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Research

How big should a mammal be? A macroecological look at mammalian body size over space and time

Felisa A. Smith^{1,*} and S. Kathleen Lyons²

¹*Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*

²*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA*

Macroecology was developed as a big picture statistical approach to the study of ecology and evolution. By focusing on broadly occurring patterns and processes operating at large spatial and temporal scales rather than on localized and/or fine-scaled details, macroecology aims to uncover general mechanisms operating at organism, population, and ecosystem levels of organization. Macroecological studies typically involve the statistical analysis of fundamental species-level traits, such as body size, area of geographical range, and average density and/or abundance. Here, we briefly review the history of macroecology and use the body size of mammals as a case study to highlight current developments in the field, including the increasing linkage with biogeography and other disciplines. Characterizing the factors underlying the spatial and temporal patterns of body size variation in mammals is a daunting task and moreover, one not readily amenable to traditional statistical analyses. Our results clearly illustrate remarkable regularities in the distribution and variation of mammalian body size across both geographical space and evolutionary time that are related to ecology and trophic dynamics and that would not be apparent without a broader perspective.

Keywords: macroecology; temporal scales; spatial scales; mammalian body mass; biogeography; the comparative method

‘For every animal there is a most convenient size’.

J. B. S. Haldane 1926 ‘On being the right size’ *Possible Worlds and Other Essays*.

1. INTRODUCTION

It is almost a tautology that mammals tend to be of a certain size—all school kids know that elephants are big and mice are small. And, most are. However, there are numerous instances where the reverse has been true. Dwarfed elephants and/or mammoths were common during the Late Cenozoic on Mediterranean islands in Europe and on the Channel Islands off the coast of California [1–5]. The tendency for rodents to become gigantic on islands is so pervasive over evolutionary history that this pattern was seminal to the formulation of the ‘island rule’ [6]. Further, the characteristic body sizes we associate with mammals today may not reflect physiological or phylogenetic constraints, but rather reflect ecological processes operating at longer or larger temporal and spatial scales. For example, modern hyraxes, which are

small, rather inconspicuous African herbivores of 2–5 kg, played a vastly different role in the Early Cenozoic. With a body mass of over 1 tonne, hyraxes were the primary terrestrial herbivore in the early African landscape for many millions of years; considerably larger than the extant Proboscideans of the time [7]. The extreme miniaturization in size of Hyracoidea was coincident with the Oligocene immigration into the African subcontinent of other herbivorous groups, namely, the Perissodactyla and Artiodactyla. Indeed, the small size we associate with hyrax today was certainly not the norm for much of their evolutionary history. So, although mammals tend to have a characteristic size, what that size is depends critically on both the environment and on their evolutionary history. Consequently, understanding the underlying mechanisms driving body size variation across time and space is a daunting task, requiring consideration of both ecological and evolutionary context.

Macroecology is a big picture, statistical approach to the study of ecology and evolution that emphasizes description and explanation of biological patterns and processes [8]. The underlying assumption is that similar statistical patterns result from similar causal mechanisms. Hence, macroecology combines both inductive and deductive reasoning. Macroecology assumes that our understanding of ecological systems

* Author for correspondence (fasmith@unm.edu).

One contribution of 10 to a Theme Issue ‘Biogeography and ecology: two views of one world’.

'improves with a broader vision' [9]. Thus, it explicitly focuses outward on broadly occurring patterns and processes at large spatial and temporal scales to uncover general mechanisms operating at organism, population and ecosystem levels of organization. In the past decade, the macroecological approach has led to some important new insights into biology. For example, the metabolic theory of ecology (MTE; [10]) models the relationships between body size, body temperature and metabolic rate across all organisms. MTE attempts to relate how basic metabolism (the rate at which organisms take up energy) and the influence of body size and temperature on metabolism, provide the fundamental constraints that govern all ecological processes. While still controversial, MTE has been extremely influential [10–16]. Similarly, macroecological approaches are often employed in conservation biology. Correlates of extinction risk have been characterized using a variety of species-level traits, such as body size and geographical range size [17–19]. Such studies indicate there are unique pathways to extinction that depend critically on life-history traits and morphology [18].

Macroecology is somewhat different from other comparative methods. It differs from typical ecological studies by using a broader spatial and/or temporal scale, and from phylogenetic comparative methods (or PCMs) in the data and focus employed. PCMs usually focus on species as the primary unit of interest and operate within an explicit phylogenetic framework [20]. Commonly, PCMs might be used to test for correlated evolutionary changes in two or more traits, or to determine whether commonalities in a trait are owing to phylogeny. Despite these differences in emphasis and scale, however, both PCMs and macroecology use a comparative method to address broad questions about the long-term history of life. The analysis of mammalian body size variation across time and space lends itself naturally to a macroecological approach. Earlier work demonstrates, for example, that body size in mammals is highly conserved within the taxonomic hierarchy [21].

Here, we briefly review the history of macroecology and use the body size of mammals as a case study to highlight current developments in the field. As is typical in many macroecological studies, we begin by using an inductive approach. We quantify empirical patterns of body size across geographical space and evolutionary time and then attempt to understand them using a more deductive process. We focus on body size not only because of its obvious ecological and evolutionary importance, but also because it offers a clear example of the utility of a macroecological approach to address fundamental scientific questions.

2. A BRIEF HISTORY OF MACROECOLOGY

Attempts to describe and explain biological patterns and processes at varying spatial and temporal scales are implicit in early publications of the eighteenth and nineteenth centuries. Indeed, one could argue that many of the great natural historians and early biogeographers viewed the world through a macroecological lens [22–26]. As data accumulated during

the early part of the twentieth century, a number of quantitative biologists began examining patterns of abundance, distribution and relatedness of species [27–31]. The macroecological approach languished during the middle and latter part of the century, however, as biology and ecology became increasingly focused on manipulative and experimental approaches [32]. However, there will always remain biological phenomena that are not amenable to study through the use of experimental manipulation. Frustration with traditional ecological approaches led Brown & Maurer [33,34] to outline a kind of 'statistical mechanics' programme for ecological systems that they dubbed 'macroecology' [35].

Since the original 1989 publication of Brown & Maurer [34], there has been a marked resurgence in using a macroecological perspective to address biological questions. The number of macroecological publications has risen exponentially; far faster than publications in general biology, biogeography or across other scientific disciplines ([32]; figure 1) and similar to the explosive growth in PCMs. This probably reflects an appreciation of the many complex biological and environmental problems that can only be addressed with new tool kits and broader perspectives. And, it also undoubtedly reflects the availability of new data on phylogenies, species distributions, abundances, remote sensing and a plethora of easily accessed abiotic information. Global change scientists, in particular, often employ a macroecological perspective. For example, recent studies examine the relationship between past and present environmental perturbations and variation in morphological, physiological, behavioural, ecological, evolutionary, phenological and phylogenetic traits [36–41].

Being a relatively young field, there is currently a lively debate concerning the validity of macroecological approaches and methods [32]. In particular, criticisms arise over data quality, the lack of appropriate experimental controls and statistics [42–44]. The scope of questions addressed means it is generally beyond the ability of a small group of scientists to collect sufficient primary data. Thus, macroecological datasets are often compiled from the literature or other sources. Consequently, considerable care must be taken with their use and interpretation. Similarly, the use of 'natural experiments' means a lack of experimental controls, which can compromise the ability to evaluate pattern and process. Interestingly, these are problems that the palaeontology community has long faced. Perhaps, this is why macroecology has been embraced within the palaeoecological community [45–53], while it remains somewhat more controversial within modern ecology [42–44].

3. WHY BODY SIZE MATTERS

Body mass is one of the most important axes of biological diversity and hence has been a key variable for many macroecological studies. Over evolutionary time, mammals have ranged over eight orders of magnitude in size, from the pygmy shrew and bumble-bee bat at approximately 2 g, mammoths, *Indricotherium* and *Deinotherium* at 10–17 tonne, to the largest animals to ever exist on the Earth, blue whales at 180–200 tonne [54]. Characterizing the minimum

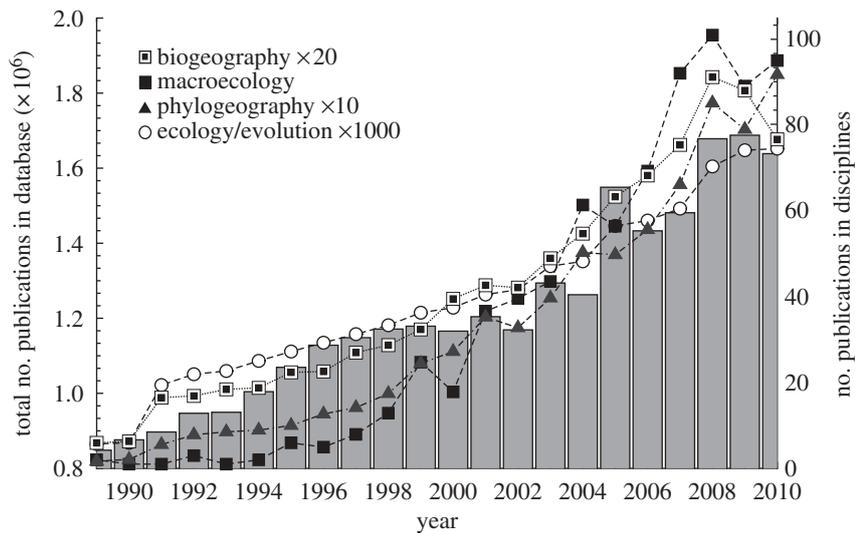


Figure 1. The number of papers published over the past 20 years as indexed by web of science (WOS) using certain key words. The grey bars represent all papers published in the expanded Science Citation Index (from 1899 to the present), the Social Sciences Citation Index (from 1898 to the present) and the Arts and Humanities Citation Index (from 1975 to the present); open circles, papers in the disciplines of ecology and/or evolutionary biology; open squares with black centres, biogeography; filled squares, macroecology; and filled triangles, phylogeography. Papers were identified by searching for ('ecolog*' and/or 'evol*'), 'biogeograph*', 'macroecolog*', and ('biogeograph*' and ('phylogen*' or 'molecul*')) as keywords in the title and/or abstract. Note scaling of disciplines as indicated in figure legend. All fields are rising significantly faster than that of WOS as a whole (t -test between each slope and WOS yields $p < 0.0001$), with both macroecology and PCMs exhibiting the fastest rates of increase (slope (\pm standard error) of log-log plots 1.888 (0.232) and 1.595 (0.059), respectively, versus 0.234 (0.024) for WOS). While publications in ecology and evolutionary biology and biogeography are each growing rapidly (slopes of 0.866 (0.048) and 0.964 (0.05), respectively), they do not vary significantly from each other, but do differ from macroecology and the comparative phylogenetic method ($p < 0.001$).

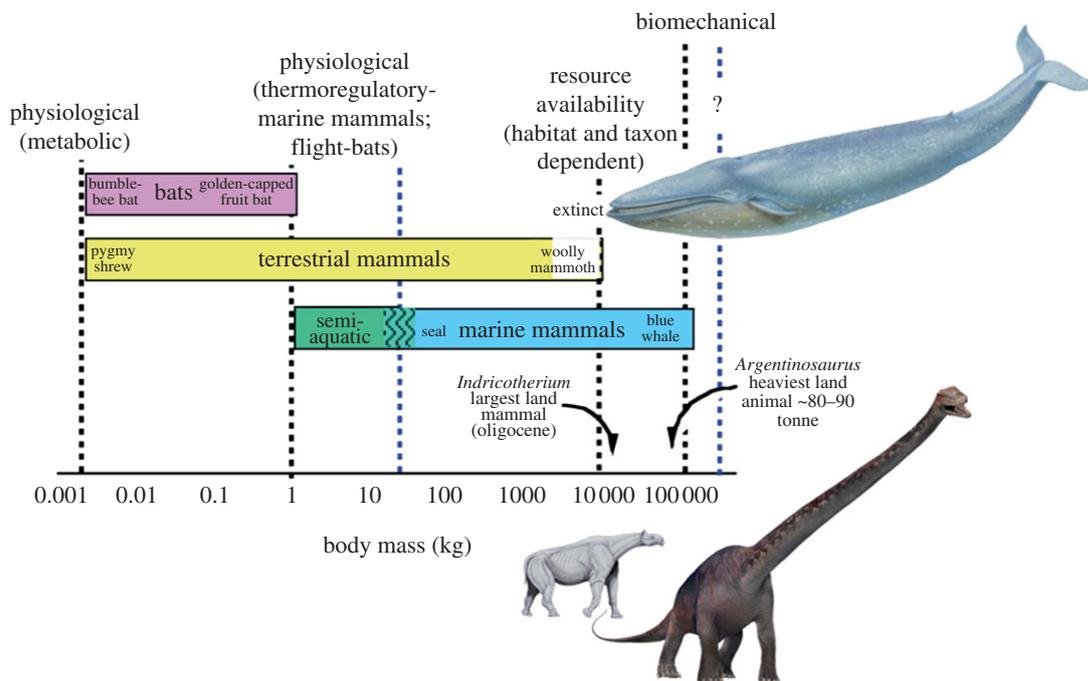


Figure 2. The limit of body size in mammals as it relates to their life history. The range of mass is shown for volant (pink), aquatic (green-blue) and terrestrial (yellow) mammals; postulated constraints on size are indicated. Redrawn after Smith & Lyons [63].

and maximum limits of size is an area of active interest [55–62]; life history may play an important role (figure 2). For example, although ultimately physiology may be responsible for constraining the minimum size for both terrestrial and aquatic mammals, this may result from different proximate

causes. The lower limit of size for marine mammals is likely set by the size of offspring (which scales with adult mass) because of the increased energetic cost of thermoregulation in aquatic environments [58]. Thus, the minimum size of marine mammals is approximately 10 kg, several orders of magnitude

greater than the 2 g minimum size found in terrestrial mammals. In contrast, energetic limitations may directly limit the minimum viable size in terrestrial species (figure 2). Mammals of very small body size face extremely high mass-specific maintenance costs; such intense energetic demands require both high quality and abundant food resources [57,64]. The lack of body size similarity among congeners for these animals has been attributed to the lack of 'physiological space' to develop novel adaptations when faced with new environments [21]. While it is likely that interactions between physiology and environment set a rigid lower boundary to mammalian body size (figure 2), it appears that factors operating on the upper limit are more diffuse. Factors such as bone density and structure, heart size and circulation, overheating and life-history parameters have all been postulated to constrain the upper limit of marine mammal size [59–61,65,66]; there remains considerable disagreement on what sets the upper limit for terrestrial mammals. Factors investigated include biomechanical constraints, resource availability [54,59–61,67] and even atmospheric oxygen content [68].

The study of body size goes beyond characterizing the limits to size and exploring the variation across space and time. A variety of fundamental geometrical and physical principles dictate how the structure and function of individual organisms scale with body mass [10,57,69,70]. These in turn, powerfully constrain nearly all aspects of an organism's ecology from life history, resource use and population density to patterns of species diversity within ecosystems. The essential activities of survival, reproduction and growth are governed by the rate that animals acquire, process and transform energy, which is largely determined by both body mass and temperature. However, we still lack an understanding of just how the complex interactions between intrinsic structure and function, environment, historical and phylogenetic evolution interact to result in particular body sizes. Certainly, the body size of an animal must reflect underlying allometric, ecological and evolutionary constraints (figure 3). Not surprisingly, examining how these factors influence or are influenced by the body mass of organisms has been an area of scientific interest for many hundreds of years [57,59,60,72–74].

But how does one go about trying to explore patterns spanning vast spatial and/or temporal scales? While this is a challenge for any scientist addressing broad-scale issues, it is particularly acute when addressing continental and global patterns of body size or other factors where no replication is possible. The macroecological programme was developed to more rigorously examine patterns at large scales in an effort to determine process. Because such an approach is both inductive and deductive, it is particularly relevant to studies examining large-scale patterns, such as those we describe here.

4. THE MACROECOLOGY OF MAMMALIAN BODY SIZE

Examining macroecological patterns of body mass across spatial and temporal scales has only become

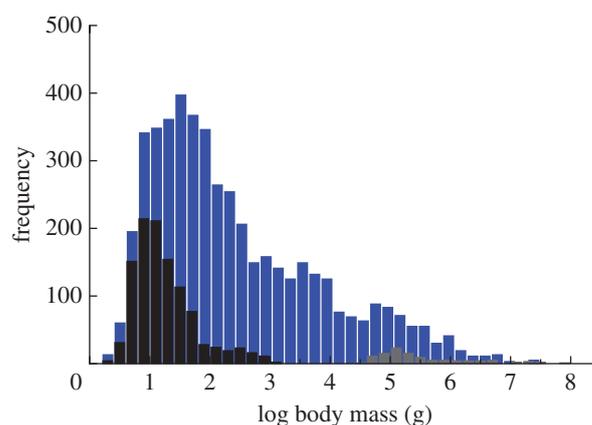


Figure 3. The global distribution of mammalian body mass at the Late Quaternary. Patterns are shown separately for volant (dark grey bars, left-hand side of graph), aquatic (grey bars, right-hand side of graph) and terrestrial (blue) mammals. Note \log_{10} scale. Data are prior to the anthropogenic extinction of megafauna in the Americas at the terminal Pleistocene, which significantly depressed the right mode and led earlier authors to characterize the overall distribution as unimodal [71].

possible by the recent compilations of large datasets. In particular, Mass of Mammals (MOM) [75] and Maximum Mass of Mammals over Time and Hierarchy (MAMMOTH) [7] provide crucial information for spatial and evolutionary analyses, respectively. MOM was constructed as an outgrowth of an NCEAS working group (<http://www.nceas.ucsb.edu/projects/2182>). It includes a complete taxonomy [76], a mass estimate for each species on each continent or island averaged across gender and geographical location ($n = 5747$), distribution information, IUCN status and trophic characterizations. These original data have been considerably updated since the publication of Smith *et al.* [75] and are freely available at the senior author's website (<http://biology.unm.edu/fasmith/>).

MAMMOTH v. 1.0 was an outgrowth of an NSF research coordination network (http://biology.unm.edu/impps_rcn/) and will be publicly accessible by the end of 2011. It contains an estimate of the maximum body mass estimate for each mammalian order, on each continent, at the sub-epoch level over evolutionary history. Data are fairly complete for some mammalian orders and the major continents, but are lacking for poorly described archaic taxa and especially for South America. Body mass estimates are mostly derived from using allometric regressions constructed on extant taxa and applied to measurements of fossil long bones or molars. Maximum body mass was chosen for statistical, taphonomic and logistical reasons: it not only tends to be reported in the literature, but is robustly related to the overall body size distribution and thus to the mean and median. At present, MAMMOTH v. 1.0 contains information on 32 extant and archaic orders, with about approximately 320 estimates.

(a) Patterns of body size across the major continents

The idea that there might be regular spatial patterns in the structuring of mammal assemblages was first

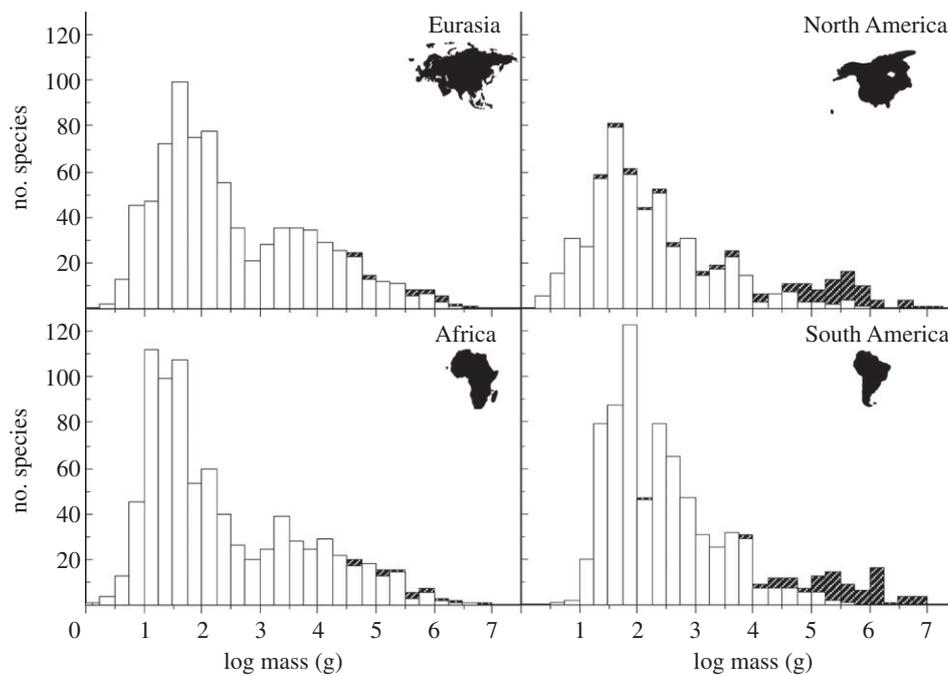


Figure 4. The distribution of mammalian body size across the major continents. Modern species are indicated by the lack of fill; species extirpated during the Late Pleistocene are indicated by hatching. Note \log_{10} scale. The overall pattern is bimodal for the major continents when extinct fauna are included; Australia lacks the mammalian diversity found on other continents. See text for details of statistical analyses. Redrawn after Alexander [59].

proposed by Brown & Nicoletto [71]. They compiled a species-level database of mammalian body mass for North America and demonstrated that the overall distribution was unimodal and right skewed, and further, changed as spatial scale was reduced. This, they argued, had both ecological and evolutionary implications and probably held for other continents. The mode of distribution (approx. 100 g) was interpreted as an optimal size for mammals; divergence from the optima resulted from a balance of opposing physiological and ecological selective constraints. Subsequent theoretical work [77] developed an energetic framework to examine optimal body mass. However, the universality of the continental pattern and their characterization of the shape of the distribution were not universally accepted. Indeed, studies employing fossils to examine body mass distributions in North America suggested that the characteristic distribution was actually bimodal [78]. Thus, evolutionary forces acting on body mass might have different effects depending on the starting position in morphospace. Subsequent research [21,79] confirmed the statistical similarities of patterns across continents proposed by Brown & Nicoletto [71], but found no support for the unimodal shape (figure 3). Rather, the unimodal pattern was owing to the anthropogenic extinction of megafauna in the Americas at the terminal Pleistocene, which selectively targeted large-bodied mammals ([79]; figure 4). By removing the second mode of large-bodied mammals, it fundamentally changed the shape of the distribution on the North and South American continents.

Analyses with an updated dataset of Late Quaternary mammals (MOM v. 4), which includes the previously unexamined Eurasian continent, clearly illustrate that prior to the Late Pleistocene extinction, the mass

distributions of species on the major continents were bimodal and right skewed ([80]; figure 4). Moreover, the overall distributions were qualitatively similar across continents. However, there were some interesting trends in the location and height of the modes. For example, insectivores, which are generally small, were particularly speciose in Africa where they evolved. This had the effect of shifting the small-bodied mode to the left (figure 5 and table 1). Similarly, the paucity of the insectivore guild in South America led to fewer small-bodied species. Consequently, the distribution for this continent is left truncated [21]. Moreover, while the second mode peaked at approximately 3.5 log units and gradually declined towards the right-hand tail in both Africa and Eurasia, the second mode was larger and dropped precipitously at 4 log units in North and South America (figure 4). Such differences may be a function of the differing evolutionary histories of the continents or they may suggest that there were more, as yet, unrecognized extinctions of medium- to large-bodied mammals in North and South America.

The consistency in the shape of mass distributions across space (figure 4) begs the question of how long these patterns have existed. Are they relatively recent in the evolutionary history of mammals, or have continental body mass distributions been bimodal and right skewed for millions of years? In his analysis of Cope's Rule for North American mammals across the Cenozoic, Alroy [78] documented a decline in the richness of medium-sized animals beginning about 40 million years ago (Mya). This 'hole' in morphospace persisted until the present, leading to a paucity of mammals weighing 1–10 kg (3–4 \log_{10} units). Moreover, when 1 Myr time slices from Alroy's [78] data are analysed following Brown & Nicoletto [71] and Smith *et al.*

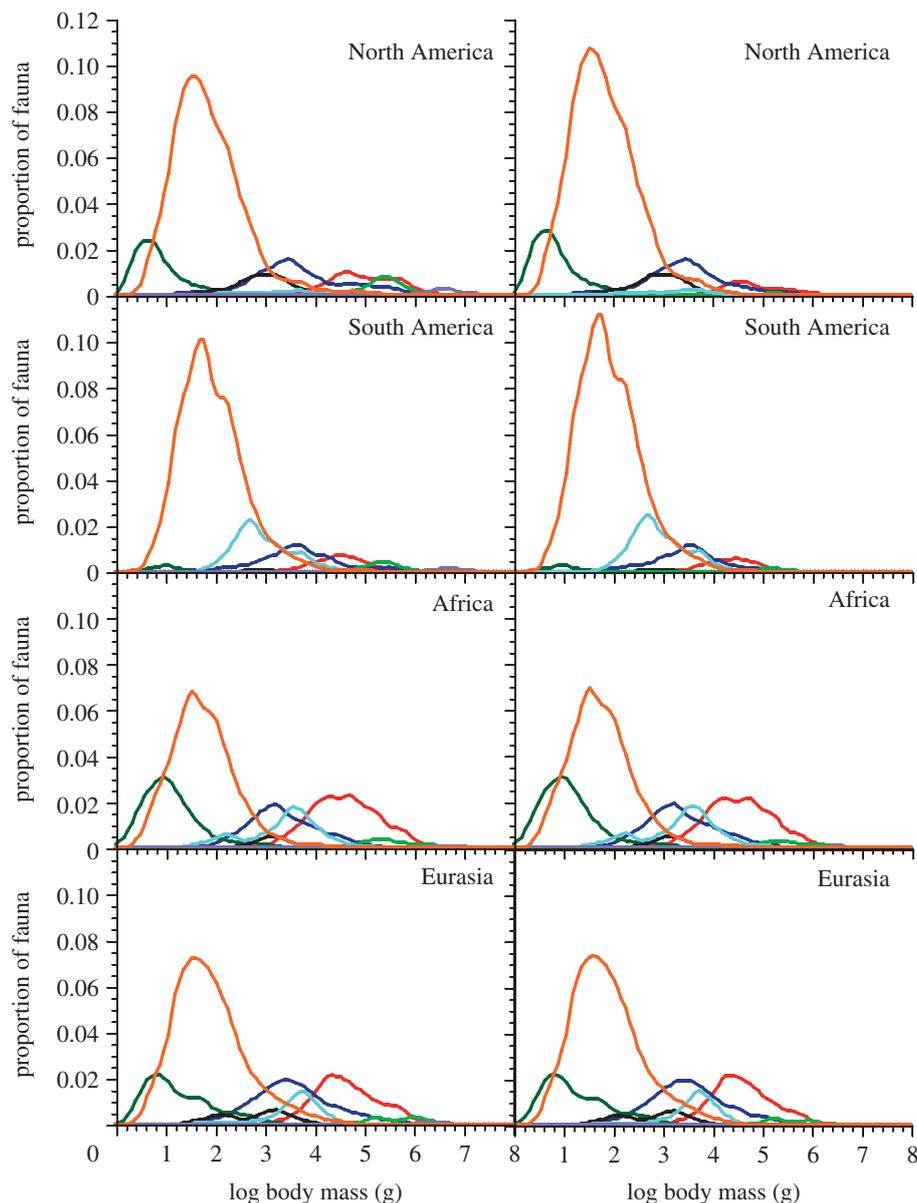


Figure 5. The proportion of each continental fauna composed of the major mammalian orders as a function of body mass. Note that there is very little change in the shape of the ordinal distribution before and after the extinction event. Orange, Rodentia; red, Artiodactyla; dark green, Insectivora; light blue, primates; purple, Proboscidea; black, Lagomorpha; dark blue, Carnivora; light green, Perissodactyla. Panels on the left represent pre-mega-faunal extinction composition; right-hand panels are post-extinction. Note \log_{10} scale.

[21], patterns similar to the ones presented in figure 4 emerge [52,80]. Beginning approximately 40 Mya, the body mass distribution for North American mammals became bimodal, and remained so until the end-Pleistocene mega-faunal extinction. Clearly, evolutionary forces act on mammalian body mass in such a way as to produce this characteristic distribution despite different geological histories and the few species shared across continents. Such results strongly suggest that body masses of 1–10 kg are suboptimal for many taxa. Indeed, many mammals of this size tend to be carnivores, which may reflect ecological or physiological selection against other life-history strategies. Perhaps, animals of 1–10 kg tend to be too big to burrow or hide effectively and are not fast enough to flee. Interestingly, this is the approximate lower limit of ruminant herbivores, where allometric, anatomical and

physiological factors interact to constrain the minimum size to approximately 5–10 kg [81].

(b) How similar are patterns of body size within orders across continents?

Body mass is evolutionarily conservative as evidenced by the similarity of congeneric species within a genus, similarity of congeneric taxa at higher levels of the taxonomic hierarchy and similarity of the overall pattern of body size across geographical space and evolutionary time [21]. This is true for placental and marsupial mammals and across all major continents. We wanted to explore how this pattern of heritability ('broad sense' >0.95) influences body mass distributions at the ordinal level, and moreover, evaluate whether patterns were affected by the extinction of large-bodied mammals at the terminal

Table 1. Descriptive statistics for mammalian orders on the continents. Species that went extinct in historical times are excluded from the analysis of after extinction of the megafauna. NA, North America; SA, South America; AF, Africa; EA, Eurasia.

order	mean	median	minimum	maximum	skew	kurtosis	<i>n</i>
<i>(a) prior to the extinction of megafauna</i>							
Artiodactyla							
NA	5.12	4.94	4.00	6.04	0.037	-1.03	37
SA	4.72	4.70	3.98	6.00	0.97	0.91	29
AF	4.73	4.74	3.40	6.15	0.16	-0.51	104
EA	4.80	4.69	3.40	5.95	0.29	-0.34	86
Carnivora							
NA	3.79	3.60	1.67	5.86	0.31	-0.19	63
SA	3.85	3.79	2.17	5.78	0.41	0.29	56
AF	3.49	3.40	2.27	5.21	0.51	-0.034	72
EA	3.69	3.54	1.89	5.63	0.38	0.14	93
Insectivora							
NA	0.92	0.85	0.38	2.15	1.42	1.58	56
SA	1.05	1.05	1.00	1.10	-0.08	-0.33	6
AF	1.20	1.16	0.24	3.10	1.15	1.84	99
EA	1.37	1.15	0.38	2.98	0.88	-0.12	81
Lagomorpha							
NA	3.08	3.18	2.11	3.68	-0.68	-0.17	26
SA	3.02	3.02	2.98	3.07	< -0.001	-2.00	2
AF	3.32	3.33	3.24	3.44	0.17	-1.38	10
EA	2.92	3.20	1.92	3.60	-0.42	-1.53	23
Perissodactyla							
NA	5.56	5.52	5.40	5.81	0.60	-0.74	15
SA	5.47	5.49	5.17	5.71	-0.48	-0.18	11
AF	5.66	5.54	5.18	6.47	0.81	-0.66	11
EA	5.86	6.10	5.36	6.46	-0.08	-1.80	11
Primates							
NA	3.38	3.58	2.45	3.86	-0.73	-0.97	6
SA	3.10	2.99	2.10	4.31	0.58	-0.55	80
AF	3.50	3.63	1.79	5.12	-0.65	-0.01	58
EA	3.74	3.85	1.89	4.33	-2.34	5.79	37
Proboscidea							
NA	6.80	6.74	6.70	7.00	0.45	-1.44	5
SA	6.79	6.79	6.70	6.88	0.10	-1.02	4
AF	6.70	6.70	6.60	6.81	< -0.001	-2.00	2
EA	6.59	6.59	6.44	6.74	< -0.001	-2.00	2
Rodentia							
NA	1.96	1.85	0.84	5.18	1.38	3.28	342
SA	2.06	1.89	0.67	5.18	1.22	2.60	452
AF	1.86	1.78	0.70	4.30	0.86	1.89	255
EA	2.02	1.93	0.59	4.60	1.00	1.20	319
<i>(b) after extinction of the megafauna</i>							
Artiodactyla							
NA	4.93	4.80	4.33	5.76	0.55	-0.88	14
SA	4.53	4.53	3.98	5.15	0.12	-0.99	20
AF	4.68	4.72	3.40	6.15	0.14	-0.45	95
EA	4.73	4.66	3.40	5.95	0.31	-0.03	82
Carnivora							
NA	3.57	3.54	1.67	5.55	0.12	0.48	50
SA	3.59	3.60	2.17	5.15	0.05	0.36	43
AF	3.49	3.40	2.27	5.21	0.51	-0.034	72
EA	3.66	3.54	1.89	5.63	0.33	0.22	91
Insectivora							
NA	0.92	0.85	0.38	2.15	1.42	1.58	56
SA	1.05	1.05	1.00	1.10	-0.08	-0.33	6
AF	1.20	1.16	0.24	3.10	1.15	1.84	99
EA	1.37	1.15	0.38	2.98	0.88	-0.12	81
Lagomorphs							
NA	3.09	3.18	2.11	3.68	-0.71	-0.10	23
SA	3.02	3.02	2.98	3.07	< -0.001	-2.00	2

(Continued.)

Table 1. (Continued.)

order	mean	median	minimum	maximum	skew	kurtosis	<i>n</i>
AF	3.32	3.33	3.24	3.44	0.17	-1.38	10
EA	2.92	3.20	1.92	3.60	-0.42	-1.53	23
Perissodactyla							
NA	5.48	5.48	5.48	5.48	—	—	1
SA	5.32	5.32	5.17	5.48	0.06	-1.50	3
AF	5.66	5.53	5.22	6.47	1.06	-0.101	8
EA	5.70	5.46	5.36	6.24	0.52	-1.66	8
Primates							
NA	3.38	3.58	2.45	3.86	-0.73	-0.97	6
SA	3.08	2.98	2.10	4.13	0.52	-0.70	79
AF	3.50	3.63	1.79	5.12	-0.65	-0.01	58
EA	3.74	3.85	1.89	4.33	-2.34	5.79	37
Proboscidea							
NA	—	—	—	—	—	—	0
SA	—	—	—	—	—	—	0
AF	6.60	6.60	6.60	6.60	—	—	1
EA	6.44	6.44	6.44	6.44	—	—	1
Rodentia							
NA	1.94	1.84	0.84	4.34	0.92	1.09	330
SA	2.05	1.89	0.67	4.80	1.03	1.54	450
AF	1.86	1.78	0.70	4.30	0.86	1.89	255
EA	2.01	1.92	0.59	4.30	0.92	0.89	318

Pleistocene. Consequently, we calculated the moments of the body mass distributions for eight major orders (Artiodactyla, Carnivora, Insectivora, Lagomorpha, Perissodactyla, Primates, Proboscidea and Rodentia) on each of the four continents (North America, South America, Africa and Eurasia) before and after the extinction event. We analysed the shapes of the overall ordinal distributions using Kolmogorov–Smirnov tests; a Bonferroni correction was applied to account for multiple comparisons. We also compared the shape of each ordinal distribution within a continent to determine the effect of the extinction event on the ‘body mass niche’ of the different mammalian orders.

Similar to Smith *et al.* [21], we find remarkable consistencies in the moments of the body mass distributions of mammalian orders on different continents (tables 1 and 2). Note the current analysis uses a greatly expanded dataset that includes Eurasian mammals and also contains much more comprehensive data for orders previously under-represented. Interestingly, the statistical moments are not appreciably influenced by the extinction of the megafauna (table 3). Moreover, we find relatively few significant differences when comparing ordinal distributions across the various continents (table 2). Of the eight mammalian orders analysed and 54 possible pairwise comparisons, only 11 are significantly different prior to the extinction of the megafauna. In general, these represent divergences in the mammalian fauna between the Old and the New World. Our results are clearly related to the geological history of the continents and presence or absence of past land bridges [82]. As expected, patterns on continents separated for longer geological times are more disparate. For example, the majority of ordinal differences are between North America and Africa or Eurasia, or between South America and Africa or Eurasia. In contrast, none of the orders yield significant

differences between Africa and Eurasia, and only one order is different in North and South America.

Interestingly, after the megafauna extinction, there are even fewer significant differences in the mammalian fauna across continents (table 2). Moreover, those we find are largely concentrated within orders mostly unaffected by the extinction (e.g. Insectivora, Primates and Rodentia). This suggests that the extinction had the interesting effect of homogenization; that is, removing the unique aspects of the ordinal distributions. This is clearly evident in figure 5, where very little difference can be detected in the shape or position of the ordinal distributions before and after the extinction. However, our results should be interpreted with some caution. Although most orders contain more than 30 species (except Perissodactyla, Proboscidea and Insectivora of South America), the sample sizes and statistical power of the analyses are lower for the ordinal comparisons than for previous studies analysing body size distributions at the continental level (e.g. [21,71,79]).

The megafaunal extinction was a highly size-selective extinction that removed the second mode of large-bodied mammals from the environment and fundamentally changed the shape of continental distributions [79,80]. Moreover, the extinction was also highly size-biased within orders [79]. However, the extinction event did not solely target large-bodied clades. Within each clade, larger-bodied members were at significantly higher risk of extinction than smaller-bodied ones. In contrast to our results for the entire fauna, the removal of large-bodied species within an order did not fundamentally change the shape of the ordinal distribution; the moments were not significantly different after the extinction on any of the major continents (figure 5 and table 3). With the obvious exception of orders such as Proboscidea where all species were extirpated, this suggests the

Table 2. Kolmogorov–Smirnov tests were used to compare the body size distributions of the orders on the different continents before and after extinction of the megafauna. For this analysis, species that went extinct in historical times are included. Upper triangle contains the test-statistic, lower triangle contains p -values. A Bonferroni correction for multiple tests per order was applied. Significance was assessed at $\alpha < 0.008$. Significant comparisons are highlighted in bold. NA, North America; SA, South America; AF, Africa; EA, Eurasia.

order	pre-extinction				post-extinction			
	NA	SA	AF	EA	NA	SA	AF	EA
Artiodactyla								
NA		10.79	12.33	12.37		4.90	5.89	3.95
SA	0.009		4.02	2.05	0.173		5.24	3.10
AF	0.004	0.268		3.63	0.105	0.146		4.57
EA	0.004	0.715	0.326		0.277	0.425	0.204	
Carnivora								
NA		2.35	8.14	1.80		1.44	4.31	1.65
SA	0.617		16.43	5.10	0.975		8.78	2.10
AF	0.034	0.001		6.17	0.232	0.025		5.53
EA	0.812	0.156	0.092		0.875	0.702	0.126	
Insectivora								
NA		12.78	29.58	34.26		12.78	29.58	34.26
SA	0.003		8.31	6.30	0.003		8.31	6.30
AF	<0.001	0.031		5.60	<0.001	0.031		5.60
EA	<0.001	0.086	0.121		<0.001	0.086	0.121	
Lagomorphs								
NA		2.15	10.94	4.83		2.00	10.33	4.26
SA	0.681		6.67	2.73	0.735		6.67	2.73
AF	0.008	0.071		7.59	0.011	0.071		7.59
EA	0.179	0.512	0.045		0.238	0.512	0.045	
Perissodactyla								
NA		2.43	1.89	7.55		1.33	0.89	1.39
SA	0.595		2.91	6.55	>0.999		2.56	3.88
AF	0.778	0.467		2.91	>0.999	0.556		1.00
EA	0.046	0.076	0.467		0.999	0.288	>0.999	
Primates								
NA		3.65	2.33	4.36		3.81	2.33	4.36
SA	0.323		32.87	48.44	0.297		34.03	49.67
AF	0.623	<0.001		10.77	0.623	<0.001		10.77
EA	0.226	<0.001	0.009		0.226	<0.001	0.009	
Proboscidea								
NA		1.42	1.43	1.43		—	—	—
SA	0.982		1.33	3.00	—		—	—
AF	0.979	>0.999		1.00	—	—		2.00
EA	0.979	0.446	>0.999		—	—	0.736	
Rodentia								
NA		13.04	5.87	3.93		13.46	5.27	4.48
SA	0.003		20.02	5.46	0.002		19.65	5.42
AF	0.106	<0.001		6.90	0.143	0.001		6.64
EA	0.280	0.130	0.064		0.213	0.133	0.072	

influence of the extinction on any particular order was relatively small. It was only in aggregate across all the affected orders that a fundamental alteration of basic macroecological and macroevolutionary patterns can be determined. Our findings add support to the idea of size-selective predation by humans as the main driver of the extinctions; other potential causes (e.g. environmental change) should target some clades more heavily than others.

(c) *Body size diversification over time*

So far, our discussion has focused largely on spatial variation in body size. But how did mammals come to occupy the full eight orders of magnitude of size

they do today (figure 3)? When and how did this diversification occur and how idiosyncratic was the evolution of body size across the different continents?

Mammals have a long evolutionary history dating back some 210 Myr. Yet, for much of this time, mammals were small and fairly inconspicuous members of ecological communities, which were dominated by dinosaurs and other reptiles [83,84]. It was only with the demise of these groups at the Cretaceous/Paleocene boundary that rapid morphological evolution in the surviving mammals took place. The fourfold post-K/Pg increase in terrestrial mammalian body mass was first quantified for North America by Alroy [78,85], who attributed the radiation to ecological release.

Table 3. Kolmogorov–Smirnov tests were used to compare the body size distributions of mammalian orders within a continent before and after the megafaunal extinction. Different continents are evaluated separately. Upper values in each square are the test-statistic, lower values are *p*-values. No extinctions represent only extant species and all extinct represents only extinct species. NA, North America; SA, South America; AF, Africa; EA, Eurasia.

order	NA	SA	AF	EA
Artiodactyla	2.291	1.927	0.277	0.320
	0.636	0.763	>0.999	>0.999
Carnivora	1.361	2.671	no extinctions	0.072
	>0.999	0.526		>0.999
Insectivora	no extinctions	no extinctions	no extinctions	no extinctions
Lagomorphs	0.100	no extinctions	no extinctions	no extinctions
	>0.999			
Perissodactyla	1.667	2.805	0.153	0.775
	0.869	0.492	>0.999	>0.999
Primates	no extinctions	0.025	no extinctions	no extinctions
		>0.999		
Proboscidea	all extinct	all extinct	0.667	0.667
			>0.999	>0.999
Rodentia	0.052	0.007	no extinctions	0.006
	>0.999	>0.999		>0.999

More recently, Smith *et al.* [54] compiled and analysed data on maximum body mass for each major continent over the entire Cenozoic at sub-epoch resolution. These data (MAMMOTH v. 1.0; [7]), based mostly on teeth measurements collected from the primary literature and/or measured by the authors, were collected at the ordinal level, thus allowing characterization of the variation within different trophic groups as well. By taking a macroecological approach and comparing the patterns across the continents, Smith *et al.* [54] were able to test among various hypotheses about body size evolution. For example, finding similarities in the rate or trajectory of body mass evolution between continents supports the concept of a universal driver rather than drivers specific to each continent or to the phylogenetic history of each lineage. Alternatively, higher species diversity can lead to larger body mass because of passive stochastic statistical effects [86–88]. This leads to the testable prediction that the largest masses are achieved during peak species diversity within lineages and for mammals overall. Alternatively, environmental conditions such as oxygen concentration and temperature may be important; previous studies have suggested that they constrain body size evolution in mammals and other organisms [6,50,89–92]. Given the recent work that provides reasonable estimates of these abiotic factors [68,93,94], it becomes possible to test macroecological patterns against such palaeoproxies.

Interestingly, Smith *et al.* [54] find remarkably consistent patterns on each continent despite little to no overlap in species composition (figure 6). The trajectory of maximum body mass, globally and on each continent, is best fit by a Gompertz model, which reflects an initial exponential-like growth phase and a saturation phase as evolutionary possibilities for increasing body size are progressively exhausted. Maximum body size increases near-exponentially in the Early Cenozoic, levels off within approximately 25 Myr, and remains approximately constant until the Recent. The difference

in the pattern for South America is likely a result of the poor fossil record for mammals on that continent. Interestingly, models of geometric Brownian motion reflecting unconstrained random walks in log space do not fit these data as well, despite previous speculation [86–88]. Indeed, the largest mammals are not correlated with times of greater species diversity. Instead, Smith *et al.* [54] find that available land area and temperature appear to explain the upper size limit of mammals, which is reached by the Oligocene on each continent (figure 6). The largest mammals evolve when the Earth is cool and terrestrial land area is at its maximal extent. The authors postulate that energetic constraints are ultimately responsible: body mass influences energy acquisition rates, which are constrained by available land area, and body mass influences energetic expenditure, which is influenced by temperature through heat loading and/or conservation. Ultimately, these data support the precepts of Bergmann's rule, a well-known ecogeographic trend for larger body size in cooler habitats found in a majority of mammal species today [90,95–97].

(d) *Body mass evolution across taxonomic groups and feeding guilds*

The highly congruent 'body size niche' of different trophic groups and taxonomic orders on the different continents today (figure 5 and table 1) strongly suggests an important role of ecological function in constraining body mass. The statistical moments for the majority of orders shared among the continents are statistically indistinguishable ([21]; tables 2 and 3). Even the size-biased Late Pleistocene extinction did not result in a significant shift in the body size 'niche' of mammalian orders (figure 5, tables 2 and 3). Such similarity is especially remarkable considering the radically different species composition; no non-introduced mammal is found on all the major continents either now or prior to the end-Pleistocene extinction [98]. Moreover, the

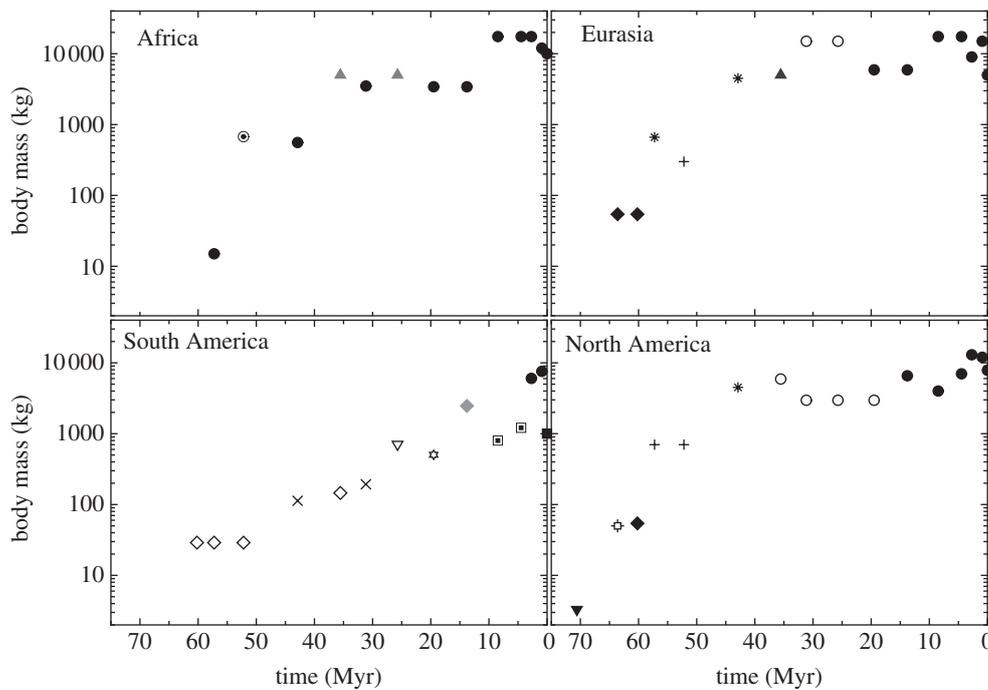


Figure 6. Turnover of the maximum body mass of mammals on the different continents over the Cenozoic. Body mass is plotted on a logarithmic scale. Note that although the same general pattern is recapitulated on each major continent, the ordinal affiliation of the largest mammal during a particular sub-epoch is often different. Data for South America are lacking because of limited sampling; thus, values for this continent should be considered an underestimate. In all cases, the trajectory of maximum body size is best fit by a Gompertz function, which suggests a saturation of the largest body size niche. Redrawn from Smith *et al.* [54].

continents have very different geographical settings and geological histories. This striking spatial pattern is also found over evolutionary time. Indeed, several archaic and modern orders exhibited the same trajectory of body mass evolution during the Cenozoic across different continents. For example, prior to the evolution of carnivorans in the middle Eocene and their eventual dominance in modern ecosystems, archaic orders such as the Creodonta and Mesonychids contained carnivorous mammals. Although displaced in time, Mesonychids, Creodonts and Carnivores each exhibit more or less the same trajectory of body mass evolution, with each clade reaching a maximal size of around 1 tonne [54]. This ‘ratcheting’ pattern of body mass evolution among carnivorous mammals is recapitulated on different continents [54].

When different trophic groups are analysed separately, the trajectories of body mass over the Cenozoic are also well characterized by the Gompertz model [54]. Interestingly, trophic affiliation appears to have significantly influenced the asymptote, but not appreciably the overall pattern of body size diversification. For example, although carnivores and herbivores evolved from insectivorous mammals of approximately the same size, within 20 Myr they reach divergent asymptotes that vary by about an order of magnitude. This consistent difference in maximal body mass has been maintained for the past 40 Myr across the different continents [54].

5. FUTURE DIRECTIONS AND CONCLUDING REMARKS

The close congruence in the patterns of mammalian body size found across both space and time is

remarkable. Mammalian taxa clearly have a ‘characteristic’ body size [73]. This occurs despite differences in geological and climatic history, turnover of lineages and differences in species composition (figures 4–6). It highlights the importance of ecological function in the evolutionary history of mammals. It is all the more surprising when one considers the abundant evidence indicating that mammals can respond to strong directional selection with large, rapid changes in body size [99–104]. For example, within 10 000 years, the body sizes of elephants and deer on continental islands fluctuated by several orders of magnitude when they were isolated by rising sea levels in the terminal Pleistocene [99,100]. Clearly, not only can body size evolution occur rapidly, but mammalian orders have sufficient evolutionary and/or morphological flexibility to evolve vastly different sizes. So why are patterns so consistent across space and time?

Our analyses suggest that the regular pattern of body mass variation reflects a common set of ecological and evolutionary processes. To some degree, similarities in the body size of taxa across different continents and across evolutionary time must reflect constraints imposed by taxonomic affiliation. However, similarities may also reflect a suite of ecological specializations and/or constraints shared by a taxonomic group. Although body size evolution must be subject to powerful constraints, our results suggest that the evolutionary diversification of size in terrestrial mammals over both geographical space and geological time cannot be explained solely in terms of phylogeny. Indeed, over evolutionary time when distantly related clades have occupied the same ecological role, they have converged on the same body size niche [54].

So what are these common ecological processes? We have suggested here that energy acquisition is key to many of the observed patterns. Energy acquisition may limit the maximal size mammals can attain over evolutionary history (figure 6), and probably sets both lower and upper boundaries (figure 2). Because the trophic strategy of mammals is both influenced by size [62,81,105,106] and influences body size [57,107], dietary strategy is a critical constraint. Future work should be directed towards investigating the patterns within lineages more carefully, both across space and time. Investigation of apparent ecological replacements across evolutionary time (e.g. hyraxes in Africa with horses and deer; [7]), and the comparison of constraints set by the major modes of life (e.g. aquatic, terrestrial and volant) will probably prove fruitful. For example, Africa today contains far fewer rodents than other major continents (figure 5). Note, however, that the modal body size of insectivores in Africa is twice as large as in other continents, and moreover, they occupy a much wider range of body masses (table 1). Perhaps, the larger body mass of insectivores reflects a response to ecological opportunities created by the paucity of rodents. Alternatively, the reduced numbers of rodents in Africa could be a direct result of the enhanced insectivore diversity owing to evolutionary history. This might well be the case if some of these insectivores are predators on rodents. Clearly, a detailed comparison of the life-history strategies and interactions of rodents and insectivores on multiple continents would be very interesting.

Use of a macroecological approach to examine body size variation in mammals has illustrated some striking statistical patterns among continents and across evolutionary time. Moving from a description of these patterns to an understanding of the mechanistic underpinnings is the focus of current research [54]. But, these efforts are complicated by the current lack of well-developed appropriate statistical tools and methodologies [32]. Macroecological studies, such as the ones described here, often employ non-experimental or 'natural' data and are moreover, typically conducted at broad geographical, taxonomic or temporal scales. Thus, the application of many modern statistical methods developed for traditional experimentally based science is inappropriate. Macroecologists are keenly aware of such limitations and are developing and employing a variety of sampling, regression, distribution testing and hypothesis-generation techniques in response [108–110]. While these are fruitful in some applications, further progress is clearly needed. Moreover, certain macroecological questions may benefit from the application of an explicitly phylogenetic framework. Such progress has been hampered by the lack of complete species-level phylogenies for many groups; even for mammals this does not yet exist. However, as well-resolved super-trees become available, they are increasingly being used to address macroecological questions within a phylogenetic context [111]. Note that such problems are not unique to macroecology; many areas of conservation biology, palaeoecology and other disciplines also employ large databases or 'natural experiments'

and face the same issues. However, the exponential growth in publications using a macroecological framework (figure 1) clearly illustrates that despite these methodological and statistical issues, macroecology has much to offer when tackling broad-scale biological patterns and processes.

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