CHAPTER FIVE

Macroecological Patterns of Body Size in Mammals across Time and Space

S. Kathleen Lyons and Felisa A. Smith

Macroecology is a way of thinking, exploring, and asking questions about complex ecological phenomena. By examining large-scale patterns across temporal, spatial, or taxonomic scales, consistent, common patterns emerge that suggest common underlying causes and processes. The field is expanding rapidly, and macroecological approaches to biology have led to new insights into the operation of general mechanistic processes that govern the structure and dynamics of individuals, populations, and complex ecological systems (Smith et al. 2008).

Here we are using a macroecological approach to examine patterns in mammalian body size distributions at multiple spatial and temporal scales. Body size is arguably one of the most fundamental attributes of an organism and has long been of interest to scientists. Many physiological and ecological traits scale with body size (Brown 1995). As a result, information about the body size of an organism can provide considerable information about its ecology and life history. There is enormous variation in the body size of extant organisms, encompassing approximately twenty-four orders of magnitude (Peters 1983; Calder 1984; Niklas 1994), and within mammals body size spans approximately ten orders of magnitude (Brown and Nicoletto 1991; Brown 1995; Alroy 1998; Marquet and Cofre 1999; Bakker and Kelt 2000; Lyons et al. 2004; Smith et al. 2004).

Much effort has focused on the consequences of being a certain size and whether taxa exhibit an optimal size (e.g., Brown and Nicoletto 1991;

Brown et al. 1993; Alroy 1998; Smith et al. 2004), and as a result, mammalian body size distributions have been well studied and found to be remarkably consistent across continents (Smith et al. 2004) and across recent time (Lyons et al. 2004). Despite these comprehensive studies, there are still holes in our understanding of the macroecology of body size. For example, the largest continent (i.e., Eurasia) has not been analyzed, and the shapes of continental body size distributions have not been evaluated across the entire Cenozoic. Community body size distributions have been studied on three of the major continents (i.e., North America [Brown and Nicoletto 1991], South America [Marquet and Cofre 1999; Bakker and Kelt 2000], and Africa [Kelt and Meyer 2009]) but have not been evaluated on Eurasia and Australia or across time. Moreover, other macroecological patterns of body size, such as the relationship between body size and range size, have not been evaluated using fossil data.

What follows is a synthetic analysis of what is known about macroecological patterns of body size in mammals. We review known patterns and extend them either spatially to previously unexamined continents or temporally into the fossil record. The majority of the chapter will focus on patterns of body size distributions at multiple spatial and temporal scales. In addition to reviewing the pertinent literature, we include new data and analyses derived from our own investigations. Building on our earlier work (Lyons et al. 2004; Smith et al. 2004), we extend our analyses to include Eurasia and a number of large islands. Moreover, we include an analysis of the shape of continental body size distribution for North American mammals across the last 65 million years. In addition, we will also include an analysis of the relationship between geographic range size and body size in mammals, and we will examine how that relationship fluctuates over time. Finally, we compare the shapes of community-level body size distributions on multiple continents and in the late Pleistocene of North America.

Taken together, the data and analyses presented herein attempt to address several questions about the macroecology of body size in mammals. First, how similar are overall body size distributions across individual continents and large islands? Second, how similar are overall body size distributions across time in North America? Are present-day patterns warped? Third, is the relationship between body size and range size consistent across time and space? Finally, are the shapes of body size distributions at the community level consistent across time and space?

Although many of these questions have been addressed previously, to our knowledge, this is the most comprehensive analysis, both spatially and temporally, of the macroecological patterns of body size to date.

Data and Analyses

The body mass data used for this review come from MOM v. 3.6, an updated version of Smith et al. (2003) that is available from either author upon request. The taxonomy used is Wilson and Reeder (1993). This dataset includes body mass estimates for the majority of the mammals of the world and the large islands. It includes estimates for extant species, species that have gone extinct in historical times, and species that went extinct during the megafaunal extinction in the late Pleistocene. Methods for data collection and handling can be found in Smith et al. (2003).

Here, we use generic averages for species without body mass estimates in order to fully characterize body size distributions. Our final dataset had estimates for 833 species from Africa, 813 species from Eurasia, 600 species from North America, 777 species from South America, 256 species from Australia, 40 species from Tasmania, 116 from Madagascar, and 150 species from New Guinea. Volant, introduced, and marine mammals were excluded from all analyses.

For each continent and large island, frequency distributions of body sizes were created and descriptive statistics were calculated for both modern (table 5.1) and late Pleistocene faunas (table 5.2). The effect of the missing values was evaluated by comparing the shapes of the body size distributions on each continent and large island with and without generic averages. Both Kolmorogorov-Smirnov two-sample tests and Mann-Whitney U tests were used. For the majority of the distributions, there was no difference between the shapes of the distributions with and without generic estimates for missing values (table 5.3). However, the shapes of the distributions for Eurasia and Africa were significantly different with and without the estimates for missing values. In each case, the missing species were primarily rare rodents and shrews and were concentrated in the lower end of the body size distribution. Because the majority of mammal genera encompass less than one order of magnitude of variation in log mass, including the estimates for missing

TABLE 5.1 Descriptive Statistics for Body Size Distributions of Extant Mammals for Each Continent and Island Separately and for All Continental Mammals Together

Land Mass	N	SD	Mean	Median	Mode	Range	Min	Max	Skewness	Kurtosis
All continents	3,057	1.160	2.378	2.059	1.130	6.353	0.243	6.596	0.876	0.153
Africa	820	1.314	2.354	1.875	1.130	6.353	0.243	6.596	0.893	−0.187
Eurasia	802	1.277	2.523	2.176	1.547	6.435	0.371	6.435	0.742	−0.304
North America	522	1.035	2.176	1.926	1.602	5.383	0.380	5.763	0.971	0.843
South America	701	0.895	2.380	2.212	2.445	5.009	0.672	5.681	0.930	0.493
Australia	211	1.032	2.402	2.121	—	4.037	0.628	4.665	0.347	−1.095
Tasmania	30	1.022	2.770	2.990	—	3.800	0.850	4.650	−0.048	−0.998
Madagascar	102	1.060	2.398	2.235	—	5.445	0.530	5.975	0.604	0.274
New Guinea	140	0.831	2.487	2.385	—	3.170	1.010	4.180	0.265	−0.972

TABLE 5.2 Descriptive Statistics for the Body Size Distributions of Late Pleistocene Mammals for Each Continent and Island Separately and for All Continental Mammals

Land Mass	Land Area (km²)	N	SD	Mean	Median	Mode	Range	Min	Max	Skewness	Kurtosis
All continents	134,344,000	3,279	1.300	2.568	2.161	1.130	6.757	0.243	7.00	0.907	0.055
Africa	30,065,000	833	1.364	2.403	1.903	1.130	6.570	0.243	6.813	0.897	−0.179
Eurasia	54,517,000	813	1.325	2.568	2.204	1.547	6.369	0.371	6.740	0.780	−0.214
North America	24,256,000	600	1.415	2.526	2.123	1.602	6.620	0.380	7.00	1.050	0.358
South America	17,819,000	777	1.279	2.683	2.360	2.445	6.208	0.672	6.880	1.219	0.873
Australia	7,687,000	256	1.364	2.847	2.708	5.176	5.548	0.628	6.176	0.395	−0.903
Tasmania	68,332	40	1.304	3.290	3.265	—	5.030	0.850	5.880	0.030	−0.875
Madagascar	581,540	116	1.228	2.644	2.545	4.00	5.445	0.530	5.975	0.563	−0.118
New Guinea	786,000	150	0.967	2.624	2.540	—	4.470	1.010	5.480	0.544	−0.312

Note: Area of major continents from www.enchantedlearning.com/geography/continents/Land.shtml. Tasmania, Madagascar, and New Guinea from Wikipedia.com. The land area for "All continents" is the sum of Africa, Eurasia, North America, South America, and Australia.

TABLE 5.3 **Comparisons of Mammalian Body Size Distributions with and without Generic Averages for Missing Values**

Land Mass	No. of Generic Values	χ^2	P	Z	P
North America	28	0.150	>0.999	−0.119	0.905
South America	3	0.052	>0.999	−0.128	0.898
Eurasia	162	10.224	0.012	−3.346	<0.001
Africa	202	21.655	<0.001	−4.418	<0.001
Australia	3	0.018	>0.999	−0.023	0.982
New Guinea	23	0.809	>0.999	−0.599	0.549
Tasmania	0	—	—	—	—
Madagascar	3	0.667	>0.999	−0.234	0.815

Note: Analyses were performed using nonparametric Kolmorgorov-Smirnov and Mann-Whitney U tests.

values should not change the shape of the binned curve (Smith and Lyons, unpublished data). Because of that, all analyses were performed on the more complete dataset that included estimates for species with missing data.

For deep-time analyses, dates and body masses of North American mammals come from the Paleobiology Database (www.pbdb.org) and from Alroy (1998, 2000). For each of four time periods (3, 20, 40, and 60 million years ago) 1-million-year time slices around those dates were taken and body size distributions of all species extant during each time period were created.

Latitudinal range sizes of extant North American mammals were obtained from an analysis of the effects of incomplete sampling on estimates of the relationship between geographic range size and body size (Madin and Lyons 2005) originally derived from (Patterson et al. 2004). Log range size was plotted as a function of log body mass, and each order of mammals was given a unique symbol. For late Pleistocene mammals, the geographic range sizes and time periods were obtained from an analysis of mammalian geographic range shifts in response to glaciation (Lyons 2003, 2005). The time periods used here (Holocene: 10,000–500 BP; Glacial: 20,000–10,000 BP; and Pre-Glacial 40,000–20,000 BP) are the same as those used by Lyons (2003, 2005) and encompass the expansion and retreat of the ice sheets during the last glaciation. The raw data are available from the FAUNMAP database (FAUNMAP Working Group 1994). In this case, geographic range sizes were calculated in km² and not degrees of latitudinal extent. As with extant mammals, log range size was plotted as a function of log body mass for each of the three time periods.

For the analyses of local community body size distributions, data and figures come from an analysis of the shapes of body size distributions over space and time (Lyons 2007). Lists of species in local communities are taken from an unpublished dataset compiled by SKL that contains 328 extant communities taken from a variety of literature and web sources, and 328 late Pleistocene and Holocene communities derived mainly from the FAUNMAP database (FAUNMAP Working Group 1994). Fossil communities are divided into late Pleistocene and Holocene communities to evaluate the effects of the megafaunal extinction on community body size distributions. Mean community age for near-time communities was calculated as the mean of the minimum and maximum age estimates for each locality as reported by FAUNMAP. For each local community, descriptive statistics that characterize the shape of the body size distribution were calculated (i.e., mean, median, skewness, and kurtosis). Because the patterns for mean and median body size were not substantially different, only median body size is reported.

Each moment of the body size distribution provides unique information about the overall shape of the distribution, and comparison of the moments gives information about the similarity or difference in different aspects of that shape. In particular, the skewness and kurtosis are extremely useful in concisely describing the shape of a distribution. The skewness measures the length of the curve relative to its height, whereas the kurtosis describes the height of the curve relative to the standard deviations. Moreover, the values of skewness and kurtosis are easily translatable to shape. For the skewness, positive values indicate right skew, negative values indicate left skew. For kurtosis, positive values indicate a peaked distribution with values around zero indicating a normal distribution. Negative values between 0 and −1 indicate a flat distribution and highly negative values greater than −1.5 indicate a bimodal distribution.

The moments of the distributions for near-time communities were compared to that of modern North American communities using t-tests to determine if the shapes of local body size distributions were significantly different because of the addition of the extinct megafauna or in the nonanalogue communities associated with glaciation. In addition, the moments describing modern communities on multiple continents were compared using t-tests to determine if there are significant differences among the continents.

Results and Discussion

The analyses presented herein are the most comprehensive to date of macroecological patterns of body size in mammals across space and time. We found that at the level of continents and large islands, there was a remarkable consistency of body size distributions across both time and space that was disrupted by the end-Pleistocene extinctions. These analyses suggest that modern body size distributions for mammals at large spatial scales have been artificially distorted by the activities of aboriginal invaders. We also find a remarkable consistency in the relationship between body size and range size across time both before and after the extinction. Finally, we find that the shapes of community body size distributions vary across both space and time and suggest that further analyses focus on the role of habitat type rather than continental associations.

Continental Patterns in Body Size

HOW SIMILAR ARE OVERALL BODY SIZE DISTRIBUTIONS ACROSS INDIVIDUAL CONTINENTS AND LARGE ISLANDS?   Despite the greater amount of data available for this analysis, our results are consistent with Smith et al. (2004). The overall shapes and ranges of the body size distributions are similar on each of the four main continents, Eurasia, Africa, North America, and South America (fig. 5.1, *white bars*). We find that the statistics that describe the body size distributions of the major continents are remarkably similar (table 5.1). The range of body sizes found on each continent differs only slightly with most of the difference attributable to the lack of elephants in the New World and the lack of insectivores in South America. Moreover, the mean and median body sizes for each continent fall within a narrow range (mean: 2.176–2.523 log units, ~150–333 g; median 1.875–2.212 log units, ~75–163 g). Even the skewness is similar, ranging from 0.742 to 0.930. However, there are noticeable differences. Although the distributions are multimodal on each continent, the position of the modes differs. Eurasia and Africa have very similar shapes, with a species-rich second mode of large-bodied mammals that is lacking in modern North and South America. In addition, the position of the small-bodied mode differs on the different continents, in part, due to the order Insectivora. Africa has a large num-
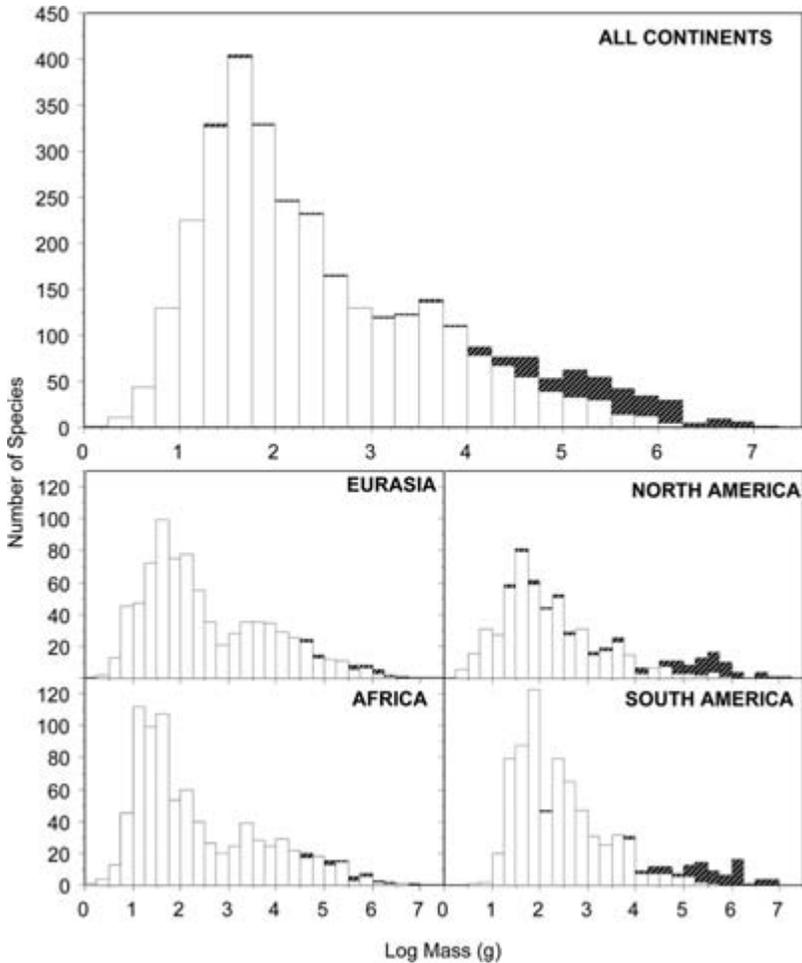
FIGURE 5.1. Frequency distributions of mammalian body size on all continents and four major continents, Eurasia, North America, Africa, and South America. Hatched bars indicate the body size distribution of species that went extinct in the late Pleistocene. Note that the timing of the extinction is not the same on all the continents. The extinction on Eurasia occurred in two pulses at 50,000 and 30,000 years ago (Stuart 1999).

ber of insectivores, causing the mode of small-bodied species to be shifted to the left relative to other continents. In contrast, insectivores do not make it into South America, and as a consequence the mode of small-bodied species is shifted to the right relative to the other continents (see Smith et al. 2004). As a result, there are statistically signifi-

cant differences between the continents, despite the overall similarity in shape.

The one small continent and the large islands (e.g., Australia, Tasmania, New Guinea, and Madagascar) have body size distributions that are distinct from those of the four main continents (fig 5.2, *white bars*). Rather than having a right-skewed distribution with a mode of small-bodied mammals, large islands have multimodal distributions that are much flatter than continental distributions. Indeed, they strongly resemble the regional distributions of Brown and Nicolleto (1991). Moreover, the degree to which the distribution is flattened appears related to island area and number of species. Tasmania has a much flatter distribution than the other large islands and also contains the fewest species (fig. 5.2, *white bars*, table 5.1) and the smallest land area (table 5.2). As with the continental distributions, the range, mean, and median of the body size distributions of the large islands are relatively similar. Moreover, as with the continents, the differences can be attributed to unique aspects of the islands' history. For example, Madagascar has a much greater body size
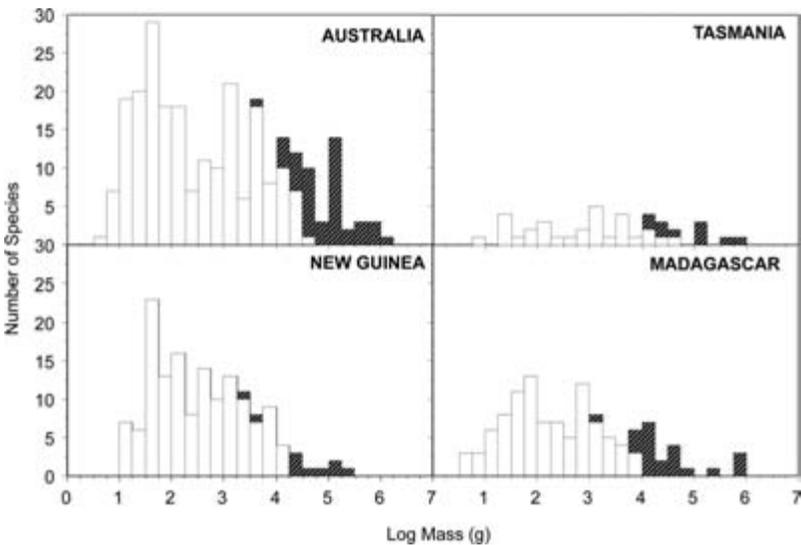

FIGURE 5.2. Frequency distributions of mammalian body size on one small continent, Australia, and three large islands, New Guinea, Tasmania, and Madagascar. Hatched bars indicate the body size distribution of species that went extinct in the late Pleistocene. Note that the timing of the extinction is not the same on all land masses, but each coincides roughly with the arrival of humans (Martin and Steadman 1999).

range because of the inclusion of the endemic pygmy hippo, *Hexaprotodon madagascariensis*. There is some question as to the timing of the extinction of this species. However, evidence suggests that the extinction occurred in historical times (MacPhee and Flemming 1999), thus warranting inclusion in a characterization of the body size distribution of modern mammals of Madagascar.

HOW SIMILAR ARE OVERALL BODY SIZE DISTRIBUTIONS ACROSS TIME IN NORTH AMERICA?   On each continent and large island, there was a size-biased extinction during the late Pleistocene that resulted in a truncation of the body size distribution (figs. 5.1 and 5.2, *hatched bars*). North and South America were strongly affected by the extinction event, losing ~70–80 species each, whereas the extinction events were relatively minor in Eurasia and Africa, with each losing ~15 species. Prior to the extinction event, the overall shapes of the continental distributions were even more similar than at present (fig. 5.1). North and South America had a second mode of large-bodied species and a large-bodied fauna that rivaled that of Africa. Similar to Lyons et al. (2004), we find remarkable similarity in the descriptive statistics that characterize the body size distributions on each continent. The mean and median body sizes fall within a narrow range of values (table 5.2). In addition, the differences in the overall range of body masses found on each continent in the present disappear when considering distributions that include the extinct megafauna. Prior to the extinction the body mass distributions on the four main continents encompassed 6.2–6.6 log units of mass. Lyons et al. (2004) found that prior to the extinction event, the shapes of the body size distributions of North and South America were not significantly different from that of Africa, although they were significantly different from each other. Here we find that all of the continents, except North America and Eurasia, are significantly different from one another even with the addition of the extinct megafauna (table 5.4). The difference between our results and that of Lyons et al. (2004) are probably due to the more complete dataset and the larger sample sizes available for this analysis. Moreover, as with the modern distributions, there are unique aspects of each continent's history that will contribute to significant differences between them.

Each of the large islands we examined also had a significantly size-biased extinction that truncated the body size distribution at the large end (fig. 5.2). Interestingly, despite the similarity in the extinction event,

TABLE 5.4 **Comparisons of Mammalian Body Size Distributions on Different Continents prior to the Extinction of the Megafauna**

	Africa	Eurasia	North America	South America	Australia
Africa	—	<0.001	<0.001	<0.001	<0.001
		<0.001	0.018	<0.001	<0.001
Eurasia	24.921	—	0.133	<0.001	<0.001
	−3.507		0.302	0.012	0.004
North America	15.670	5.429	—	<0.001	<0.001
	−2.377	−1.032		<0.001	<0.001
South America	78.613	22.298	19.530	—	<0.001
	−6.555	−2.514	−3.608		0.128
Australia	29.090	16.660	24.553	23.227	—
	−5.001	−2.849	−3.430	−1.523	

Note: Analyses were performed using nonparametric Kolmorgorov-Smirnov and Mann-Whitney U tests. Values in the bottom triangle are test statistics, and values in the upper triangle are p values. Upper values are for the Kolmorgorov-Smirnov test, and lower values are for the Mann-Whitney U test. Continent-specific generic averages were substituted for missing body sizes.

the extinction did not occur at the same time on each island (Grainger et al. 1987; Flannery 1995; Strahan 1995; Bonaccorso 1998 ; Garbutt 1999). Indeed, for Madagascar, there is some debate concerning the timing of the extinction of the different species that were affected (Garbutt 1999; MacPhee and Flemming 1999). However, as with the continental distributions, the shapes and the statistics that characterize the body size distributions of mammals on large islands were similar prior to the extinction event (fig. 5.2, table 5.2). In particular, the range of body masses on each island was more similar prior to the extinction event despite the differences in land area (compare table 5.2 to table 5.1). Interestingly, for island distributions, the megafaunal extinction events did not substantially change the shape of the distribution. Because the distributions tend to be flatter and less skewed in general, the removal of large-bodied species simply truncated the distributions rather than removing a second mode, as with the continental distributions.

At the continental level, body size distributions of modern mammals and late Pleistocene mammals are significantly different (Lyons et al. 2004). The lack of megafauna in present-day faunas has had a profound effect on the shape of body size distributions. The question then becomes, Which time period is unique? Are present-day distributions unusual or is there something unique about the late Pleistocene? To answer these questions, we examined the shape of body size distributions for mammals in North America in 1-million-year intervals at four different time periods over the Cenozoic (4, 20, 40, and 60 million years ago).

Because these distributions were generated entirely from fossil data, they are unlikely to be perfect representations of the faunas of the time. First, sampling is a problem, and not all species present at a particular time will be represented in the fossil record. Second, this bias is likely to be stronger for small-bodied species. An analysis of the late Pleistocene record of North America has shown that small-bodied species are less likely to be represented, either because they are less robust and therefore less likely to be fossilized or because they are less likely to be recovered without special collecting techniques (Lyons and Smith 2006a, 2010). However, these biases should be similar throughout the Cenozoic, making comparison among the deep-time faunas possible. Despite these problems, there are similarities between these deep-time faunas and the late Pleistocene that suggest general patterns. First, after the Cretaceous/Paleogene extinction, mammals very quickly filled the full range of body sizes occupied by mammals (fig. 5.3, *bottom panel*; see also Alroy 1998; Smith et al. 2004). Moreover, the mean body masses for the different orders of mammals stayed relatively constant over time and across continents (Smith et al. 2004). Second, the body size distribution of mammals became bimodal by 40 million years ago and stayed that way until the extinction of the megafauna in the late Pleistocene (fig. 5.3; see also Alroy 1998).

The similarity of extinction events on multiple continents and large islands suggests that there should be predictability in the shape of mammalian body size distributions at continental and regional scales. Continental body size distributions should be right skewed and multimodal with two major modes—one for small-bodied species and one for the large-bodied species that are lacking from many modern faunas. Indeed, mammalian body size distributions became bimodal early on in the history of mammals, first occurring around 40 million years ago. Moreover, our results for large islands suggest that regional distributions should have the predictable shape that was first characterized by Brown and Nicoletto (1991). They should be somewhat right skewed and flatter than continental distributions, and they should become increasingly less skewed and flatter as the spatial scale decreases. This similarity in distribution shape implies there are underlying mechanisms that shape these distributions over ecological and evolutionary time. Moreover, it suggests that humans have manipulated the environment by default or design since they became a dominant species (e.g., Lyons et al. 2004; Donlan et al. 2005; Surovell et al. 2005; Donlan et al. 2006). Therefore,
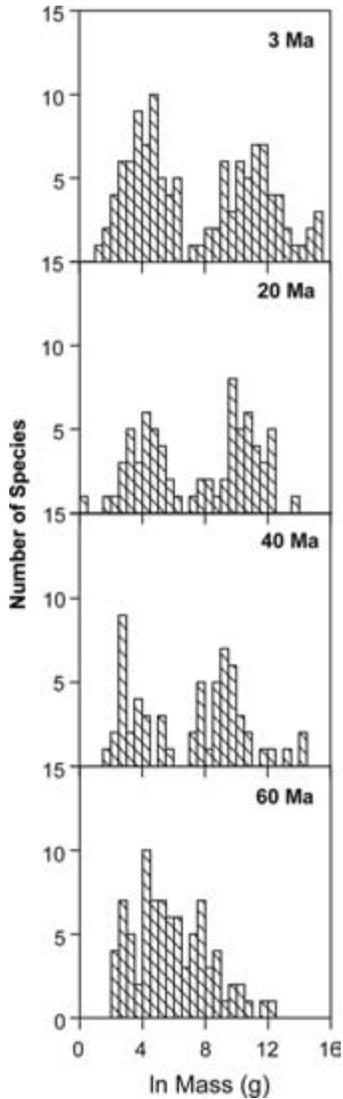
FIGURE 5.3. Frequency distributions of body size of North American mammals at four different points in time across the Cenozoic: 60, 40, 20, and 3 million years ago. Note that continental body size distributions are bimodal by 40 million years ago and remain that way until the end-Pleistocene extinctions. (Data courtesy of J. Alroy [Alroy 1998, 2000].)

present-day macroecological patterns must be interpreted with the realization that anthropogenic effects may have altered the patterns from their "natural" state. If we truly think that the repeatable macroecological patterns we are seeing have underlying ecological processes, then we must be sure that the patterns we are trying to explain are not unduly artificially altered.

Continental Patterns of Body Size and Range Size

The relationship between body size and range size, for most groups examined, is a triangular relationship in which large-bodied species tend to have large ranges and small-bodied species have a large amount of variation in the shape of their geographic range (Brown 1995; Blackburn and Gaston 1996; Gaston and Blackburn 1996; Gaston 2003). Mammals in the present-day New World show this pattern (fig. 5.4, *left-hand panel*) both across all mammals and within the different orders (J. Madin, pers. comm.). Moreover, this pattern is consistent across the last 40,000 years in North America (fig. 5.4, *right-hand panels*). In fact, we see this messy, triangular relationship before and after the extinction of large mammals. Nonetheless, there are some differences. The body size/range size plots for the Holocene, Glacial, and Pre-Glacial time periods (fig. 5.4, *right-hand panels*) have some large-bodied mammals that had small ranges. However, examination of the identity of these points indicates that in each case, they are species that subsequently went extinct or are species whose distributions are truncated, as the majority of the range falls outside the United States (i.e., the range of the FAUNMAP data). For example, in the Pre-Glacial plots, the three largest mammals with small ranges are *Homotherium serum*, *Hydrochoerus holmesi*, and *Equus scotti*. Each of these species is now extinct. In the Glacial time periods, the large mammals with the smallest ranges are *H. holmesi* and *E. niobrarensis*. The other large-bodied species with small ranges are species like *Alces alces* that have a large portion of their current range outside of the range of the FAUNMAP data. Finally, in the Holocene the large-bodied species with small ranges tend to be species like the peccary and the mountain goat, whose ranges extend outside the United States.

The consistency over time of the relationship between body size and range size, the pattern that large-bodied mammals have large ranges and small-bodied mammals have great variation in range size, suggests that small mammals can be either coarse or fine grained in how they perceive
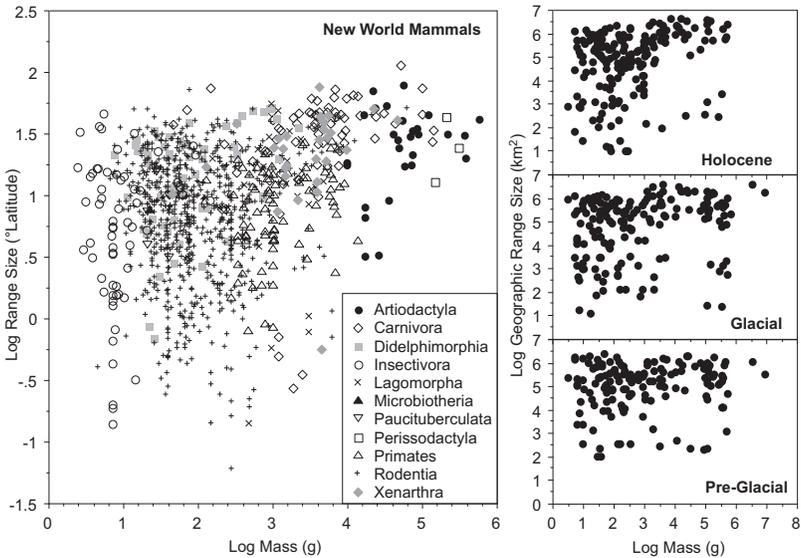
FIGURE 5.4. The relationship between body size and range size for New World mammals (*left-hand panel*) and for North American mammals at three time periods during the Quaternary: Holocene (last 10,000 years), Glacial (20,000–10,000 years ago), and Pre-Glacial (40,000–20,000 years ago). Data for New World mammals are coded according to ordinal affiliation.

the environment, but that large mammals can only be coarse grained. This difference in how large- and small-bodied mammals perceive and use the environment could help explain the triangular shape of the relationship, because it explains why the smallest range size within a body size bin increases with body size. However, it does not explain the top constraint line, or lack thereof. Maximum range size in all body size bins is similar and seems to be related to available space. That is, at all body sizes, some species will have the maximum range size allowable given the available land area. Why are there small-bodied species that use a lot of space? One possibility is that there are constraints imposed by life history traits or phylogenetic history. However, this has yet to be explored across all mammals.

Interestingly, the overall triangular shape cannot be attributed to turnover in the ordinal identity across the *x* axis. The triangular-shaped relationship holds within orders as well as across all mammals (fig. 5.4, *left-hand panel*; J. Madin, pers. comm.), suggesting that mode of life influences the steepness of the relationship, but not the overall triangular

shape. If the triangular shape were attributable simply to differences in how body size relates to range size in different orders of mammals, we would not expect to see the same pattern recapitulated within the different orders. Indeed, the fact that larger insectivores (fig. 5.4, *left-hand panel, open circles*) or larger artiodactyls (fig. 5.4, *left-hand panel, solid circles*) tend to have larger ranges and less variation in range size than smaller-bodied members of their order suggests that there is something about body size per se that influences the overall shape.

Community-Level Patterns of Body Size

There are two main findings concerning body size distributions at the community level. The first is that they tend to be flatter than distributions at regional or continental scales (Brown and Nicolleto 1991). In general, this means that as the spatial scale of the analysis decreases, the number of species in the modal size classes is reduced. Brown and Nicolleto (1991) first showed this pattern for North American mammals and pointed out that this meant that beta diversity among communities was due to turnover in species from the modal size class (i.e., 100 g) and that smaller- and larger-bodied species were occurring in multiple communities. Studies that have extended these analyses to South America (Marquet and Cofre 1999; Bakker and Kelt 2000) and Africa (Kelt and Meyer 2009) have also found a flattening of the body size distribution with decreasing spatial scale.

The second main finding first recognized by Brown and Nicolleto (1991) is that the shapes of body size distributions change with spatial scale. They found that although North American continental body size distribution was unimodal and right skewed, local body size distributions were essentially uniform. The uniform shape of the distribution was consistent for all of the different habitats they examined. However, subsequent studies for South America (Marquet and Cofre 1999; Bakker and Kelt 2000) and Africa (Kelt and Meyer 2009) have not replicated these findings. Non–rain forest communities in South America showed the uniform distribution common to North America; however, rain forest communities had more unimodal and peaked distributions (Marquet and Cofre 1999; Bakker and Kelt 2000). The difference was attributed to the arboreal habitat available in rain forests and the additional medium-sized mammals that it could support. Interestingly, Africa shows a third pattern. In Africa, local body size distributions are

flatter than continental body size distributions but never completely lose the bimodality found at larger spatial scales (Kelt and Meyer 2009). Kelt and Meyer (2009) attribute this difference to the second mode of large-bodied mammals still present in Africa and argue that any coevolutionary accommodations between early human hunters and large-bodied mammals that allowed the African fauna to escape anthropogenic extinction may also be responsible for the bimodality of local body size distributions. Interestingly, this predicts that other continents such as Eurasia that also retained their second mode of large-bodied mammals and avoided the end-Pleistocene extinction should show similar patterns to that of Africa.

ARE THE SHAPES OF BODY SIZE DISTRIBUTIONS AT THE COMMUNITY LEVEL CONSISTENT ACROSS SPACE?   Our analyses of the moments of community body size distributions across space and time found significant differences in the shapes of community body size distributions among continents (fig. 5.5, tables 5.5, 5.6, and 5.7) and across time (fig. 5.6). However, there were notable exceptions. First, pairwise analyses of the median ln body mass of communities on different continents found significant differences among only three pairs of continents: Africa and North America, Eurasia and Australia, and Australia and South America (fig. 5.5, table 5.5). Africa had the highest median body size of its communities, followed by South America. As might be expected from the results of Kelt and Meyer (2009), the majority of the differences in median ln body size are driven by differences with Africa. Because Africa still retains its large-bodied fauna and the second mode in the continental body size distribution (fig. 5.1), African communities could have a higher median body size, because they contain more individuals of larger size. However, we did not find the expected similarity between Eurasian and African communities, despite the fact that the continental body size distributions of Africa and Eurasia are remarkably similar and both continents retain a significant portion of their large-bodied fauna (fig. 5.1). This may reflect the wider range of temperate latitudes in Eurasia than in Africa.

We found no difference in the skewness of the communities on different continents (fig. 5.5, table 5.6). The average skewness on each continent was close to zero, but the range of values was much greater on Australia, Eurasia, and South America (fig. 5.5). Clearly African communities did not attain higher median ln body sizes by having communities with radically different skewness. Indeed, the average skewness
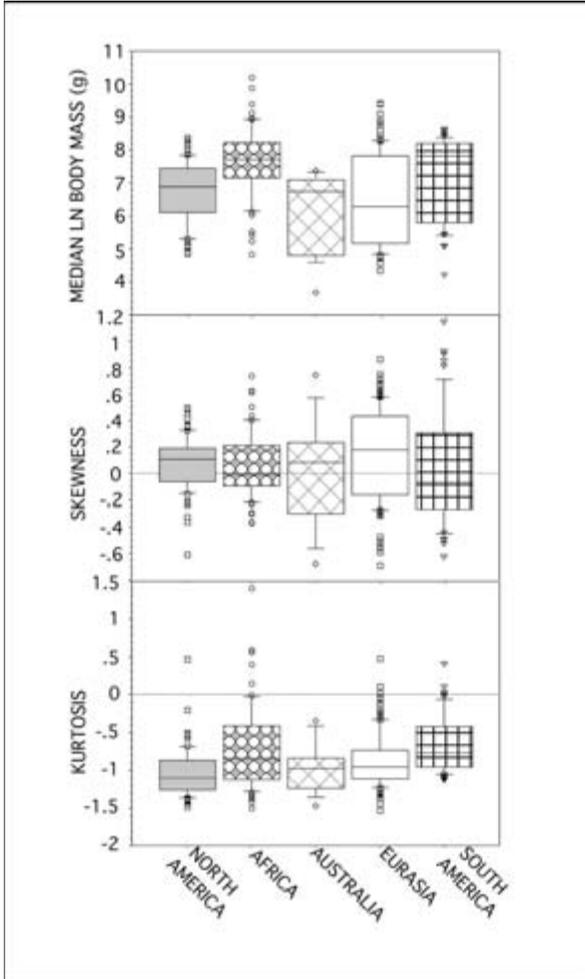
FIGURE 5.5. Box plots comparing the moments of body size distributions of modern mammal communities for five different continents, North America (*gray bar*), Africa (*circle hatching*), Australia (*x hatching*), Eurasia (*white bar*), and South America (*square hatching*). Each panel represents a different moment: median ln body mass, skewness, and kurtosis.

for African communities is approximately zero (fig. 5.5), consistent with the findings of bimodality reported by Kelt and Meyer (2009). Although it is not a significant difference, it is worth noting that Eurasia has the highest average skewness and that the values tend to be positive, indicating a right skew. Despite having a second mode of large-bodied mam-

TABLE 5.5 **Comparisons of ln Median Body Size for Body Size Distributions of Local Communities on Different Continents**

	Africa	Eurasia	North America	South America	Australia
Africa	—	**<0.001**	**<0.001**	0.05	**<0.001**
Eurasia	5.19		0.38	0.007	0.23
North America	−5.39	0.875		0.01	0.03
South America	2.03	−2.75	−2.48		**0.005**
Australia	4.71	−1.20	2.20	−2.95	

Note: Analyses were performed using *t*-tests. Values in the bottom triangle are test statistics, and values in the upper triangle are *p* values. Continent-specific generic averages were substituted for missing body sizes. A Bonferroni correction puts the alpha needed for significance at 0.005. Significant *p* values are highlighted in bold.

TABLE 5.6 **Comparisons of Skewness Values for Body Size Distributions of Local Communities on Different Continents**

	Africa	Eurasia	North America	South America	Australia
Africa	—	0.09	0.64	0.67	0.58
Eurasia	−1.70		0.11	0.07	0.17
North America	0.47	−1.61		0.40	0.34
South America	0.42	1.85	0.84		0.88
Australia	0.56	−1.40	0.96	−0.15	

Note: Analyses were performed using *t*-tests. Values in the bottom triangle are test statistics, and values in the upper triangle are *p* values. Continent-specific generic averages were substituted for missing body sizes. A Bonferroni correction puts the alpha needed for significance at 0.005. There are no significant *p* values.

mals still extant (fig. 5.1), Eurasian communities are more likely to have a peak in smaller-bodied species and a long tail of large-bodied species rather than a second mode. Again, this is unlike Africa and suggests that simply having a continental biota that was less affected by the megafaunal extinction is not sufficient to explain African community body size distributions.

Analyses of the kurtosis values of the communities on different continents found significant differences largely between North and South America and the other continents (fig. 5.5, table 5.7). Specifically, the distribution of kurtosis values describing North American communities was significantly different from that of African, Eurasian, and South American communities. In addition to being significantly different from North America, South America was also significantly different from Eurasia. On all continents, the majority of communities had kurtosis values less than zero, indicating a relatively flat distribution. However, the variation in community kurtosis values on the different continents is infor-

TABLE 5.7 **Comparisons of Kurtosis Values for Body Size Distributions of Local Communities on Different Continents**

	Africa	Eurasia	North America	South America	Australia
Africa	—	0.02	**<0.001**	0.56	0.08
Eurasia	2.33		**<0.001**	**<0.001**	0.23
North America	−4.27	−3.37		**<0.001**	0.59
South America	−0.59	−3.56	−6.20		**0.003**
Australia	1.80	−1.20	−0.54	−3.09	

Note: Analyses were performed using *t*-tests. Values in the bottom triangle are test statistics, and values in the upper triangle are *p* values. Continent-specific generic averages were substituted for missing body sizes. A Bonferroni correction puts the alpha needed for significance at 0.005. Significant *p* values are highlighted in bold.

mative (fig. 5.5). North America and Australia had kurtosis values that fell within a narrow range, with the average being close to −1, indicative of the flat distributions documented in Brown and Nicoletto (1991). Eurasia and South America also had kurtosis values that fell within a narrow range. However, the average for Eurasia was close to −1, whereas the average for South America was closer to −0.75. For both continents, the average values indicate a majority of communities with relatively flat distributions; however, the body size distributions of South American communities were slightly more peaked than those of Eurasian communities. This is consistent with the findings of more peaked distributions in South American rain forests (Marquet and Cofre 1999; Bakker and Kelt 2000). Interestingly, the range of values for Eurasian communities is much greater than for any other continent save Africa. This suggests that Eurasian community body size distributions run the gamut from highly bimodal to uniform to highly peaked.

African community body size distributions show the greatest range of kurtosis values and the highest average (fig. 5.5). Moreover, the communities with the absolute highest kurtosis values occur in Africa. This is in sharp contrast to the bimodality at all spatial scales reported by Kelt and Meyer (2009). The difference may be due to the area of the local communities used in the different studies and the greater number of local communities analyzed here. Our communities were constrained to be <10,000 km^2, whereas Kelt and Meyer's (2000) were not. Moreover, we analyzed a much larger number of local communities covering a wider range of habitats (57 vs. 14). Although some communities are peaked, it is not a consistent feature of African communities. Our analyses indicate that the majority of African communities have peaked distribu-

tions, but that they run the gamut from bimodal to uniform to highly peaked. Interestingly, in this respect African and Eurasian communities are similar.

The analyses presented here confirm and extend the findings previously reported concerning the shapes of community body size distributions. First, community body size distributions across the globe are flatter than either regional- or continental-level distributions. The flattening with spatial scale first noted by Brown and Nicoletto (1991) is a consistent characteristic of community body size distributions regardless of continent, clade composition or habitat and biome membership. Second, the shapes of the body size distributions are not consistently uniform as they are for North America. There are significant differences among and within all the continents. These differences are probably associated with differences in habitat type and clade composition. However, more research comparing body size distributions as a function of habitat type irrespective of continental association is necessary to evaluate that claim.

ARE THE SHAPES OF BODY SIZE DISTRIBUTIONS AT THE COMMUNITY LEVEL CONSISTENT ACROSS TIME?   For each of the moments analyzed (median, skewness, and kurtosis), >60% of the values for the fossil communities fell within the same range as the values for modern North American communities. However, we did find significant differences in some of the moments in the different time periods. There were no significant differences in the median ln body size of late Pleistocene, Holocene, and modern North American communities (fig. 5.6, late Pleistocene vs. Holocene: $t = 1.91$, $p = 0.057$; late Pleistocene vs. modern: $t = -1.67$, $p = 0.10$; Holocene vs. modern: $t = -0.28$, $p = 0.78$). This is despite the fact that late Pleistocene communities still contained the megafauna that went extinct after the arrival of humans (Martin 1966, 1967, 1984; Martin and Klein 1984). The late Pleistocene communities have a greater variation in median ln body size than the more recent time periods, but this difference is not significant. It is possible that this is due to poorer sampling of the large-bodied species in the community. However, that is unlikely. Large-bodied species are more likely to be recorded than small-bodied species (Lyons and Smith 2006, 2010). In North America, approximately 80 species of large-bodied mammals went extinct at the end of the Pleistocene (Lyons et al. 2004). The greater range values of median ln body size may reflect greater competition for resources and community membership among large-bodied species when so many more of them are extant.
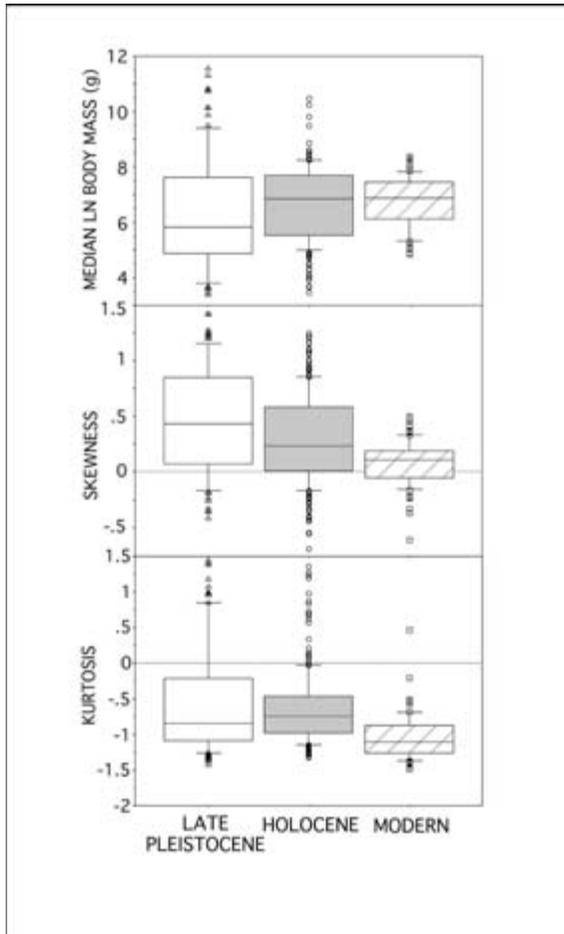
FIGURE 5.6. Box plots comparing the moments of body size distributions of late Pleistocene (*white bar*), Holocene (*gray bar*), and modern (*diagonal hatching*) mammal communities. Each panel represents a different moment: median ln body mass, skewness, and kurtosis.

The value of the median ln body size will be dependent on which and how many of the large-bodied species are present. If it is highly variable, median ln body size of communities should be as well.

Our analysis found significant differences in the skewness of communities for all pairwise combinations of time periods (fig. 5.6, late Pleistocene vs. Holocene: $t = -3.56$, $p < 0.001$; late Pleistocene: $t = 6.99$,

$p < 0.001$; Holocene vs. modern: $t = 4.68$, $p < 0.001$). Indeed, skewness decreased toward the present, with late Pleistocene communities significantly more right skewed than Holocene communities, which were in turn significantly more skewed than modern communities. However, what seems to really be driving the pattern is the much greater range of skewness values describing the fossil communities (fig. 5.6). There are two possible explanations for this. The first is that it is a sampling problem and the use of fossil data is introducing noise into the data that is increasing variation. To some degree, this is probably the case. The second possibility is that the climate change and its affect on communities is affecting community body size distributions. The climate change associated with glaciation had significant effects on the distributions of mammalian species (Graham 1984, 1986; Graham and Mead 1987; Graham et al. 1996; Lyons 2003) and there was considerable turnover in community composition (Lyons 2005). Moreover, late Pleistocene communities were more diverse than Holocene and modern communities (Graham et al. 1996). Although it has been less well studied, it is possible that the rapid climate flickers during the Holocene also affected community composition and diversity. These differences in other aspects of community structure may have translated into differences in community body size distributions as well.

With respect to the kurtosis, we found that the fossil communities in the late Pleistocene and Holocene were significantly different from the modern communities, but not significantly different from each other (fig. 5.6, late Pleistocene vs. Holocene: $t = -1.67$, $p = 0.10$; late Pleistocene vs. modern: $t = 5.56$, $p < 0.001$; Holocene vs. modern: $t = 6.59$, $p < 0.001$). Moreover, the average kurtosis for both Holocene and late Pleistocene communities was higher than for modern communities, suggesting at least some communities with more peaked and less uniform distributions. Indeed, the smallest kurtosis values in each time period were similar, but the late Pleistocene and Holocene contained communities with much higher kurtosis values than found in modern communities (fig. 5.6). The differences in kurtosis probably have the same explanation as differences in skewness and are a result of noise introduced by the fossil data and real differences resulting from differences in community structure of North American communities over the last 40,000 years.

Although the analyses presented here document significant differences in some of the moments of the body size distributions of mamma-

lian communities in North America over the last 40,000 years, it is worth emphasizing that the majority of communities (>60%) had values for each of the moments that fell within the range of modern North America. This suggests that the majority of communities had the flat distributions documented by Brown and Nicoletto (1991) and that relatively flat, uniform distributions are common to temperate North America. However, the greater range of values suggests that the changes in climate and differences in community composition and diversity did play a role in the shapes of body size distributions. Moreover, it implies that, as with differences on the different continents, habitat type is likely to be an important predictor in the shapes of these distributions across both time and space.

Summary and Conclusions

Our comprehensive analysis of the macroecology of body size in mammals across space and time shows that there are gross similarities in these macroecological patterns across land masses and throughout evolutionary time. Although there are unique aspects to the patterns on individual continents, the shapes of body size distributions and the moments of the distributions are remarkably similar despite their different evolutionary and geological histories (figs. 5.1 and 5.2). Moreover, the overall shape of the continental body size distribution seems to have developed by 40 million years ago and remained consistent until the extinction of the megafauna at the end of the Pleistocene (fig. 5.3). At a local scale, studies have shown that the shape of the body size distribution differs depending on your continent and biome (Brown and Nicoletto 1991; Marquet and Cofre 1999; Bakker and Kelt 2000; Kelt and Meyer 2009). Our analysis confirms that there are differences among the three continents studied and extends the finding to Australia and Eurasia (fig. 5.5). However, we also find a similarity to the patterns across the late Pleistocene, suggesting that the habitat- and biome-level factors that shape community-level body size distributions have done so consistently across time (fig 5.6). Finally, we find that other macroecological patterns, such as the relationship between body size and range size, are recoverable in the fossil record and that any discrepancies between modern patterns and fossil patterns can be attributed to the anthropogenic extinction of the late Pleistocene megafauna.

References

Alroy, J. 1998. "Cope's rule and the dynamics of body mass evolution in North American fossil mammals." *Science* 280 (5364): 731–734.

———. 2000. "New methods for quantifying macroevolutionary patterns and processes." *Paleobiology* 26 (4): 707–733.

Bakker, V. J., and D. A. Kelt. 2000. "Scale-dependent patterns in body size distributions of Neotropical mammals." *Ecology* 81 (12): 3530–3547.

Blackburn, T. M., and K. J. Gaston. 1996. "Spatial patterns in the geographic range sizes of bird species in the New World." *Philosophical Transactions of the Royal Society B: Biological Sciences* 351 (1342): 897–912.

Bonaccorso, F. J. 1998 *Bats of Papua New Guinea*. Conservation International Tropical Field Guide Series 2. Washington DC: Conservation International.

Brown, J. H. 1995. *Macroecology*. Chicago: University of Chicago Press.

Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. "Evolution of body size: Consequences of an energetic definition of fitness." *American Naturalist* 142 (4): 573–584.

Brown, J. H., and P. F. Nicoletto. 1991. "Spatial scaling of species composition: Body masses of North American land mammals." *American Naturalist* 138 (6): 1478–1512.

Calder, W. A., III. 1984. *Size, function, and life history*. Cambridge, MA: Harvard University Press.

Donlan, C. J., J. Berger, C. E. Bock, D. A. Burney, J. A. Estes, D. Foreman, P. S. Martin, G. W. Roemer, F. A. Smith, M. E. Soulé, and H. W. Greene. 2005. "Rewilding North America." *Nature* 436:913–914.

———. 2006. "Pleistocene rewilding: An optimistic agenda for twenty-first century conservation." *American Naturalist* 168:660–681.

FAUNMAP Working Group. 1994. *A database documenting late Quaternary distributions of mammal species in the United States*. Vol. 1. Illinois State Museum Scientific Papers, vol. 25. Springfield: Illinois State Museum.

Flannery, T. 1995. *Mammals of New Guinea*. Rev. and updated ed. Ithaca: Cornell Unversity Press.

Garbutt, N. 1999. *Mammals of Madagascar*. New Haven: Yale University Press.

Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.

Gaston, K. J., and T. M. Blackburn. 1996. "Range size body size relationships: Evidence of scale dependence." *Oikos* 75 (3): 479–485.

Graham, R. W. 1984. "Paleoenvironmental implications of the Quaternary distribution of the eastern chipmunk (Tamias-Striatus) in central Texas." *Quaternary Research* 21 (1): 111–114.

———. 1986. "Response of mammalian communities to environmental changes

during the late Quaternary." In *Community Ecology*, edited by J. Diamond and T. J. Case, 300–313. New York: Harper and Row.

Graham, R. W., E. L. Lundelius, M. A. Graham, E. K. Schroeder, R. S. Toomey, E. Anderson, A. D. Barnosky, J. A. Burns, C. S. Churcher, D. K. Grayson, R. D. Guthrie, C. R. Harington, G. T. Jefferson, L. D. Martin, H. G. McDonald, R. E. Morlan, H. A. Semken, S. D. Webb, L. Werdelin, and M. C. Wilson. 1996. "Spatial response of mammals to late Quaternary environmental fluctuations." *Science* 272 (5268): 1601–1606.

Graham, R. W., and J. I. Mead. 1987. "Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America." In *North American and adjacent oceans during the last deglaciation*, edited by W. F. Ruddiman and H. E. Wright, Jr., 372–402. Boulder, CO: Geological Society of America.

Grainger, M., E. Gunn, and D. Watts. 1987. *Tasmanian mammals: A field guide*. Hobart: Tasmanian Conservation Trust.

Kelt, D. A., and M. D. Meyer. 2009. "Body size frequency distributions in African mammals are bimodal at all spatial scales." *Global Ecology and Biogeography* 18 (1): 19–29.

Lyons, S. K. 2003. "A quantitative assessment of the range shifts of Pleistocene mammals." *Journal of Mammalogy* 84 (2): 385–402.

——. 2005. "A quantitative model for assessing community dynamics of Pleistocene mammals." *American Naturalist* 165 (6): E168–E185.

——. 2007. "The relationship between environmental variables and mammalian body size distributions over the space and time." Paper read at the annual meetings of the Ecological Society of America, San Jose, CA.

Lyons, S. K., and F. A. Smith. 2006. "Assessing biases in the mammalian fossil record using late Pleistocene mammals from North America." *Geological Society of America Abstracts with Programs* 38: 307.

——. 2010. "Using a macroecological approach to study geographic range, abundance, and body size in the fossil record." In *Quantitative methods in paleobiology*, edited by J. Alroy and G. Hunt, Paleontological Society Papers 16, 117–141.

Lyons, S. K., F. A. Smith, and J. H. Brown. 2004. "Of mice, mastodons and men: Human-mediated extinctions on four continents." *Evolutionary Ecology Research* 6 (3): 339–358.

MacPhee, R. D. E., and C Flemming. 1999. "Requiem aeternam: The last five hundred years of mammalian species extinctions." In *Extinctions in near time: Causes, contexts, and consequences*, edited by R. D. E. MacPhee, 333–372. New York: Kluwer Academic/Plenum.

Madin, J. S., and S. K. Lyons. 2005. "Incomplete sampling of geographic ranges weakens or reverses the positive relationship between an animal species'

geographic range size and its body size " *Evolutionary Ecology Research* 7:607–617.

Marquet, P. A., and H. Cofre. 1999. "Large temporal and spatial scales in the structure of mammalian assemblages in South America: A macroecological approach." *Oikos* 85 (2): 299–309.

Martin, P. S. 1966. "Africa and Pleistocene overkill." *Nature* 212 (5060): 339–342.

———. 1967. "Prehistoric overkill." In *Pleistocene extinctions: The search for a cause*, edited by P. S. Martin and H. E. Wright Jr., 75–120. New Haven: Yale University Press.

———. 1984. "Prehistoric overkill: The global model." In *Quaternary extinctions: A prehistoric revolution*, edited by P. S. Martin and R. G. Klein, 354–403. Tucson: University of Arizona Press.

Martin, P. S., and R. G. Klein. 1984. *Quaternary extinctions: A prehistoric revolution*. Tucson: University of Arizona Press.

Martin, P. S., and D. W. Steadman. 1999. "Prehistoric extinctions on islands and continents." In *Extinctions in near time: Causes, contexts, and consequences*, edited by R. D. E. MacPhee, 17–55. New York: Kluwer Academic/Plenum.

Niklas, K. J. 1994. *Plant allometry: The scaling of form and process*. Chicago: University of Chicago Press.

Patterson, B. D., G. Geballos, W. Sechrest, M. Toghelli, G. T. Brooks, L. Luna, P. Ortega, I. Salazar, and B. E. Young. 2004. *Digital distribution maps of the mammals of the Western Hemisphere*. Version 1.0. Nature Serve 2003. Cited February 2004. Available from http://www.natureserve.org/getData/mammalmaps.jsp.

Peters, R. H. 1983. *The ecological implications of body size*. Cambridge: Cambridge University Press.

Smith, F. A., J. H. Brown, J. P. Haskell, S. K. Lyons, J. Alroy, E. L. Charnov, T. Dayan, B. J. Enquist, S. K. M. Ernest, E. A. Hadly, K. E. Jones, D. M. Kaufman, P. A. Marquet, B. A. Maurer, K. J. Niklas, W. P. Porter, B. Tiffney, and M. R. Willig. 2004. "Similarity of mammalian body size across the taxonomic hierarchy and across space and time." *American Naturalist* 163 (5): 672–691.

Smith, F. A., S. K. Lyons, S. K. M. Ernest, and J. H. Brown. 2008. "Macroecology: More than the division of food and space among species on continents." *Progress in Physical Geography* 32 (2): 115–138.

Smith, F. A., S. K. Lyons, S. K. M. Ernest, K. E. Jones, D. M. Kaufman, T. Dayan, P. A. Marquet, J. H. Brown, and J. P. Haskell. 2003. "Body mass of late Quaternary mammals." *Ecology* 84 (12): 3403–3403.

Strahan, R. 1995. *Mammals of Australia*. . Washington, DC: Smithsonian Institution Press.

Stuart, A. J. 1999. "Late Pleistocene megafaunal extinctions: A European perspective." In *Extinctions in near time: Causes, contexts, and consequences*, edited by R. D. E. MacPhee, 257–270. New York: Kluwer Academic/Plenum.

Surovell, T., N. Waguespack, and P. J. Brantingham. 2005. "Global archaeological evidence for proboscidean overkill." *Proceedings of the National Academy of Sciences of the United States of America* 102 (17): 6231–6236.

Wilson, D. E., and D. M. Reeder. 1993. *Mammal species of the world: A taxonomic and geographic reference*. 2nd ed. Washington, D.C: Smithsonian Institution.