their ecology, morphology, physiology and genetics. With this accumulated knowledge, we may be able to predict the responses of these taxa to future environmental fluctuations. However, these species may be the exception, and for most species, only a part of the relevant information is known, and predictions on their response to climate change may be less accurate (Holt 1990). Moreover, there may be several evolutionary solutions for a given species to adapt to its new environment (Mayr 1956). Yet, more and more data are becoming available, and there is abundant empirical evidence for the impact of climate change on living organisms (Hughes 2000). The consistent patterns of ecotypic variation observed across varied taxa, and across wide geographical and temporal scales, provide strong evidence for the non-negligible effect of climate warming on the biology of species (McCarty 2001). Both historical and fossil records suggest that there is some convergence across different temporal scales of patterns associated with climate change. Moreover, these consistent patterns are evident despite the possibly confounding influences of human activities.

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APPENDIX 1: SOME EXAMPLES OF BERGMANN'S RULE AND THE ISLAND RULE IN THE LITERATURE

Section A	Bergmann's rule in some living species
Mammals	Ashton, K.G., Tracy, M.C. & de Queiroz, A. (2000). Is Bergmann's rule valid for mammals? *Am. Nat.*, **156**, 390–415
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	Freckleton, R.P., Harvey, P.H. & Pagel, M. (2003). Bergmann's rule and body size in mammals. *Am. Nat.*, **161**, 821–825
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Amphibians	Ashton, K.G. (2002). Do amphibians follow Bergmann's rule? *Can. J. Zool.*, **80**, 708–716
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Fishes	Belk, M.C. & Houston, D.D. (2002). Bergmann's rule in ectotherms: a test using freswater fishes. *Am. Nat.*, **160**, 803–808
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Sloths	Anderson, R.P. & Handley, C.O. Jr (2002). Dwarfism in insular sloths: biogeography, selection, and evolutionary rate. *Evolution*, **56**, 1045–1058
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