Chapter 10

Mammal Ecology as an Indicator of Climate Change

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On 12 January 2002, weather stations in New South Wales, Australia recorded air temperatures exceeding 42 °C, which is more than 16 °C hotter than the 30-year average daily maximum. On this day, more than 3500 flying foxes (large fruit bats in the genus Pteropus) from nine colonies in the region succumbed to hyperthermia. Mass die-offs of flying foxes associated with heat waves are known to have occurred 3 times in the century prior to 1990, 3 times in the decade between 1990 and 2000, and 13 times in 7 years between 2000 and 2007 [1].

1. INTRODUCTION: A PRIMER ON MAMMAL THERMOREGULATION AND CLIMATE IMPACTS

Fruit bats, like other mammals and birds, use a combination of physiological and behavioural mechanisms to regulate their body temperature [2]. This thermoregulatory capacity decouples their core body temperature from air temperature. Thus, despite exposure of the body surface to very cold or very hot air temperatures, appropriate physiological and behavioural thermoregulatory responses ensure that core body temperature never varies by more than a few degrees centigrade between birth and death [3]. Even birds and mammals that express torpor do not abandon thermoregulation, but rather lower their thermoregulatory setpoint [4]. For all endotherms, the abandonment of thermoregulation is fatal.

The capacity for mammals to thermoregulate might be expected to enable a degree of thermal independence that reduces their vulnerability to environmental conditions and their sensitivity to climate change. But 3500 dead flying foxes suggest any such expectation would be incorrect [1]. To understand why, we must broaden our consideration of how climate affects mammals, both directly and indirectly.

The defining feature of endotherms is their use of metabolic heat to regulate their body core at a constant set-point temperature that is independent of air temperature [2]. This means that under cool environmental conditions, where the body loses heat to the environment, maintenance of a constant body temperature requires that heat production, and thus metabolism, increases with declining air temperature along a slope that equals thermal conductance [2]. Under hot conditions, where the body gains heat from the environment, endotherms must begin actively dissipating heat through panting, perspiration, saliva spreading, and in the case of bats, wing fanning [2]. Because these responses increase heat production (i.e. contribute to the problem that it solves), the slope of the increase in metabolism at warm temperatures is always much steeper than the slope of the increase below the lower critical temperature. As a result of the inefficiencies of metabolic solutions to heat dissipation, endotherms are particularly vulnerable to heat stress and, whenever possible, occupy microenvironments that reduce heat stress [5]. Between the lower critical temperature (where thermoregulation begins to require heat production) and the upper critical temperature (where thermoregulation begins to require heat dissipation) is a region referred to as the thermal neutral zone where metabolic rate does not vary with air temperature because small, energetically insignificant adjustments in conductance (e.g. vasodilation, piloerection and postural changes) are sufficient to maintain a constant body temperature [2]. The metabolic rate (or energy expenditure) of an endotherm is minimised when they are at rest, in their thermoneutral zone, and not digesting food; metabolism measured under these circumstances is referred to as basal metabolic rate [2].

Thus, although endotherm thermoregulation permits maintenance of a constant body temperature that is independent of air temperature, air temperature has a direct and major effect on an endotherm's metabolic rate, which in turn determines their resource requirements. Endotherms exposed to environmental temperatures above or below their thermal neutral zone require more resources to stay alive than endotherms exposed to temperatures within their thermoneutral zone. Furthermore, the capacity for endotherms to produce and dissipate heat is not without limits. Exposure to extreme temperatures that cause thermoregulatory capacity to be exceeded, lead first to hypo- or hyperthermia, then, if exposure continues, to death.

Thus, air temperature has direct effects on the metabolism and resource requirements of endotherms and exposure to extreme air temperatures can have direct effects on survival.

Climate exerts additional, indirect effects on mammals through its effects on their resources, competitors and predators. Temperature has a fundamental effect on all biological processes [6], and thus climate variation should profoundly affect all organisms sharing the same environment. In fact, these indirect effects, acting via resources, competitors and predators, are likely to be so strong and pervasive that they will frequently supersede or mediate most direct effects of climate. The mass die off of flying foxes provides a potent example of a direct effect of climate operating independently of any indirect effects [1]. It was the heat that killed them, directly and outright. But even here, it is likely that more complex climate and biotic factors played a role. For example, although 1453 flying foxes from the Dallis Park colony succumbed to hyperthermia on 12 January 2002, more than 25 000 flying foxes present in the same colony and presumably exposed to the same thermal conditions survived [1]. Many factors are likely to dictate thermoregulatory capacity under such extreme situations, such as body size, age, social rank, reproductive condition, body composition and aerobic capacity [2], most of which will, in turn, be influenced by an individual's lifetime experience with resources, competitors and predators. More commonly, climate impacts on mammals are much more complex and multi-faceted, encompassing effects on thermoregulation and other forms of homeostasis, the distribution and abundance of resources, competitors and predators, as well as the interactions among all these biotic elements. Examples of climate impacts acting primarily on biotic interactions include the influence of snow cover on resource access [7] susceptibility to predation [8] and drought on the spatial overlap of competitors and predators [9]. Most climate impacts on mammals are perhaps best envisioned as climate setting the stage for a complex play involving competitors, resources and predators. Changing the stage changes the play, but often in indirect and nuanced ways.

2. DEMONSTRATED IMPACTS OF CLIMATE CHANGE ON MAMMALS

Demonstrated impacts of climate change on mammals is a broad topic, in evolutionary time, geographic scope and taxonomic diversity, which cannot be covered comprehensively in a short chapter. There is much research interest in this area, and many excellent reviews have appeared recently. For more detailed treatments, I refer the reader to the following reviews of climate change impacts on arctic marine mammals [10], Australian fauna [11], tropical ecosystems [12], fossil mammals [13], mammal morphology [14], mammal population dynamics [15] and mammal demographics [16].

2.1. Temporal Approaches

2.1.1. Geological Climate Variation, Mammal Assemblages and Body Size

Most paleo studies demonstrate that climate change has pronounced effects on the diversity and composition of mammal communities [17,18]. Evidence for long-period climate impacts on mammal diversity is provided by a 22 Ma (million years) record of fossil rodents from southern Spain that is characterised by pulses of species turnover at 1–2 Ma intervals coinciding with Milankovitch oscillations [19]. Gingerich [20] reviews faunal responses to the Paleocene–Eocene thermal maximum, a 20 000 a (year) interval of rapid, greenhouse warming marking the transition between the Paleocene and Eocene 55 Ma ago. The faunal responses to the resulting 5–7 °C warming of deep oceans and 4–5 °C warming of mid-latitude terrestrial regions were extreme, including the simultaneous disappearance of up to 50% of benthic foraminifera (associated with rising water temperature and associated reduction in dissolved oxygen) and the simultaneous appearance of several modern orders of mammals, including Artiodactyla, Perissodactyla and Primates. The small size of many of the mammals during this thermal maximum suggests a pattern of dwarfism, which Gingerich [20] attributes to the negative impacts of elevated CO_2 on plant growth and herbivore nutrition. Research using ancient DNA to reconstruct trends in the abundance of Beringian steppe bison (*Bison* spp.) during the Pleistocene has established that the onset of pre-extinction population declines coincided with periods of climate warming and forest expansion [21]. Related genetics research suggests a similar pattern of climate-driven population declines in Pleistocene bears, horses and mammoths [22], but there is also compelling evidence that humans contributed to several megafaunal extinctions in other regions of the world [23].

The strong associations between climate and faunal composition observed across paleo timescales suggest the maintenance of some degree of thermal niche conservatism during prolonged periods of climate change spanning evolutionary time. Direct evidence of this thermal niche conservatism is provided by Martinez-Meyer et al.'s [24] demonstration that 23 extant North American mammals with fossil records spanning back to the Last Glacial Maximum have spatially tracked consistent climate profiles for the last 18 000 a. Associations between paleoclimate reconstructions and the contemporary diversity and composition of fossil mammal assemblages are sufficiently strong that recent literature has advocated using fossil mammal assemblages to reconstruct paleo-climates (e.g. [25,26]).

2.1.2. Recent Climate Variation and Mammal Miscellany

Studies in this category examine mammal responses to annual-, decadal-, and century-scale climate variation. Responses examined are a miscellany of traits, including but not limited to morphology, phenology, life history traits, population abundance and species distribution. The consequences of anthropogenic climate change are best illustrated by long-term data extending back prior to the industrial revolution or, at least, the mid-twentieth century acceleration of greenhouse gas emissions and warming trends (e.g. [27–29]), but such long-term studies of mammals are largely lacking. Thus, most studies in this category examine mammal responses to climate variation occurring across much shorter timescales, ranging from a few years to several decades. Multi-decadal studies frequently encompass climatic variability induced by large scale climate drivers such as North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), Arctic Oscillation or El Nino Southern Oscillation (ENSO). Interestingly, wildlife population responses to these climatic phenomena are often of greater magnitude and greater consistency than effects observed in meteorological records, suggesting that animal populations can be sensitive integrators and indicators of subtle and complex climatic events [30,31].

Several long-term studies have documented changes in body size that correlate with changing climate conditions. In many but not all cases, body size has been observed to decrease as climate warms [14], consistent with the biogeographical association between small body size and warm climates referred to as Bergmann's Rule [32,33]. For example, the body mass of woodrats (*Neotoma albigula*) in New Mexico decreased by 15% during a decade when summer temperatures warmed by 3 °C ([34]; Fig. 1a). Intriguingly, this short-term association between small body size and warm temperatures matches a much longer, evolutionary-timescale relationship between climate and woodrat body size as inferred from the size of faecal pellets preserved in paleomiddens ([35]; Fig. 1b.). However, other studies have documented the opposite trend, with body size increasing as climate warms, perhaps because of increased resources and enhanced growth rates [36,37]. These (relatively) short-term, observational studies of morphological and climate variation frequently have limited potential to discriminate phenotypic plasticity from evolutionary responses to climate, and to isolate responses to climate from other factors that may also vary over-time (e.g. habitat succession, density-dependence, competition, predation).

Changes in phenology, such as the annual timing of reproduction or dormancy, are among the best documented impacts of climate change on animals and plants in general [38,39]. Examples among mammals are few, but striking. The date when yellow-bellied marmots (*Marmota flaviventris*) emerge from hibernation in Colorado, USA advanced by 38 d (days) over 25 a with 60% of the observed variation in emergence date linked to variation in spring air temperature ([40]; Fig. 2). Although springs became warmer and earlier over the study period, increases in winter snow depth during the same time meant that snow cover persisted longer as marmots emerged earlier, creating a potential mismatch between energy demands and supply in early spring (see Ref. [41]). Réale et al. [42] showed that the parturition date of red squirrels (*Tamiasciurus hudsonicus*) in Yukon, Canada advanced by 18 d over 10 years. Applying

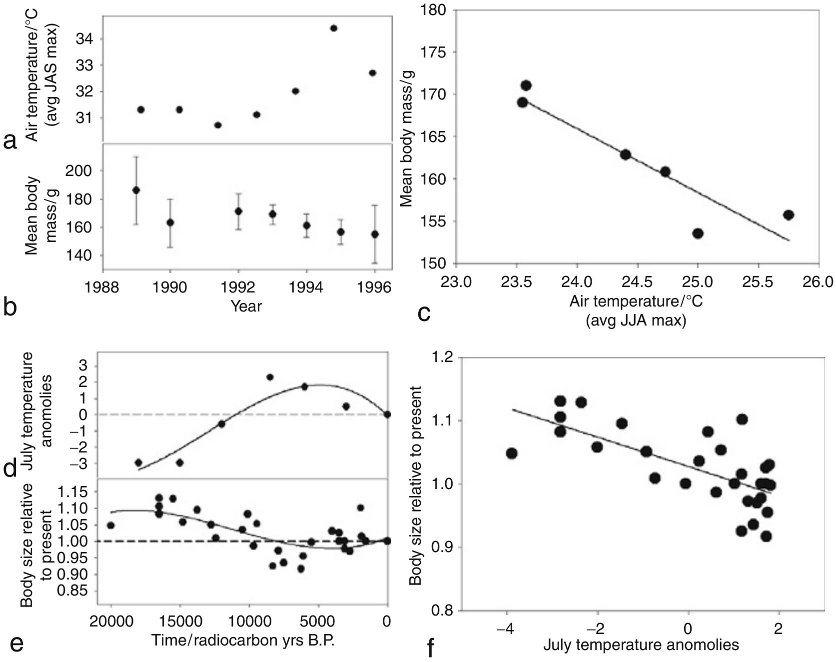

FIGURE 1 The negative influence of warm air temperatures, *t*, on the body size of *Neotoma* woodrats over decadal (a–c) and geological timescales (d–f) in southwestern USA. During a decade of warming air temperatures (a; with air temperature expressed as the average of monthly maximums in July, August and September; redrawn from Fig. 2b, pp. 143 of Smith et al. 1998) the average body mass of woodrats declined by more than 15% (b; redrawn from Fig. 5, pp. 147 of Smith et al. 1998), generating a negative correlation between summer air temperature and body mass (c; redrawn from Fig. 6b, pp. 147 of Smith et al. 1998). During 20 000 a of fluctuating summer air temperatures (d; redrawn from Fig. 3b, pp. 2013 of Smith et al. 1995), the body size of woodrats (as inferred from the size of fecal pellets in paleomiddens) decreased during warm intervals (e; redrawn from Fig. 3a, pp. 2013 of Smith et al. 1995), again generating a negative correlation between summer air temperature and body mass (f; redrawn from Fig. 3, pp. 2013 of Smith et al. 1995).

quantitative genetic approaches to this study population's known pedigree revealed that two-thirds of this advancement involved phenotypic plasticity whereas one-third involved genetically-based microevolution [42]. This study represents one of the few demonstrations that mammals have the evolutionary capacity to adapt to rapid, contemporary climate change, but the taxonomic generality and long-term sustainability of this evolutionary potential is unclear [43].

Many studies have documented climatic influences on mammal population dynamics, usually operating in combination with a complex array of biotic influences such as density dependence, competition, predation, and in the case of large mammals, human harvest [15]. Rigorous demonstration of population-level impacts of climate change impacts requires long-term monitoring of population abundance as well as potential climatic and biotic

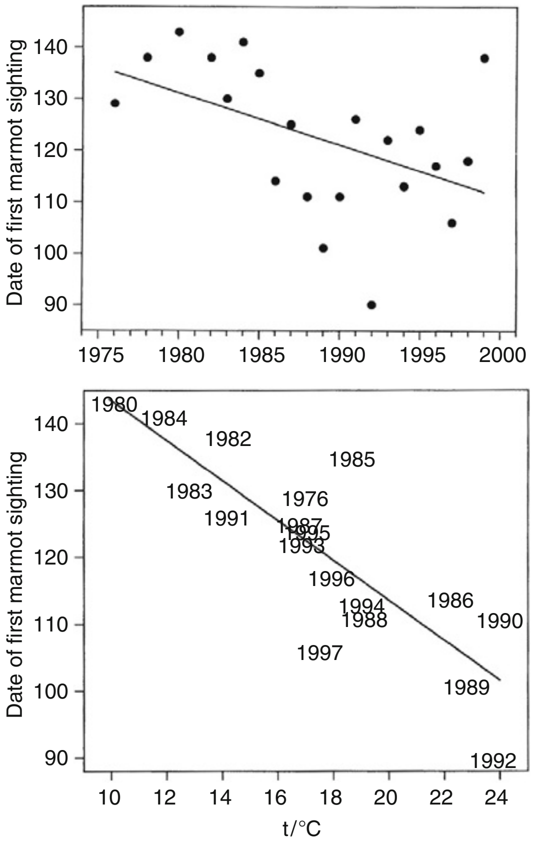

FIGURE 2 Advancement in the date of first appearance of yellow-bellied marmots (*Marmota flaviventris*) following hibernation over a twenty-five year warming period in Colorado, USA. During this period, the strongest predictor of the timing of emergence was the average of daily minimum air temperatures, t', during April. (Reprint from Fig. 4 and 5, pp. 1631–1632 of Inouye et al. 2000; Copyright (2000), National Academy of Sciences, U.S.A.).

drivers of abundance. The relatively long generation time and transience of mammal population dynamics creates additional challenges in establishing cause and effect relationships between climate and mammal population parameters. However, several case studies provide compelling evidence of localised impacts of climate change on mammals. Polar bears (*Ursus maritimus*) have played a prominent role in public and scientific discourse on the impacts of climate change on wildlife because they rely on sea ice that has been observed and projected to decline as a result of climate change [44]. The strongest evidence for a negative effect of climate change on polar bears comes from a 20 a time series on a population occurring at the southern edge of the species' distributional range [45]. This study establishes that reduced survival of juvenile, sub-adult and senescent-adult polar bears in years of early sea ice breakup caused bear populations to decline by 24% over a period when spring ice breakup advanced by 3 weeks. Although comparable data are lacking for most other polar bear populations and current trends in sea ice coverage and polar bear populations vary widely across the Arctic, there is general consensus that if the climate continues to warm and sea ice continues to decline at the rates recently observed and projected, it is only a matter of time before most polar bear populations are detrimentally affected by climate change [46]. Evidence of climate change impacts on other mammal species arise from demonstrated influence of large-scale climate oscillations on population demography and dynamics in a diverse and growing list of species, including muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus*; [47]), soay sheep (*Ovis aries*) and red deer (*Cervus elaphus*; [48]), wolves (*Canis lupus*) and moose (*Alces alces*; [8]), ibex (*Capra ibex*; [49]) grey-sided voles (*Myodes rufocanus*; [50]), lynx (*Lynx canadensis*; [51]), pikas (*Ochotona collaris*; [52]), South American leaf-eared mice (*Phyllotis darwini*; [53]) and Savanna ungulates [54]. A wide array of statistical time series and population modelling are used in these studies to relate population demographic time series to current and prior climatic conditions [15]. These long-term data and quantitative approaches provide detailed examination of climatic influences on particular populations, and frequently identify the demographic basis of population-level effects. However, these studies provide a weaker basis to predict future climate impacts requires extrapolation because expected warming far exceeds the amplitude of monitored climate variation. The general absence of simultaneous monitoring of prey and predator populations, as well as any associated landscape change, clouds interpretation of the mechanisms by which climate influences populations.

Climate change has also been blamed for the recent disappearance or dampening of many of the renowned mammal population cycles that have been so important in the development of animal ecology over the last century [55]. Large-scale spatial variation in cycle amplitude and period, including the well described northern hemisphere pattern of cyclic dynamics at high latitudes transitioning to stable dynamics at more southerly latitudes, has been attributed to geographical variation in the degree of seasonality [55]. The recent collapse of many of these population cycles from disparate high latitude localities coincides with a period of accelerated climate warming and reduced seasonality ([56;] Fig. 3.) Thus, the climate conditions responsible for the collapse of population cycles at low latitudes may be spreading north as the climate warms.

2.1.3. The Temporal Scale of Mammal Responses to Climate Change

The nature, extent, and significance of observed temporal responses to climate change depend on the timescale of the comparison [17]. Very short timescale comparisons offer insight into how mammals respond to and are affected by weather, as well as seasonal and annual climate differences. Frequently the

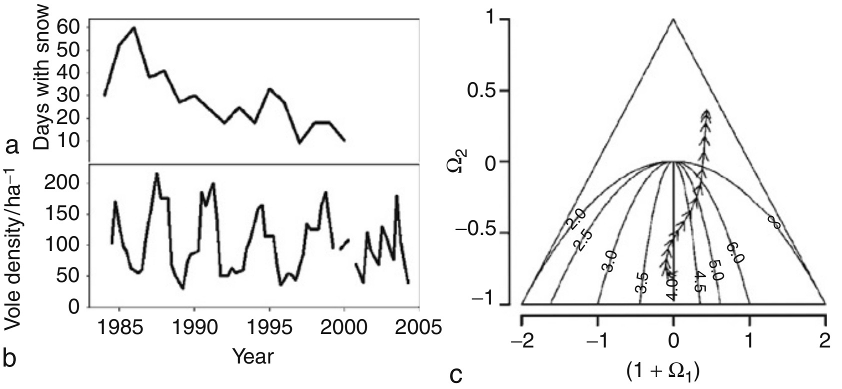

FIGURE 3 Twenty-year time series of declining snow cover duration (a) and disappearance of cyclic dynamics in a population of field voles (*Microtus agrestis*) from Kielder Forest, England (b). Changes over time in the form of direct $(1 + \Omega_1)$ and delayed density dependence (Ω_2) affecting vole population dynamics are shown in (c). Cyclic dynamics are predicted for combinations of the parameters that fall below the semi-circle, with the period of the cycle increasing from left to right. Stable dynamics are predicted for combinations lying above the semi-circle. The line with upward pointing arrows tracks the population from early in the time series, when dynamics are cyclic with a period of ~4 a, to later in the time series when the cycle period extends to >6 a then disappears. Population fluctuations apparent at the end of the time series in (b) are within-year seasonal variations, which appear to increase in magnitude following the transition to non-cyclic dynamics. Redrawn (a, b) and reprinted (c) from Ref. [56]. (Adapted from Am. Nat/University of Chicago Press).

responses detected by these comparisons involve behaviour and other forms of phenotypic plasticity [43]. But these studies reveal less about the likely impacts of longer-term directional climate change, particular when climate change will, by definition, involve conditions outside the contemporary range of variation. On the other hand, very long scales of comparison can obscure the significance of events occurring at shorter timescales. For example, Gingerich [20] argues that the failure of previous studies to detect a relationship between climate and diversity over the entire 65 Ma Cenozoic resulted from averaging of climate and diversity over 1 myr intervals when most significant climate fluctuations and evolutionary responses to them occurred on 1000 a time scales. The consequences of anthropogenic climate change might be similarly obscured if extinction rates during the twentieth and twenty-first century were averaged with extinction rates prevailing, for example, 10 000 a prior to and following these two centuries. Thus, there is a continuum of temporal scales available to study the effects of climate change on mammals, and studies situated at either end of this continuum contribute less to predicting the responses of mammals to current anthropogenic climate change. Short-term ecological studies are confined to studying climate fluctuations of much shorter period and lower amplitude than the phenomenon of interest. Long-term, paleontological studies are, for reasons of temporal resolution and the nature of past environmental change, confined to studying episodes of directional climate change that are much more gradual than the phenomenon of interest. Additional insight into the responses of mammals to current anthropogenic climate change will be provided by ecological time series of longer duration that incorporate more climate variation and paleontological time series of finer temporal resolution focused on brief periods of rapid climate change.

2.2. Spatial Approaches

Latitudinal gradients in climate and biodiversity provide valuable null models for predicting the future impacts of a warmer climate [57]. According to this latitudinal shift or climate envelope approach, to the extent that species range limits are imposed by climatic tolerance, climate warming will cause the plants and animals in a given region to more closely resemble the plants and animals currently found at lower latitudes [58]. The validity of these predictions depends critically on: (1) emission scenarios that correctly predict future greenhouse gas emissions based on current economic and demographic trends, (2) general circulation models (GCM) that correctly predict regional climates based on these emission scenarios and (3) species climate models that correctly predict species' responses to climate change based on a mechanistic understanding of how climate influences their distribution and abundance [59]. Although more research is needed on all fronts, there is enough consensus in emission scenarios and GCM's to render species climate models as far and away the weakest link in biotic climate change predictions. In fact, in many regions of the world, little is known about how much plants and animals actually vary across regional climate gradients (i.e. across hundreds to thousands of kilometres), much less how and why any observed variation across these scales is correlated to climate. In the following sections, I briefly review empirical relationships between spatial climate variation and mammal diversity as well as evidence for the mechanisms by which climate determines species range limits and spatial variation in abundance.

2.2.1. Spatial Climate Variation and Mammal Diversity

Latitudinal gradients in species diversity are among the strongest and most general patterns in ecology [60,61]. With the exception of extremely arid areas, warm regions of the globe host a much greater diversity of mammals (and other organisms) than cold regions. Within North America, measures of local mammal diversity (in this case, the number of terrestrial mammal species occurring in 58 275 km^2 quadrats) varies from 178 species in tropical regions of southern Nicaragua and northern Costa Rica to 20 species in arctic regions of north-central Canada ([62;] Fig. 4). Almost 90% of this variation can be accounted for by five environmental variables, representing seasonal extremes of temperature, annual energy and moisture and elevation [62]. Examples of latitudinal diversity gradients from regions outside of North

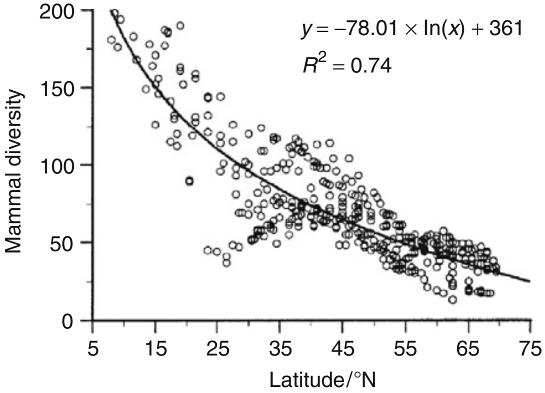

FIGURE 4 Latitudinal variation in the diversity of North American mammals. The diversity measure is the number of terrestrial mammal species present in 58 275 km^2 quadrats systematically distributed across the continent. Five environmental variables, representing seasonal extremes of temperature, annual energy and moisture, and elevation, predicted 88% of continental variation in this variable. From Ref. [62] (Adapted from Journal of Biogeography, Blackwell Science Ltd).

America are dominated by non-mammalian taxa, but the taxonomic and geographic consistency of latitudinal diversity gradients [61], suggests that the distribution of most of the world's mammal species will contribute to a pattern of more species in warmer regions. Climate variables usually outperform landcover variables as predictors of species diversity or distribution [63,64], particularly when scales of comparison are large [65], but it is unclear whether this is because climate is the more important mechanistic driver of diversity or because it is difficult to classify land cover appropriately for multiple species across a variety of landscapes. Regardless, the remarkable generality and strength of climate-diversity correlations across biogeographical space, together with their correspondence with patterns over geological time, has caused them to occupy a central role in approaches to examining and predicting the impacts of climate change on mammals and other animals.

2.2.2. *Spatial Climate Variation and the Distribution and Abundance of Mammals*

Climatic constraints are thought to impose biogeographic range boundaries on individual wildlife species. The breeding distribution of gray seals (*Halichoerus grypus*) may be limited by the effects of cold air temperatures on the fasting endurance of recently weaned pups [66]. The winter distribution of little brown bats (*Myotis lucifugus*) is limited to latitudes where hibernacula are warm enough to ensure that the energetic costs of hibernation do not exceed maximum autumn fat reserves [67]. The northward range limit of nine-banded armadillos (*Dasypus novemcinctus*) and virginia opossums (*Didelphis virginiana*) seems to be constrained by long bouts of cold winter weather [68,69]. Relatively few studies have examined variation in abundance of mammal species across latitudinal gradients, but the abundance of red foxes in northern Eurasia decreases with declining winter temperature and increased seasonality [70], and the abundance of beaver in north-eastern North America decreases with declining potential evapotranspiration and spring temperatures [71]. There is a need for more studies of spatial variation in abundance across species ranges, because how abundance varies as range limits are approached will dictate whether climate change impacts will be greater at the edge or in the core of species' ranges [71].

The range limits of many mammals have shifted poleward as the climate has warmed in the past century, but it has frequently been difficult to isolate the impact of climate change on these range shifts from other forms of environmental change and historical factors. A classic example is the southern range contraction of arctic foxes concomitant with the northern range expansion of red foxes, which is hypothesised to be mediated by climate driven changes in primary productivity and prey base [72]. This hypothesis is partially supported by recent work comparing ecosystem characteristics of sites abandoned and still occupied by arctic foxes, but there are many site-specific contingencies and alternative explanations [73]. In North America, many of the mammals characterised by prominent poleward range expansions are species that are also affiliated with human-modified habitats, including red foxes, Virginia opossums [73], raccoons [74], white-tailed deer [75] and coyotes [76], making it difficult to identify whether anthropogenic climate change or landscape modification are most responsible for the expansions. However, climate change is clearly contributing to the poleward range shifts of many mammals, as well as other animals and plants, and this will be an important impact on mammals over the next century [38,39,77]. Species of particular concern are those whose poleward range limit is imposed by physical barriers, such as coastlines or mountain ranges, leaving them nowhere to go as their non-poleward range limit moves towards the barrier.

2.2.3. Spatial Climate Variation and Mammal Morphology, Metabolism and Life Histories

All else being equal, mammals occupying warm environments are smaller, metabolically slower and have smaller litter sizes than mammals occupying cold environments. The tendency for animals to be larger in cooler environments, referred to as Bergmann's rule, is well supported by comparisons of populations or species of mammals distributed along latitudinal and climatic gradients [32,33,78]. There are many notable exceptions, but in general, more than two-thirds of mammals conform to this trend. The original explanation for Bergmann's rule, related to heat conservation in cold environments, is no longer widely accepted because the trend is supported by both large and small endotherms, as well as many ectotherms [32,78]. However, mammals occupying cold environments are characterised by increased heat production and reduced heat loss relative to their warm-climate counterparts [79,80]. Classic work in this area was conducted by Scholander comparing the metabolism and pelage insulation of arctic and tropical mammals [81,82], which has since been expanded using phylogenetically-informed analyses on a wider diversity of species [79,80]. An example of the influence of climate variability rather than average climate conditions is provided by Lovegrove's [83] analysis of mammal metabolism showing species inhabiting regions influenced by large scale climate fluctuations have lower resting metabolism than species located outside of these regions. The field metabolic rate of mammals tends to increase with declining air temperature, but also tends to be less variable in cold environments than in warm environments [85]. According to the metabolic niche hypothesis, this pattern suggests that cold environmental temperatures limit diversity by restricting the range of energetically feasible lifestyles [84,86]. Latitudinal and climatic variation in the life history traits of mammals has not been explored as thoroughly as in other vertebrates, but there are theoretical expectations and some empirical evidence for litter size being larger in cold, seasonal environments than warm environments [87–89].

2.2.4. The Spatial Scale of Mammal Responses to Climate Change

The nature, extent, and significance of correlations between mammal ecology and spatial variation in climate depend on the spatial scale of the comparison. At continental and hemispheric scales, climate frequently emerges as powerful predictor of ecological variation in phenomena ranging from diversity, abundance, body size and metabolism. Of course, the term climate captures a wide array of temperature, precipitation and related variables. Which climate variables have the highest predictive power varies according to the region and taxa under consideration, with, unsurprisingly, precipitation and temperature variables performing better in arid and cold regions, respectively. Furthermore, because most climate variables are highly correlated, it is difficult to proceed from correlative to causal models focused only on the best or the top few climate predictors without considering the potential influence of the many covarying climate variables. At a local and regional scale, habitat and other biotic and physical variables emerge as much more powerful predictors of ecological variation than climate. However, it would be erroneous to conclude that climate has not been a major driver of the form and extent of ecological variation observed at a local and regional scale (lack of observed correlation does not, necessarily, imply lack of causation). On the other hand, it would also be erroneous to conclude that climate is the major driver of the form and extent of ecological variation observed at continental and hemispheric scales (correlation does not imply causation). In both cases and at all spatial scales, it should be clear that ecological variation is driven by a complex interaction between climate, physical features, biotic interactions and historical contingencies. But our capacity to quantify and detect those influences varies with spatial scale. Returning to an earlier analogy of climate setting the stage for a complex play involving competitors, resources and predators, the perceived importance of the stage is diminished by watching different plays on the same stage and enhanced by watching the same play on different stages. Instead of sitting in the same theatre and waiting for the stage to change to see if it changes the play, why not visit some different stages where the same play is being performed. Instead of hopping from theatre to theatre and only counting the number of actors on the stage, why not sit down and watch some plays to understand what is happening on the stage. Opportunities to combine watching many different plays on the same stage and the same play on many different stages are rare, but are necessary to assess the relative importance of the stage (climate) and the play (biotic interactions).

3. LINKING TIME AND SPACE IN MAMMAL CLIMATE RESPONSES

Better documentation of the impacts of climate change on mammals awaits integration of temporal and spatial approaches, with careful attention paid to the scales of comparison. I end with a brief review of two approaches, one historical and one contemporary, with considerable promise in this regard.

Phylogeography, as its name implies, integrates spatial and temporal approaches by examining historical influences on geographical distribution. Much of phylogeography is based on genetic approaches, but palaeontology spread across geographical gradients provides similar insights [18]. For example, comparison of the geographical distribution of woolly mammoths (*Mammuthus primigenius*; based on dated fossil discoveries) and reconstructed climates at different time intervals during the Pleistocene provide insight into the role of climate change and human hunting in this species' range contraction and eventual extinction [90]. Genetic estimates of the timing of population and species divergence linked with paleoclimate and habitat reconstructions can provide critical insight into the influence of past environmental change on contemporary diversity. The divergence of Antarctic minke whales (*Balaenoptera bonaerensis*) and common minke whales (*Balaenoptera acutorostrata*) is estimated to have occurred during an extended warming period in the Pliocene, when elevated ocean temperatures would have disrupted the spatial homogeneity of oceanic upwelling and promoted allopatric speciation [91].

A contemporary analog to phylogeography is provided by spatially extensive, long-term monitoring of species diversity, population abundance and individual traits. Unfortunately, the best of these programs, such as breeding and winter bird surveys conducted for many decades over continental spatial scales [92], involve non-mammalian taxa. Nevertheless, these programs can serve as a model for the type and spatial extent of long-term data needed to document the effects of anthropogenic climate change on mammals. They also provide a warning of the difficulty in disentangling the effects of climate change from other forms of environmental change, even with fantastic data [93]. As anthropogenic climate change accelerates, we need to continue and expand the few global examples of spatially-extensive, long-term monitoring of mammal diversity (e.g. [94,95]) and for the many mammal taxa and regions currently excluded, we need to initiate rigorous monitoring programs before it is too late.

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REFERENCES

1. J.A. Welbergen, S.M., Klose, N., Markus, P. Eby, Proc. R. Soc. B-Biol. Sci. 275 (2008) 419–425.
2. B.K. McNab, The Physiological Ecology of Vertebrates: A View from Energetics, Cornell University Press, Ithaca, New York, 2002, pp. 576.
3. B. Heinrich, Am. Nat. 111 (1977) 623–640.
4. F. Geiser, Ann. Rev. Physiol. 66 (2004) 239–274.
5. C.R. Vispo, G.S. Bakken, Ecology 74 (1993) 377–389.
6. J.F. Gillooly, J.H., Brown, G.B., West, V.M., Savage, E.L. Charnov, Science 293 (2001) 2248–2251.
7. K.S. Chan, A., Mysterud, N.A., Oritsland, T., Severinsen, N.C., Stenseth, Oecologia 145 (2005) 556–563.
8. E. Post, R.O., Peterson, N.C., Stenseth, B.E., McLaren, Nature 401 (1999) 905–907.
9. S.A.R. Mduma, A.R.E. Sinclair, R. Hilborn, J.Anim. Ecol. 68 (1999) 1101–1122.
10. H.P. Huntington, S.E. Moore, Ecol. Appl. 18 (2008) S1–S2.
11. L. Hughes, Austral Ecology 28 (2003) 423–443.
12. S.J. Wright, Trends Ecol. Evol. 20 (2005) 553–560.
13. A.D. Barnosky, B. P. Kraatz, Bioscience 57 (6) (2007) 523–532.
14. V. Millien, S.K., Lyons, L., Olson, F.A., Smith, A.B., Wilson, Yom-Tov, Y. Ecol. Lett. 9 (2006) 853–869.
15. M.C. Forchhammer, N.M. Schmidt, T.T., Hoye, T.B., Berg, D.K., Hendrichsen, E. Post, Population Dynamical Responses to Climate Change, in Advances in Ecological Research, vol. 40, Elsevier Academic Press Inc., San Diego, 2008, pp. 391–419.
16. V. Grosbois, O., Gimenez, J.M., Gaillard, R., Pradel, C., Barbraud, J., Clobert, A.P., Moller, H. Weimerskirch, Biol. Rev. 83 (2008) 357–399.
17. A.D. Barnosky, E.A. Hadly, C.J. Bell, J. Mammal. 84 (2003) 354–368.

18. G.M. MacDonald, K.D., Bennett, S.T., Jackson, L., Parducci, F.A., Smith, J.P., Smol, K.J., Willis, Prog. Phys. Geogr. 32 (2008) 139–172.
19. J.A. van Dam, H.A., Aziz, M.A.A., Sierra, F.J., Hilgen, L.J., Ostende, Lwvdh, Lourens, P., Mein, A.J., van der Meulen, P., Pelaez-Campomanes, Nature 443 (2006) 687–691.
20. P.D. Gingerich, Trends Ecol. Evol. 21 (2006) 246–253.
21. B. Shapiro, A.J., Drummond, A., Rambaut, M.C., Wilson, P.E., Matheus, A.V., Sher, O.G., Pybus, M.T.P., Gilbert, I., Barnes, J., Binladen, E., Willerslev, A.J., Hansen, G.F., Baryshnikov, J.A., Burns, S., Davydov, J.C., Driver, D.G., Froese, C.R., Harington, G., Keddie, P., Kosintsev, M.L., Kunz, L.D., Martin, R.O., Stephenson, J., Storer, R., Tedford, S., Zimov, A., Cooper, Science 306 (2004) 1561–1565.
22. Regis Debruyne, Genevieve Chu, Christine E. King, Kirsti Bos, Melanie Kuch, Carsten Schwarz, Paul Szpak, Darren R. Gröcke, Paul Matheus, Grant Zazula, Dale Guthrie, Duane Froese, Bernard Buigues, Christian de Marliave, Clare Flemming, Debi Poinar, Daniel Fisher, John Southon, Alexei N. Tikhonov, Ross D.E. MacPhee, Hendrik N. Poinar., Curr. Biol. 18 (2008) 1320–1326.
23. D.A. Burney, T.F. Flannery, Trends Ecol. Evol. 20 (2005) 395–401.
24. E. Martinez-Meyer, A. Townsend Peterson, W.W. Hargrove, Global Ecol. Biogeogr. 13 (2004) 305–314.
25. S. Legendre, S., Montuire, O., Maridet, G., Escarguel, Earth Planet. Sci. Lett. 235 (2005) 408–420.
26. M.H. Fernandez, P. Pelaez-Campomanes, Global Ecol. Biogeogr. 14 (2005) 39–56.
27. W. Buermann, B.R., Lintner, C.D., Koven, A., Angert, J.E., Pinzon, C.J., Tucker, I.Y., Fung, Proc. Natl. Acad. Sci. USA 104 (2007) 4249–4254.
28. J. Esper, U., Buntgen, D.C., Frank, D., Nievergelt, A., Liebhold, Proc. R. Soc. B – Biol. Sci. 2007 (2007) 671–679.
29. M.S.V. Douglas, J.P. Smol, W. Blake, Science 266 (1994) 416–419.
30. N.C. Stenseth, A. Mysterud, C. Ottersen, J.W. Hurrell, K.S. Chan, M. Lima, Science 297 (2002) 1292–1296.
31. T.B. Hallett, T., Coulson, J.G., Pilkington, T.H., Clutton-Brock, J.M., Pemberton, B.T., Grenfell, Nature 430 (2004) 71–75.
32. K.G. Ashton, M.C. Tracy, A. de Queiroz, Am. Nat. 156 (2000) 390–415.
33. T.M. Blackburn, B.A. Hawkins, Ecography 27 (2004) 715–724.
34. F.A. Smith, H. Browning, U.L. Shepherd, Ecography 21 (1998) 140–148.
35. F.A. Smith, J.L. Betancourt, J.H. Brown, Science 270 (1995) 2012–2014.
36. Y. Yom-Tov, S. Yom-Tov, Biol. J. Linn. Soc. 82 (2004) 263–267.
37. Y. Yom-Tov, J. Yom-Tov, J. Anim. Ecol. 74 (2005) 803–808.
38. G.R. Walther, E., Post, P., Convey, A., Menzel, C., Parmesan, T.J.C., Beebee, J.M., Fromentin, O., Hoegh-Guldberg, F., Bairlein, Nature 416 (2002) 389–395.
39. C. Parmesan, Ann. Rev. Ecol. Evol. Syst. 37 (2006) 637–669.
40. D.W. Inouye, B. Barr, K.B. Armitage, B.D. Inouye, Proc. Natl. Acad. Sci. USA 97 (2000) 1630–1633.
41. N. Pettorelli Pettorelli, N., Pelletier, F., von Hardenberg, A., Festa-Bianchet, M., Cote, S. D., Ecology 88 (2007) 381–390.
42. D. Reale, A.G., McAdam, S. Boutin, D., Berteaux, Proc. R. Soc. Lond. Ser. B – Biol. Sci. 270 (200) 591–596.
43. D. Berteaux, M.M., Humphries, C.J., Krebs, M., Lima, A.G., McAdam, N., Pettorelli, D., Reale, T., Saitoh, E., Tkadlec, R.B., Weladji, N.C., Stenseth, Int. Comp. Biol. 44 (2004) 140–151.

44. A.E. Derocher, N.J. Lunn, I. Stirling, Int. Comp. Biol. 44 (2004) 163–176.
45. E.V. Regehr, N.J., Lunn, S.C., Amstrup, L., Stirling, J. Wildlife Manage. 71 (2007) 2673–2683.
46. COSEWIC, COSEWIC Assessment and Update Status Report on the Polar Bear Ursus Maritimus in Canada, Committee on the Status of Endangered Wildlife in Canada: Ottawa, 2008, p. 75.
47. M.C. Forchhammer, E., Post, N.C., Stenseth, D.M., Boertmann, Popul. Ecol. 44 (2002) 113–120.
48. J. Hone, T.H. Clutton-Brock, J. Anim. Ecol. 76 (2007) 361–367.
49. V. Grotan, B.E., Saether, F., Filli, S., Engen, Global Change Biol. 14 (2008) 218–228.
50. T. Saitoh, B., Cazelles, J.O., Vik, H., Viljugrein, N.C., Stenseth, Clim. Res. 32 (2006) 109–118.
51. N.C. Stenseth, D., Ehrich, E.K., Rueness, O.C., Lingjaerde, K.S., Chan, S., Boutin, M., O'Donoghue, D.A., Robinson, H., Viljugrein, K.S., Jakobsen, Proc. Natl. Acad. Sci. USA 101 (2004) 6056–6061.
52. S.F. Morrison, D.S. Hik, J.Anim. Ecol. 76 (2007) 899–907.
53. M. Lima, N.C. Stenseth, F.M. Jaksic, Proc. R. Soc. Lond. Ser. B – Biol. Sci. 269 (2002) 2579–2586.
54. J.O. Ogutu, N. Owen-Smith, Ecol. Lett. 6 (2003) 412–419.
55. R.A. Ims, J.A. Henden, S.T. Killengreen, Trends Ecol. Evol. 23 (2008) 79–86.
56. S.M. Bierman, J.P., Fairbairn, S.J., Petty, D.A., Elston, D., Tidhar, X., Lambin, Am. Nat. 167 (2006) 583–590.
57. D.J. Currie, Ecosystems 4 (2001) 216–225.
58. M.B. Araujo, R.J., Whittaker, R.J., Ladle, M., Erhard, Global Ecol. Biogeogr. 14 (2005) 529–538.
59. R.K. Heikkinen, M., Luoto, M.B., Araujo, R., Virkkala, W., Thuiller, M.T., Sykes, Prog. Phys. Geogr. 30 (2006) 751–777.
60. D.J. Currie, Am. Nat. 137 (1991) 27–49.
61. K.J. Gaston, Nature 405 (2000) 220–227.
62. C. Badgley, D.L. Fox, J. Biogeogr. 27 (2000) 1437–1467.
63. W. Thuiller, M.B. Araujo, S. Lavorel, J. Biogeogr. 31 (2004) 353–361.
64. B. Huntley, R.E., Green, Y.C., Collingham, J.K., Hill, S.G., Willis, P. J., Bartlein, W., Cramer, W.J.M., Hagemeijer, C.J., Thomas, Ecol. Lett. 7 (2004) 417–426.
65. W. Thuiller, L., Brotons, M.B., Araujo, S., Lavorel, Ecography 27 (2004) 165–172.
66. S. Hansen, D.M. Lavigne, Physiol. Zool. 70 (1997) 436–443.
67. M.M. Humphries, D.W. Thomas, J.R. Speakman, Nature 418 (2002) 313–316.
68. L.L. Kanda, Ecography 28 (2005) 731–744.
69. J.F. Taulman, L.W. Robbins, J. Biogeogr. 23 (1996) 635–648.
70. K.A. Barton, A. Zalewski, Global Ecol. Biogeogr. 16 (2007) 281–289.
71. S.I. Jarema, J., Samson, B.J., McGill, M.M., Humphries, Global Change Biol. 15 (2009) 508–522.
72. P. Hersteinsson, D.W. Macdonald, Oikos 64 (1992) 505–515.
73. S.T. Killengreen, R.A., Ims, N.G., Yoccoz, K.A., Brathen, J.A., Henden, T., Schott, Biol. Conserv. 135 (2007) 459–472.
74. S. Lariviere, Wildlife Soc. Bull. 32 (2004) 955–963.
75. A.M. Veitch, Can. Field-Nat. 115 (2001) 172–175.
76. H.D. Cluff, Can. Field-Nat. 120 (2006) 67–70.

77. T.L. Root, J.T., Price, K.R., Hall, S.H., Schneider, C., Rosenzweig, J.A., Pounds, Nature 421 (2003) 57–60.
78. S. Meiri, T. Dayan, J. Biogeogr. 30 (2003) 331–351.
79. B.G. Lovegrove, J. Comp. Physiol. B – Biochem. Syst. Environ. Physiol. 173 (2003) 87–112.
80. B.G. Lovegrove, J. Comp. Physiol. B – Biochem. Syst. Environ. Physiol. 175 (2005) 231–247.
81. P.F. Scholander, V., Walters, R., Hock, L., Irving, Biol. Bull. 99 (1950) 225–236.
82. P.F. Scholander, R., Hock, V., Walters, L., Irving, Biol. Bull. 99 (1950) 259–271.
83. B.G. Lovegrove, Am. Nat. 156 (2000) 201–219.
84. K.J. Anderson, W. Jetz, Ecol. Lett. 8 (2005) 310–318.
85. M.M. Humphries, S. Boutin, D.W. Thomas, J.D. Ryan, C. Selman, A.G. McAdam, D. Berteaux, J.R. Speakman, Ecol. Lett. 8 (2005) 1326–1333.
86. A. Clarke, K.J. Gaston, Proc. R. Soc. B 273 (2006) 2257–2266.
87. R.D. Lord Jr., Am. Midland Nat. 64 (1960) 488–499.
88. M.S. Boyce, Am. Nat. 114 (1979) 569–583.
89. J.R. Whorley, G.J. Kenagy, J. Mammal. 88 (2007) 1404–1411.
90. D. Nogues-Bravo, J., Rodiguez, J., Hortal, P., Batra, M.B., Araujo, Plos Biol. 6 (2008) 685–692.
91. L.A. Pastene, M., Goto, N., Kanda, A.N., Zerbini, D., Kerem, K., Watanabe, Y., Bessho, M., Hasegawa, R., Nielsen, F., Larsen, P.J., Palsboll, Mol. Ecol. 16 (2007) 1481–1495.
92. A.H. Hurlbert, E.P. White, Ecol. Lett. 8 (2005) 319–327.
93. C. Rahbek, G.R. Graves, Proc. Natl. Acad. Sci. USA 98 (2001) 4534–4539.
94. J. Pellikka, et al., Annales Fennici Zoologici 42 (2005) 123–134.
95. S. Harris, D.W. Yalden, Mammal Rev. 34 (2004) 157–167.