

Similarity of Mammalian Body Size across the Taxonomic Hierarchy and across Space and Time

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ABSTRACT: Although it is commonly assumed that closely related animals are similar in body size, the degree of similarity has not been

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examined across the taxonomic hierarchy. Moreover, little is known about the variation or consistency of body size patterns across geographic space or evolutionary time. Here, we draw from a data set of terrestrial, nonvolant mammals to quantify and compare patterns across the body size spectrum, the taxonomic hierarchy, continental space, and evolutionary time. We employ a variety of statistical techniques including “sib-sib” regression, phylogenetic autocorrelation, and nested ANOVA. We find an extremely high resemblance (heritability) of size among congeneric species for mammals over ~18 g; the result is consistent across the size spectrum. However, there is no significant relationship among the body sizes of congeneric species for mammals under ~18 g. We suspect that life-history and ecological parameters are so tightly constrained by allometry at diminutive size that animals can only adapt to novel ecological conditions by modifying body size. The overall distributions of size for each continental fauna and for the most diverse orders are quantitatively similar for North America, South America, and Africa, despite virtually no overlap in species composition. Differences in ordinal composition appear to account for quantitative differences between continents. For most mammalian orders, body size is highly conserved, although there is extensive overlap at all levels of the taxonomic hierarchy. The body size distribution for terrestrial mammals apparently was established early in the Tertiary, and it has remained remarkably constant over the past 50 Ma and across the major continents. Lineages have diversified in size to exploit environmental opportunities but only within limits set by allometric, ecological, and evolutionary constraints.

Keywords: heritability, macroecology, evolution, Cenozoic, niche differentiation.

For there is a limit of size in all animals.
(Aristotle, *De Generatione Animalium*)

Body size is the most obvious and fundamental characteristic of an organism and accordingly has long been a subject of interest. At least since the time of Aristotle, scientists and philosophers alike have been intrigued by the enormous variation in the body size of living organisms

spanning some 24 orders of magnitude (Peters 1983; Schmidt-Nielsen 1984; Niklas 1994). The influence of an organism's size goes beyond its physical footprint in the ecosystem, however; many fundamental features of life history, ecology, and evolution scale nonlinearly with size (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). In recent years, considerable research has gone into describing allometric relationships and into developing a theoretical underpinning to explain them (Charnov 1993; West et al. 1997, 1999).

Although scientists now have a clearer understanding of the consequences of being a certain size, we have yet to understand how the complex interactions between intrinsic structure and function, environment, and historical and/or phylogenetic evolution interact to result in particular body sizes. Certainly the range and mode of body size of a taxonomic or functional group must reflect underlying allometric, ecological, and evolutionary constraints. Just what these constraints are, however, and how pervasive they are over evolutionary time or how consistent over geographic space remains unclear. Here we describe a study undertaken to investigate the influence of environmental conditions and historical and/or evolutionary constraints on body size. We examine the repeatability (or heritability) of body size across a variety of spatial, temporal, and taxonomic scales. Our study focuses on mammals because body size is easily characterized and data can be compiled readily, and moreover, taxonomic relationships for the entire class have been established (Wilson and Reeder 1993).

We first determine the repeatability or heritability of body size within the taxonomic hierarchy. How similar in body size are species within a genus or families within an order? Several studies have found that mammalian body size is highly heritable from ancestor to descendant (e.g., Galton 1889; Sumner 1932; Falconer 1973; Rutledge et al. 1973; Leamy 1988), and so we might expect closely related species or genera also to be similar in size. Further, allometric scaling laws may restrict size-related variation unless evolutionary innovations in body plan and physiology accompany substantial changes in body size. Conversely, selection pressures to avoid competition with relatives or to exploit new resources could lead to divergent body sizes. Directional selection has been invoked to explain patterns of spatial and temporal variation within species (e.g., Grant et al. 1976; Lomolino 1985; Grant and Grant 1989; Lister 1989; Roth 1990; McShea 1994; Smith et al. 1995, 1998; Dayan and Simberloff 1998; Smith and Betancourt 1998; Carroll 2001), and it may affect interspecific variation as well (Kappeler and Heymann 1996). There is ample evidence that mammals have the capacity to respond to directional selection with large, rapid changes in body size (Lister 1989; Roth 1990). Within a few hundred genera-

tions, for example, artificial selection has produced breeds of dogs and horses that differ in body mass by about two orders of magnitude. Moreover, given sufficient time and genetic variation, random drift could also lead to disparate sizes even among closely related species (Falconer 1989). Thus variation in body size might increase over time as random or selected changes accumulate while lineages speciate and diversify.

Second, we investigated the influence of body size on the degree of resemblance among congeners. Mammals at either end of the body mass spectrum (e.g., <10 g or >10⁶ g) may be approaching physiological and/or biomechanical limits on size, shape, and life-history processes (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Charnov 1993; West et al. 1997, 1999). These biomechanical, thermoregulatory, and other fundamental constraints on the very smallest and very largest mammals may restrict the direction of evolutionary alterations in body size or shape. The high metabolic rate characteristic of extremely small mammals, for example, necessitates a more or less continuous supply of high-quality food. Consequently, most small mammals are insectivores, specializing on a ubiquitous and high-energy food source. Other trophic strategies may not be viable without substantial modifications of body shape and size. Hence, we might expect to see more tightly constrained body size in these animals, leading to greater similarity among congeners than for mammals of intermediate size.

Third, we examine the influence of mammalian phylogeny on the pattern and similarity of body size. By examining the similarity of congeners within and across the taxonomic hierarchy, we characterize the body size "space" occupied by mammalian genera, families, and orders. Specifically, we ask whether taxa tend to occupy narrowly defined and evolutionarily conserved body size niches with little overlap or whether they overlap extensively. Is there something intrinsic to mammals in the order Rodentia, for example, that results in a weight of ~10–1,000 g? How many other orders also contain animals found within this body size range?

Fourth, we examine the patterns of mammalian body size across four different continents—North America, South America, Africa, and Australia—that differ substantially in species composition, environment, and geologic history. Given the almost complete lack of species overlap among these continents and their very divergent geological histories, we expect few consistencies in the overall body size distribution of animals on each continent and even fewer at different levels of the taxonomic hierarchy. Nonetheless, recent studies of North and South America demonstrate similarities in the overall body size distribution of mammals (Marquet and Cofre 1999; Bakker and Kelt 2000). We compare these patterns at the

continental scale and also at each level of the taxonomic hierarchy.

Finally, we use an extensive compilation of fossil data for North America (Alroy 1998) to examine the evolutionary history of mammalian body size over the past 60 Ma. At the beginning of the Cenozoic, mammals were still small, largely forest-dwelling creatures (Janis 1993). By the end of the Paleocene, mammals were already becoming much larger and more diverse; all major groups were present by the Eocene. How rapidly after this radiation of eutherian mammals did the body sizes of lineages converge on the spatial patterns seen today? Have the various mammalian orders maintained the same overall body size space despite the very disparate climatic and vegetative regimes characteristic of different epochs? Or has the range of body size of each mammalian order changed over time in response to differing abiotic and biotic conditions?

Material and Methods

Body Size Data and Taxonomy

Our analyses draw on a recently compiled comprehensive database of mammalian body mass, distribution, and taxonomy (MOM version 3.1; Smith et al. 2003). We assembled standardized data on body mass and taxonomy for most species of extant terrestrial nonvolant mammals in North America, South America, Australia, and Africa using a variety of literature sources, mammalian species accounts, and unpublished field notes (Kingdon 1982; Eisenberg 1989; Emmons 1990; Brown and Nicoletto 1991; Redford and Eisenberg 1992; Wilson and Reeder 1993; Silva and Downing 1995; Eisenberg and Redford 1999; Marquet and Cofre 1999; for individual species accounts, see the American Society of Mammalogy Web site at <http://www.mammalsociety.org>). We were unable to obtain reliable mass data for a small subset of rare species (~150); those are excluded from the analysis. For each of the 1,892 other species, a single body mass estimate was derived from the various sources by averaging male and female body mass in grams. The body mass range represented in our data varied from 0.25 log units (1.8 g) for the shrew *Suncus etruscus* to 6.6 log units (3,940,034 g) for the African elephant *Loxodonta africana*. For mammals on the North American continent, we were able to obtain fossil data for the past 60 Ma, spanning the radiation of mammals from the K/T extinction event to the present (<http://www.nceas.ucsb.edu/~alroy/nampfd.html>). Alroy (1998, 1999, 2000) translated measurements of first molars for North American fossil mammals into estimates of body mass using regression equations for each mammalian order. The database includes more than 23,000 molars and 1,969 species. The fossil mammal data compiled by Alroy

represent one of the only data sets for an assemblage over a long period of evolutionary time; no comparable data are available for South America, Australia, or Africa. All body masses were log transformed before analysis.

We used the taxonomy of Wilson and Reeder (1993), which is the most comprehensive one currently available. At present, there is no fully resolved phylogeny for all mammals. While there is a family-level phylogeny that includes most placental orders (Liu et al. 2001), and phylogenies have been proposed for several clades (Butler 1988; Jaeger 1988; Hooker 1989; Marshall et al. 1990; Schneider et al. 1993; Wyss and Flynn 1993; Milinkovitch et al. 1994; Nedbal et al. 1994), few species-level supertrees (consensus trees) exist for mammals (but see Purvis 1995; Bininda-Emonds et al. 1999; Jones et al. 2002). Moreover, many existing phylogenies are resolved only to the familial level, leaving the upper branches of the tree as unresolved polytomies, which is insufficient for our purposes (i.e., Butler 1988; Liu et al. 2001).

Implicit in our use of the Wilson and Reeder taxonomy as a proxy for phylogeny are a number of underlying assumptions. First, we assume that the relationships of species within genera, genera within families, and families within orders are represented by hard polytomies. Second, we assume that the evolutionary age of a genus or family is unrelated to the pattern of body size diversification within it. Indeed, our analysis is likely to underestimate heritabilities because a polytomy assumes that all congeneric taxa are equally old and equally related. Clearly, older species within a taxon have had more time to differentiate and may well exhibit more divergent body sizes. Third, we assume that evolutionary age and the number of species within a taxon are not related. This is in opposition to the notion of cladogenesis, which underlies many studies, where lineages continually speciate but extinctions are largely ignored. Note, for example, that the oldest mammalian order is Monotremata, which contains only three extant species. Within the placental mammals, geological ranges of species-rich genera (>15 species) vary from <2 to >20 Ma (Maglio and Cooke 1978; Mones 1986; <http://www.nceas.ucsb.edu/~alroy>; <http://www.angellis.net>). While these assumptions introduce some noise into our analysis, they should lead to underestimates of the similarity of congeneric taxa.

Statistical Analyses

Similarity of Body Size within Genera and across the Body Size Spectrum. We examined the degree of similarity among congeneric species by conducting a correlation analysis of the pooled mammalian database (e.g., Jablonski 1987). For the handful of species found on more than one continent, we randomly picked one of the masses assigned, and the

duplicates were excluded from the analysis. We were left with 1,844 species representing 548 genera, of which 278 were monotypic. We began by selecting one random species pair for each genus containing two or more species. These were plotted against each other, and a regression was conducted through the values. We employed both least squares and Type II regressions; results were similar in both instances. Species were as just as likely to be smaller or larger than their siblings, so the variation in the x and y direction is approximately equivalent. Because these species pairs represent the analogue of “full sibs” in quantitative genetics (Falconer 1989), the correlation between them is analogous to broad-sense heritability or resemblance. We repeated the analysis in a number of ways. First, we plotted half as many species pairs as were present in each genus. However, genera with odd numbers of species were underrepresented. A genus with three species, for example, could only yield one species pair without redundancy. Second, we plotted as many species pairs as there were species in the genus. This had the advantage of weighting each species equally; all were paired twice. Although more diverse genera had a greater influence, this scaled arithmetically (i.e., ditopic genera had two pairs, tritopic genera had three pairs, etc.). Third, we plotted all possible pairwise combinations of species within a genus. In this latter analysis, species-rich genera had an increasingly larger influence on the overall pattern. Finally, we repeated each of these analyses for discrete logarithmic body size categories (0.25–1.25, >1.25–2.25, >2.25–3.25, etc.), so that we could determine whether the degree of resemblance between relatives varied with body size. When assigning species pairs into discrete body size categories, the category a pair was assigned to was determined by the body mass of the first member of the pair.

Similarity of Body Size across the Taxonomic Hierarchy. To pictorially examine the overlap of body size across the taxonomic hierarchy on each continent, we plotted log body mass versus the position in the taxonomic hierarchy (species, genus, family, and order). Species-specific masses were plotted in the first column, and values for each successively higher level of the hierarchy were calculated by averaging the log-transformed values of the lower level. Generic values, for example, were obtained by averaging species means, family values were obtained from averaging generic means, and ordinal values were obtained by averaging family means. For each mammal species, the values at each level of the hierarchical classification were connected by a line. The resulting diagram depicted variation in size within each taxon as well as overlap with other taxa at the same hierarchical level.

We quantified the partitioning of body size variation among the hierarchical levels in several ways, which pro-

vided different perspectives into body size evolution. First, we estimated the phylogenetic correlation for North American mammals using the spatial autocorrelation statistic Moran's I (Gittleman and Kot 1990; Gittleman et al. 1996). This is widely employed to assign phylogenetic correlation among taxonomic levels (i.e., Martins and Hansen 1997). When standardized, values of Moran's I vary from +1 to -1. Positive values indicate that a trait (e.g., body size) at a particular phylogenetic level is more similar than random, whereas negative values indicate that they are more different. More details can be found in Gittleman and Kot (1990) and Gittleman et al. (1996). Second, we conducted mixed-model nested ANOVA on the data for each continent, as has been done in the life-history literature (i.e., Pagel and Harvey 1988; Read and Harvey 1989). Body mass was the dependent variable, and the taxonomic classifications (genus, family, order) were the nested independent variables. The “Proc Mixed” procedure in SAS was used because it can handle unbalanced designs (SAS Institute 1989).

Both Moran's I and nested ANOVA tests were conducted on the actual data as well as on several null models. Our purpose in devising null models was to provide a framework for the interpretation of our results. Thus we chose them to span the spectrum of possibilities of body size evolution, ranging from a perfectly ordered hierarchy to a completely randomized one. The ordered hierarchy was obtained by subjecting the log-transformed data to cluster analysis, which reassigned taxonomic affiliations so that at each level, taxa of most similar size were members of the same taxon at the next highest level (SAS Institute 1989). The number of orders, families, genera, and species were thus constrained to be the same as in the real data. This necessarily resulted in maximal partitioning of the body size spectrum. We view this model as representing the extreme of possible phylogenetic inertia, where the body size of an animal perfectly reflects its taxonomic affiliations.

Randomized hierarchies were created by randomly reassigning Latin binomials (without replacement) to body masses contained in our data set. Then on the basis of these binomials, the species were assigned to genus, family, and order. Thus any species potentially could have been assigned any body mass within each continental pool, although some sizes were more likely than others to be selected because the randomizations were constrained by the real distribution. We maintained the same number of taxa at each hierarchical level as were present in the real data. This model represents an evolutionary scenario where body size is completely independent of phylogeny and any species can evolve to any available body size within the seven orders of magnitude. Although there is only one perfectly ordered hierarchy, there are many possible ran-

domized ones, so we repeated the randomization procedure 100 times.

Body Size Diversification across Geographic Space. To examine the similarity of body size across geographic space, we plotted the log-transformed frequency distributions for each continent as well as for the pooled data. Frequency distributions were also plotted for each mammalian order within each continent as well as for the pooled mammalian orders. For each continent and taxonomic group, we calculated the moments and other descriptive statistics using standard procedures in SAS. Body size distributions between continents were directly compared using Mann-Whitney and Kolmogorov-Smirnov two-sample tests and with a series of randomizations. Kolmogorov-Smirnov tests are sensitive to differences in skew and kurtosis as well as location, so they potentially could yield additional insights into similarities and differences in overall size distributions among continents and orders (Sokal and Rohlf 1981). Our aim in the simulations was to determine whether the distributions on each continent were more similar than expected on the basis of chance. Thus we measured the similarity among various continental distributions and compared the measured statistical distance with a frequency distribution of randomly derived distributional differences. We did this in three ways. First, we compared each continent with randomly constructed simulated continents drawn from the entire species pool. The number of species drawn was equivalent to that of the continent in question. For each of the 10,000 randomizations, a similarity index with the actual continental distribution was computed. We then plotted a frequency distribution of these indices and quantified the proportion of randomizations that fell above or below the actual observed similarities. This allowed us to compute the likelihood that the actual similarity value would arise by chance. Although a number of different metrics could be used to measure similarity, we chose 1-D ($D =$ the Kolmogorov-Smirnov statistic) because the behavior of this statistic is reasonably well characterized. The test measures the maximum difference between two distributions, which is a measure of dissimilarity. Thus we computed similarity by subtracting this metric from 1.

Second, we directly contrasted each pair of continents. We randomly drew from the entire species pool sufficient animals to construct two artificial continents, each containing the appropriate number of species. A similarity index between these two continents was computed, and the procedure was repeated 10,000 times. The actual computed similarity index was compared with the overall distribution of similarity indices as described above. This entire simulation was repeated six times, representing each

pairwise combination of continents (i.e., Africa vs. North America, Africa vs. South America, Africa vs. Australia, North America vs. South America, North America vs. Australia, South America vs. Australia).

Third, we repeated the entire 100,000 simulations described above (comparing each continent against random reconstructions and comparing each pair of continents) but restricted species draws so that the number of species drawn from each order was constrained to that contained within the actual continental distributions. Thus we conserved the unique taxonomic hierarchy and structure of each continent. Finally, all simulations were repeated yet again so that draws were conducted with and without replacement.

Body Size Diversification across Evolutionary Time. We binned the North American fossil mammal database into 10-Ma increments and calculated a mean for each order present. Subdivision of the data into smaller time intervals was hampered both by the coarse resolution of the dating and by the desire to maintain reasonable sample sizes. The average body mass of each order was plotted versus the time bin; orders were connected by dotted lines to highlight body size trajectories. Note that because of the substantial taxonomic turnover during the Cenozoic, not all orders were present at all time intervals. Further, the species composition of each order often differed substantially even between successive time slices. Ordinal means for contemporary mammals on the three major continents were also plotted for comparative purposes.

Research Questions. These techniques were used to address the five major questions outlined in the introduction: How similar is mammalian body size among congeneric species? Does similarity of body size vary across the size spectrum? How similar is body size across the taxonomic hierarchy (genus, family, and order) for a given continent? How do patterns of body size vary among the major continents that differ in taxonomic composition and degree of historical isolation? and How has the diversity of North American mammal body sizes changed over evolutionary history?

Results

Similarity among Congeneric Species and across the Size Spectrum

For the most part, the body sizes of congeneric species within a genus were extremely similar. Overall we estimated the broad-sense heritability or resemblance of body size to be ~ 0.94 (fig. 1A). The result was quite robust; we obtained nearly identical heritability (0.93–0.95) estimates

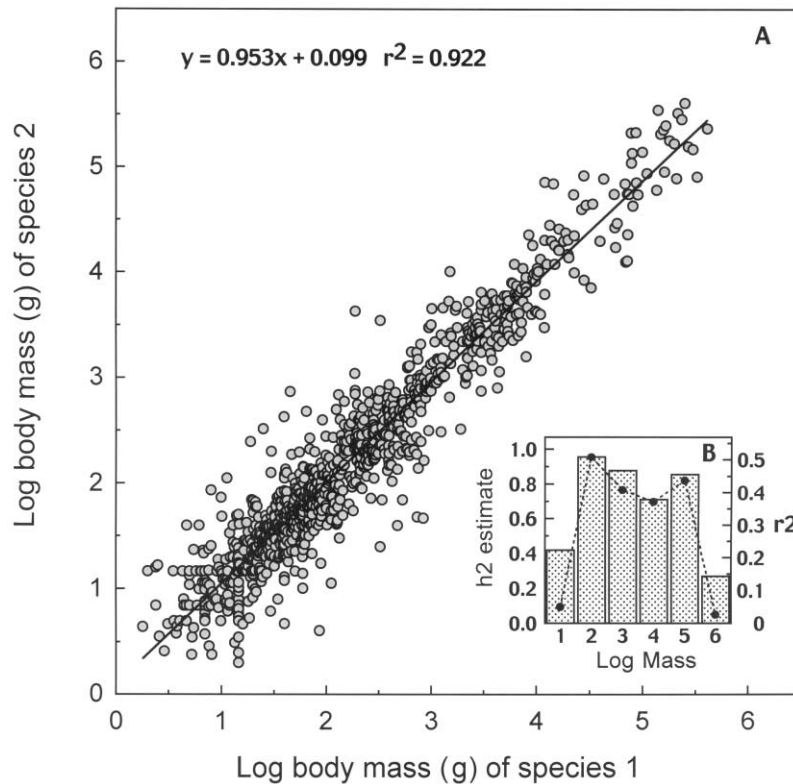


Figure 1: “Sib-sib” analysis of mammalian species. *A*, Regression of species pairs for all genera with more than two species. If five species are present within a genus, then five random species pair combinations were plotted. Results were very similar regardless of whether a single species pair per genus or all potential pairwise combinations were used. The broad sense heritability for “full sibs” is estimated by the correlation coefficient; this is equivalent to multiplying the estimate of the slope by the ratio of the standard deviations for each variable. *B*, Heritability estimates obtained for discrete logarithmic size categories. Also shown are the r^2 values for each regression (solid circles connected with dotted line for clarity). Units shown indicate the mean body size within the bin. The first bin, for example, contains mammals from 0.25 to 1.25 log units (~ 1.8 – 18 g); the second, from 1.25 to 2.25 (>18 – 180 g); and so forth. Note that the heritability estimates for mammals >1.25 log units (>18 g) are consistently high (~ 0.9) with more than half the variation explained by the regression. Small mammals (<1.25 log units), however, not only yield a much lower estimate, but very little variation is explained by the relationship. Although not shown, for example, the bin from 0.25 to 1.0 (1.8 – 10 g) explains $<4\%$ of the variation. Values for the largest bin should be viewed with caution because they may be the result of small sample size.

regardless of whether the analysis was conducted with all possible species pairs within a genus, as many species pairs as there were species within a genus, or a single arbitrarily selected species pair. Moreover, we assumed a polytomy (i.e., all congeners were equally related), whereas actually they exhibit different degrees of relatedness. Not incorporating a completely resolved phylogeny should increase the variation present in our data and might well result in a reduced estimate of heritability.

When regression analysis was conducted separately for each \log_{10} body size bin, however, we found a difference in the degree of resemblance among congeners with body size (fig. 1*B*). Although the heritability estimate was strikingly consistent for animals larger than ~ 18 g (>1.25 log

units), averaging over 0.9, this was not true for the smallest mammals. We found no significant relationship among the body sizes of congeneric species for the very smallest mammals (i.e., the bin from 0.25 to 1.25 log units; ~ 1.8 – 18 g). The similarity between congeneric species and the explained variation decreased even further if only mammals <10 g (1 log unit) were included (h^2 estimate = 0.378, $r^2 = 0.039$, $df = 80$).

Because this was surprising and potentially important, we conducted a number of tests to verify the validity of this result. First, we examined the influence of sample size by calculating the correlation between the sample size and either the heritability estimate or the correlation coefficient. There was no relationship in either case; the low

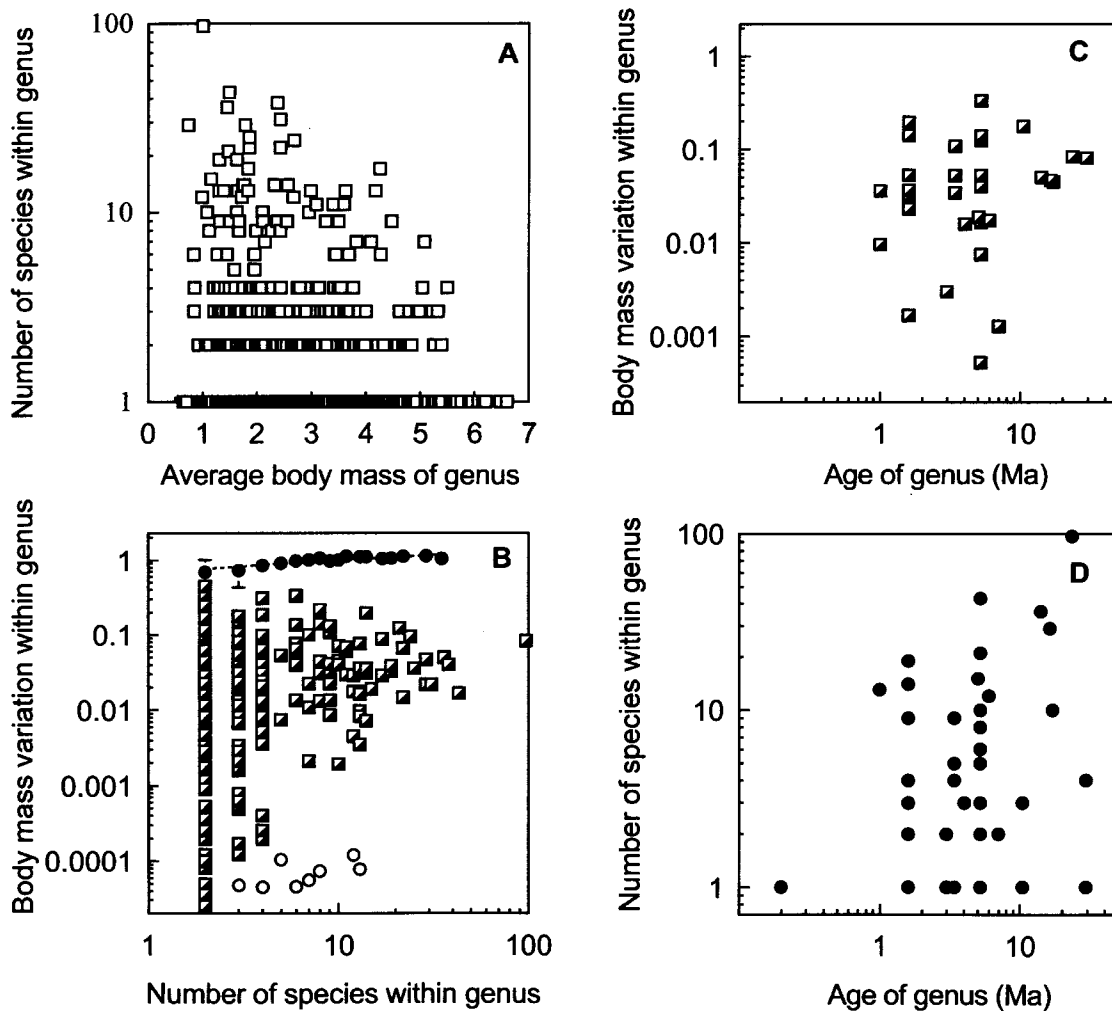


Figure 2: Exploration of the influence of taxon age and diversity on body size variation. *A*, The number of species within mammalian genera plotted as a function of the average body size of the genus. Note that while genera containing 20 or fewer species are found across the entire body size spectrum, the most species-rich genera are found at smaller body sizes. *B*, Body mass variation within each genus plotted as a function of the number of species within the genus. The real data (*partially filled squares*) are shown compared with those obtained by the randomizations (*solid circles*) and the ordered data (*open circles*). For randomizations, the mean of 100 runs is shown; error bars represent the standard deviation. There is no relationship between body size variation and genera diversity (regression analysis, $P > .05$). Ditypic genera are not only the most variable overall but also contain genera with the greatest body size variation within them. *C*, Body mass variation as a function of the age of the genus. Only genera containing species of 1.25 log units or less are included. There is no tendency for older genera to exhibit increased body size divergence (regression analysis, $P > .05$). *D*, Species diversity of genera as a function of age. There is no relationship between the age of the genus and its species diversity (regression analysis, $P > .05$).

estimate of heritability at extremely small size was not a consequence of small samples ($P > .05$, $df = 5$). Note that our data set contained 235 species of less than 17.8 g (1.25 log units) from five different mammalian orders and from all four continents.

Second, we examined the potential influence of our binning technique on our results by rerunning the analysis using a “sliding window” where bin size increased in 0.1 log units. For example, the first bin covered the range

from 0.25 to 1.25 log units, the second from 0.35 to 1.35, and so forth across the entire body size spectrum. Regressions were conducted independently for each size bin. Again, our results were robust, with low heritability estimates and little explained variation consistently found for the smallest size classes. The similarity between congeneric species and the r^2 values increased rapidly and converged by the bin averaging 1.35 log units (0.85–1.85).

Third, we explicitly examined the potentially dispro-

Table 1: Results of nested ANOVAs on mammalian body mass for each continent

Variance source	Mean square	Variance component	Percentage of total variance
North America:			
Order	39.16	1.25	71.62
Family	4.24	.26	14.86
Genus	.70	.20	11.30
Error	.04	.04	2.23
Total	1.09	1.74	100.00
South America:			
Order	30.60	.61	56.34
Family	5.30	.32	29.93
Genus	.42	.11	10.61
Error	.03	.03	3.11
Total	.75	1.08	100.00
Africa:			
Order	80.86	1.80	74.73
Family	3.62	.41	16.92
Genus	.38	.15	6.34
Error	.05	.05	2.01
Total	1.96	2.41	100.00
Australia:			
Order	21.78	.84	46.36
Family	3.18	.72	39.46
Genus	.37	.23	12.76
Error	.03	.03	1.42
Total	1.49	1.82	100.00

Note: Because this was a mixed-model nested ANOVA with unequal sample sizes, significance tests could not be performed.

portionate influence that the most species-rich genera might have on our results. Although genera with up to 25 species are found across the entire body size spectrum, the most species rich are found at body masses from 1 to 3 log units (10–1,000 g; fig. 2A). The most species-rich mammalian genus is *Crociodura*, a group of ~180 small insectivores found primarily in Africa and Eurasia (Wilson and Reeder 1993). Although ~97 are extant in Africa, we were able to obtain species-specific body masses for only 45 of these. As lineages speciate to leave more descendants and adapt to different environmental conditions, the range of body size might be expected to increase. An increase in variance with number of species per taxon might be expected even from a random model of evolutionary change (Gould 1988). Thus a more species-rich taxon might be predicted to exhibit a larger range of body mass. We examined the validity of this prediction in several ways. First, we reran our sliding window excluding all genera with more than 25 species. Although this potentially complicated the interpretation because of a decrease in sample size, we nonetheless obtained the same results; estimates

of heritability were low, and little variation was explained in the smaller size classes. Again, results converged rapidly. Second, we plotted the variation of body size as a function of the number of species in the genus (see table A1 in the online edition of the *American Naturalist*). We compared this with values obtained for the ordered and randomized data sets (fig. 2B). There was no significant trend in the amount of variation in a genus with species abundance. In fact, the genera with the most variation tended to be those with the fewest species (ditypic or tritypic). Thus as lineages diversified, the descendants did not occupy a greater range of body size. Whether this is because of a lack of evolutionary flexibility or whether “outliers” have a greater probability of extinction is unclear. As expected, the randomized data displayed a pattern of increased variance with species abundance, while the perfectly ordered data displayed very little. Thus the real data consistently fell between the randomized and the perfectly ordered data, suggesting that the process of evolutionary differentiation was neither random nor completely constrained by phylogeny but approximately intermediate between these extremes.

Fourth, we examined the potential influence of evolutionary age of a lineage on the estimated heritability estimate. The two insectivore genera *Crociodura* and *Sorex*, for example, are both fairly old lineages, dating to 23.3 and 16.3 Ma, respectively (Maglio and Cooke 1978). If divergence time does equate with greater species differentiation, it is possible that a low heritability estimate could result if most species within a bin are old. Although this would only add to an underestimate of the high values obtained for larger mammals, it could be a factor resulting in the observed lack of body size similarity for the smaller ones. Thus we examined this only for small body size classes. Using published values in the paleontological literature (Maglio and Cooke 1978 and references therein; Kurten and Anderson 1980; Mones 1986; Alroy 1999; <http://www.angellis.net>; <http://www.nceas.ucsb.edu/~alroy/nampfd.html>), we obtained estimates of origination times for genera containing one or more species with body sizes of 1.25 log units or less (~18 g; see table A1). This included 47 genera. For nine of these, however, we were unable to obtain estimates of the age of first appearance, presumably because they lacked well-developed fossil records. Because the origination dates were generally reported in terms of the epoch (i.e., late Oligocene, middle Miocene, etc.), we assigned standardized dates to these terms (table A1). With a few notable exceptions, most genera of extremely small mammals are fairly young. The mean age of the 38 genera for which we obtained data was 6.75 (± 7.28) Ma (table A1). Longer divergence time clearly does not equate with greater species differentiation; regression analysis indi-

cated that <2% of the variation in body mass was attributable to the age of the genus ($P > .05$, $df = 36$; fig. 2C). The smallest mammal in our database, for example, is *Suncus etruscus*, with a body mass of 1.8 g (Y. Yom Tov, personal communication). This relatively young genus (~5.2 Ma) also contains *Suncus murinus*, which can reach body masses of >100 g (Hasler et al. 1977). Thus the body mass range within *Suncus* exceeds that seen in much older genera (table A1). What role, if any, that selective extinctions may have played is unknown. In contrast to assumptions implicit in many models of cladogenesis, we also did not find a relationship between the age of the genus and the number of species it contains (fig. 2D). Indeed, the oldest small genus is monotypic (i.e., *Acrobates* at 29.3 Ma) and some of the youngest are the most species rich (i.e., *Akodon* at 5.2 Ma; *Sminthopsis* at 1.6 Ma). As a final test, we reran our sliding window excluding the oldest genera (>17 Ma). As expected, we found that removing these lineages did not influence the results. Again, we found low heritability and little variation explained for the smaller size classes and the opposite pattern for the larger sizes (results not shown here). Thus we conclude that the pattern we found—no body size heritability for congeneric species of small size, and high and very consistent heritability for mammals of other sizes—is extremely robust.

Similarity of Body Size across the Taxonomic Hierarchy

Both Moran's I and the nested ANOVA suggested that mammalian body size was highly correlated with evolutionary history (table 1; table A2 in the online edition of the *American Naturalist*; fig. 3). Not only were closely related species within genera significantly more similar in body size than would be expected by chance (Moran's $I = 0.80$, $Z = 20.6$, $P \ll .05$), but this pattern was maintained across the taxonomic hierarchy (i.e., genera within families and families within orders). Interestingly, mammalian orders showed the opposite pattern; they were more dissimilar in body mass than would be predicted from random (Moran's $I = -0.51$, $Z = -52.8$, $P \ll .05$, fig. 3). The nested ANOVA supports this conclusion but from a different perspective. It too suggested that body masses of mammalian orders were significantly divergent (tables 1, A2), confirming the earlier conclusion by Read and Harvey (1989). Moreover, by attributing most of the variation in body size across the taxonomic hierarchy to the ordinal level, the nested ANOVA indicates that genera and families within an order are much more similar to each other than they are to genera or families in other orders. For example, for both North America and Africa, over 70% of the total variance was attributed to the ordinal level and successively less to the familial and generic levels.

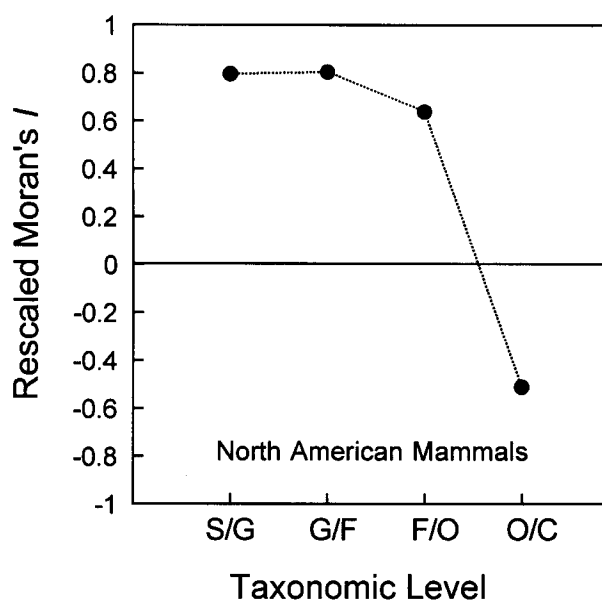


Figure 3: Phylogenetic correlogram illustrating the results of a Moran's I procedure conducted on the body mass of North American mammals. The Y-axis represents rescaled Moran's I (where I is rescaled for comparability across taxonomic levels; see Gittleman and Kot 1990); the X-axis is the taxonomic level, where *S/G* represents trait phylogenetic correlation of species within genera, *G/F* represents genera within families, *F/O* represents families within orders, and *O/C* represents orders within Mammalia. Significance is indicated by values close to ± 1 (Gittleman and Kot 1990), which represent a trait completely phylogenetically correlated (i.e., corresponding to our ordered reconstruction of the data) or completely uncorrelated, respectively. Values of 0 indicate no phylogenetic autocorrelation (i.e., corresponding to our random reconstruction of the data). Note that values at all taxonomic levels are highly significant.

The ordinal level explained somewhat less variance in South America and Australia (~56% and 46%) and the familial level more (~30% and 39%) than on other continents (tables 1, A2). Note that the patterns were strikingly different for both the ordered and randomized reorganizations of the data. In the perfectly ordered data set, >94% of the variation on each continent was attributed to the ordinal level, and the remainder was attributed to family. In contrast, very little variation (<2%) was explained by any taxonomic level in the randomizations (tables 1, A2). These results suggested that mammals within the same order exhibit a limited range of size variation, so that the real data were actually fairly similar to the maximally ordered data set. Further, results were extremely similar for both North America and Africa, and those for South America and Australia showed less precise but qualitative agreement.

Although the nested ANOVA indicated that much of the variation could be attributed to the ordinal level, the statistics generated did not easily permit interpretation of

the complicated pattern of overlap and variance within and between taxonomic levels. By plotting the actual data on a \log_{10} body size axis and then superimposing the taxonomic hierarchy, the full pattern of overlap and variation was depicted (fig. 4; fig. A1 in the online edition of the *American Naturalist*). Both the ordered and randomized reorganizations of the data yielded very different patterns. The ordered data display maximal segregation of species, genera, families, and orders. In contrast, the randomizations showed a central tendency, with most orders clustered in the 100 g–1 kg range (fig. A1). Not only did the randomizations display greatly reduced variation in body size at each successively higher level, but also there was much more overlap at all levels. Although we illustrate only one randomization for North America, this procedure was repeated 100 times for each continent with very similar results. Both the real and the ordered data were similar in spanning a broad and similar spectrum of sizes at each taxonomic level, but they differed conspicuously in that the real pattern had substantial overlap at all levels (fig. A1 vs. fig. 4). Another way to express this pattern is that the species within a limited range of sizes may belong to many genera, families, and orders. In North America, for example, the 50–100-g size range includes 31 species belonging to 10 genera, five families, and four orders; the 5–10-kg category includes 11 species from 11 genera, eight families, and three orders. Such patterns were consistent on other continents as well (fig. 4).

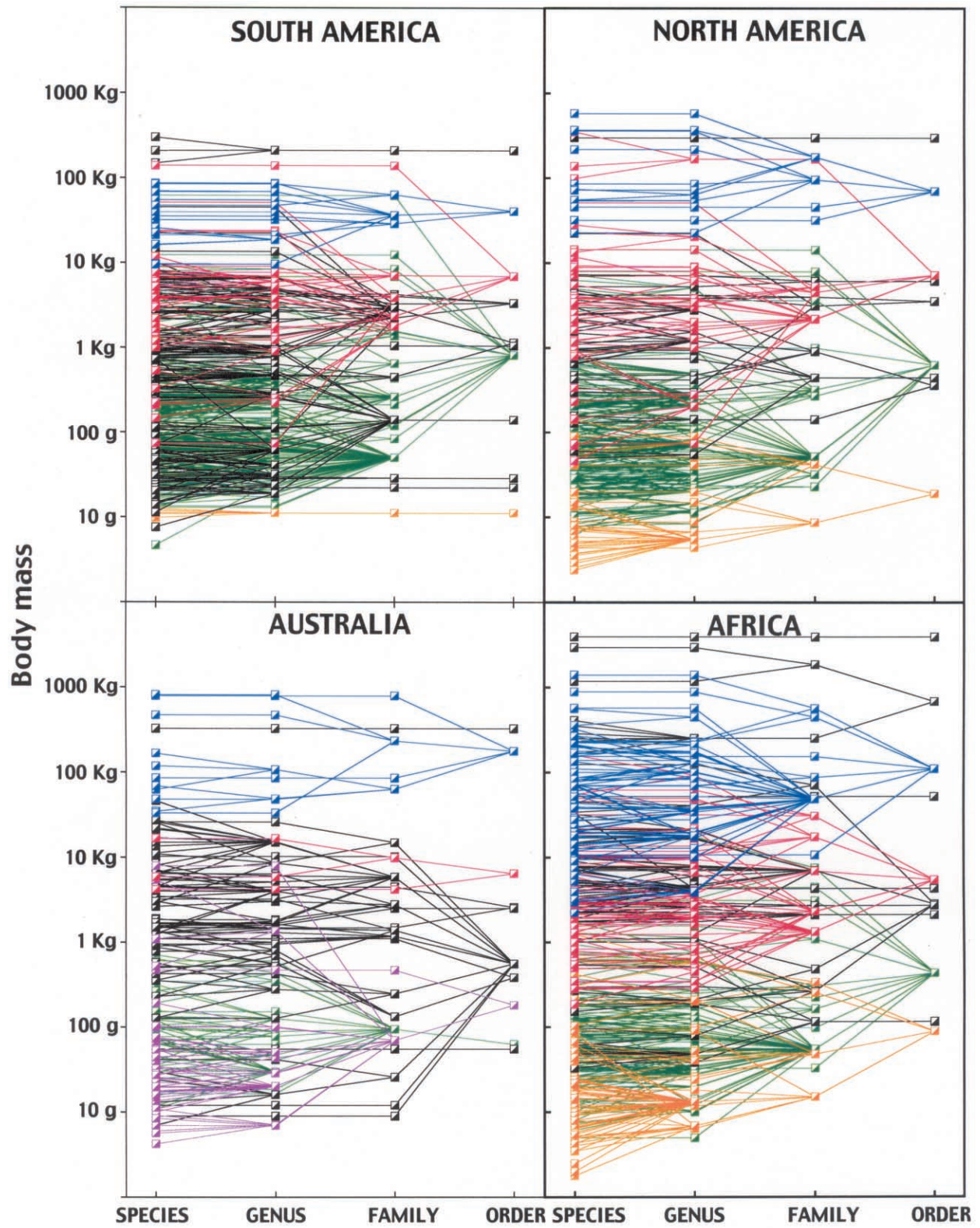
Body Size Diversification across Geographic Space

The overall distribution of mammalian body size was qualitatively similar across all three major continents (fig. 5; fig. A2 in the online edition of the *American Naturalist*). All were strongly right skewed and contained multiple modes (table A3 in the online edition of the *American Naturalist*). The overall size range found on each continent was quite similar (about five orders of magnitude; table A3; figs. 4, A2), with the noticeable exception of Africa. The presence of several groups of large-bodied lineages in Africa, not currently found elsewhere, resulted in a wider range of size than that found on other continents (6.3 orders of magnitude; table A3). Moreover, the greater maximum size also resulted in a flatter, more multimodal distribution (figs. 5, A2), which was significantly different from the other continents (Mann-Whitney *U*-test and Kolmogorov-Smirnov two-sample tests, $P < .001$). Note, however, that both North and South America were influenced to a much greater degree than Africa by the terminal Pleistocene extinctions, which largely targeted megafauna (Martin and Wright 1967). Recent work has demonstrated that there was no significant difference in the overall body size range between Africa and either North or South Amer-

ica when the entire late Pleistocene mammalian fauna is considered (i.e., the extinct mammals are added to the current distribution; Lyons et al. 2004). Thus past anthropogenic influences are likely the reason for any differences found today. There was also a significant difference between the body mass distributions of North and South America (Kolmogorov-Smirnov two-sample test, $P < .001$). Kolmogorov-Smirnov two-sample tests are known to be sensitive to differences in skew and kurtosis as well as in location (Sokal and Rohlf 1981). Thus a lack of quantitative similarity between the continental distributions may derive from significant differences in species richness and kurtosis between continents (table A3; fig. 5).

The simulation analysis also yielded significant differences between each continent and the overall species pool and, moreover, between all pairwise comparisons of continents. Although the similarity indices for the continent pairs were very high ($1 - KS \approx 0.8$ for all comparisons), those for the random continents were almost identical (mean of 10,000 simulations for each comparison yielded a mode of >0.96 for each). Thus random simulations were always very similar to the actual overall species pool. This meant that any small differences in the actual location of the modes translated into significant differences from the random and from other continents (fig. A2). These high similarities persisted when simulations were restricted by order and when draws were conducted with or without replacement. The large numbers of species contained in each distribution (~ 700) and the large proportion of the overall species pool drawn at one time ($\sim 25\%$ – 30%) may have contributed to the high similarities obtained in the random simulations.

Despite quantitative differences in the overall distributions, the moments and other descriptive statistics characterizing the individual mammalian orders were generally similar across continents (table A3). The mean body mass for orders shared across continents is statistically indistinguishable, and similar patterns hold for the median, mode, and range (*t*-tests conducted on values presented in table A3). Thus the differences in the overall body mass distribution among the continents are probably attributable to the unique orders found on each (table A3; figs. 4, 5, A2). That the mean body size of each order is the same is especially interesting because there is little overlap in taxonomic composition. That is, no mammal occurred on all continents and even among the three major continents, only seven mammalian orders were shared. For example, although the body size of the order Carnivora was statistically indistinguishable among continents (3.6, 3.6, and 3.5 log units for North America, South America, and Africa, respectively), each mean resulted from a vastly different species pool. No carnivores are shared between



Position in taxonomic hierarchy

South America and Africa, only two species occur on both North America and Africa, and despite close proximity, North and South America share only 11 species, or ~26% of their carnivore fauna (table A3). For the most part, ordinal distributions were right skewed, although the degree varied (table A3; fig. 5). We did find some differences in the degree of asymmetry and kurtosis among continents even when only those orders with large sample sizes (>20 animals) are considered. This probably reflects the subtle differences in the overall distribution that were suggested by the simulation results. Note that we have excluded Australia from analysis of ordinal patterns because of the extremely limited taxonomic overlap with the other continents, especially if only nonintroduced species are considered.

The overall distribution for Australia was significantly different from that of the three much larger continents (fig. 5; Kolmogorov-Smirnov test, $P < .02$; similarity index from simulations ranged from 0.827 to 0.877). This difference persists even when late Pleistocene mammalian fauna are added (Lyons et al. 2004). Moreover, Australia supports a much reduced mammalian diversity compared with the three larger continents ($N = 212$ vs. 433, 694, and 543 species for North America, South America, and Africa, respectively), although the range of body size found is approximately the same as on the others (table A3).

Body Size Diversification across Evolutionary Time

The pattern of body size variation was also very similar across evolutionary time (fig. 6). By 50 Ma, there were orders of mammals representing nearly the entire range of body sizes seen today (Alroy 1998, 1999). The size spectrum established during the Eocene radiation of eutherian mammals was maintained throughout the remainder of the Cenozoic, although many orders became extinct and others originated. Note that by 10 Ma, North America supported a distribution of ordinal body sizes very similar to that seen on all three major continents today (fig. 6). There were two major exceptions. First, at 10 Ma, North America had representatives of Proboscidea, with body masses of approximately 10^6 g. Elephants of this size still persist in Africa, but in North and South America they were extirpated in the early Holocene, presumably because

of human hunting (Martin and Wright 1967; Kurten and Anderson 1980; Alroy 2001). Second, at 10 Ma, orders with average body sizes between approximately 10^2 and 10^4 g were absent from North America. The gap in this size range may simply reflect the problems of resolution and sampling inherent in the fossil record. However, ancestors of some mammals in that size range immigrated from South America to North America ~3 Ma after the emergence of the Central American land bridge (Stehli and Webb 1985). Perhaps their successful colonization was due in part to a paucity of native North American species in that size range.

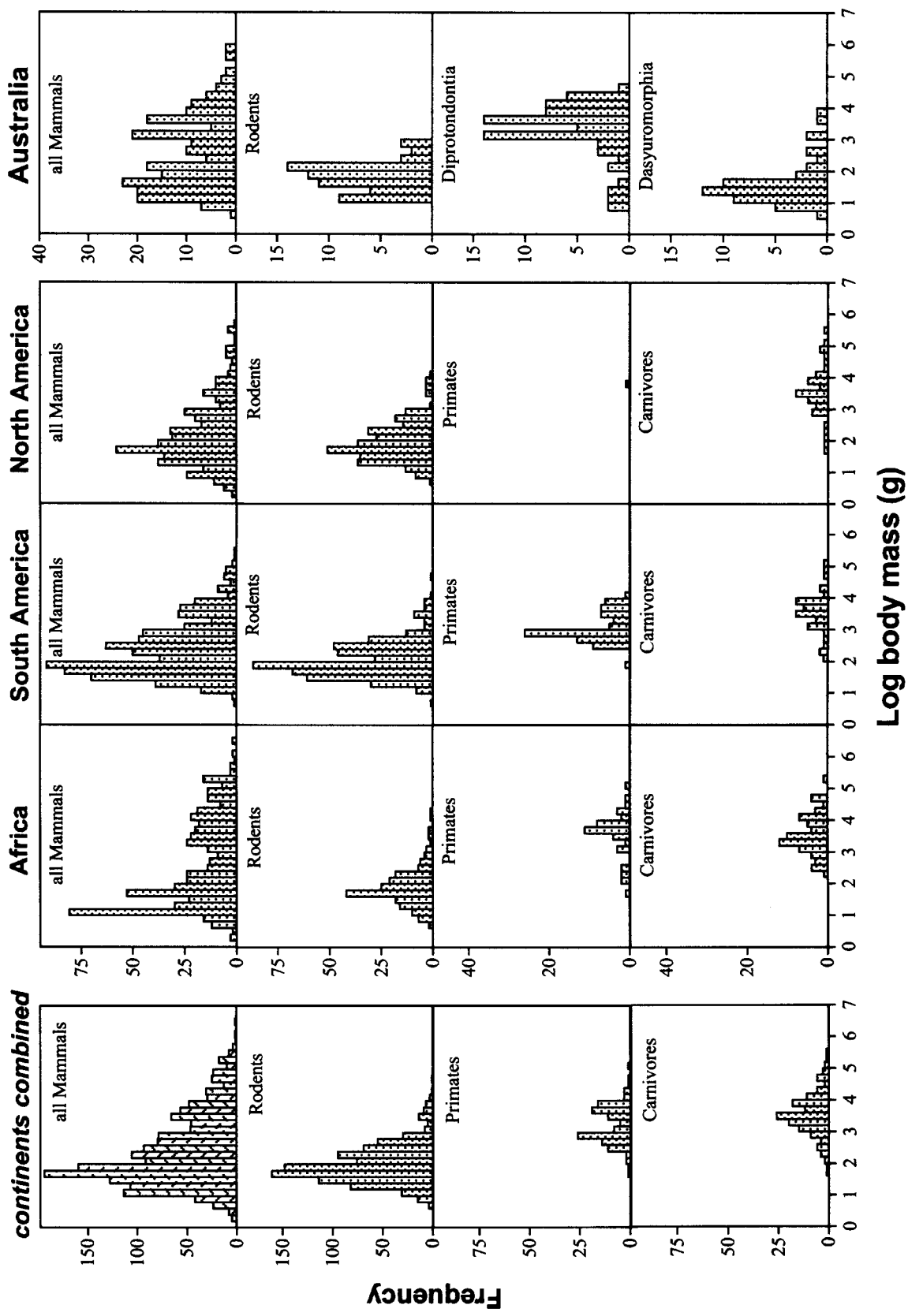
Discussion

But in all our speculations concerning nature, what we have to consider is the general rule. (Aristotle, *Partibus Animalium*)

Our analyses strongly support the idea that mammalian taxa have a “characteristic” body size (Haldane 1928). Body size is highly heritable, as evidenced by the similarity of congeneric species within a genus (fig. 1), similarity of congeneric taxa at higher levels of the taxonomic hierarchy (figs. 3–5), and similarity of the overall pattern of body size across geographic space (figs. 4, 5, A2) and evolutionary time (fig. 6). This is true of both placental and marsupial mammals and across all four continents we examined. Our investigations employed a variety of statistical approaches with different assumptions and properties, yet all yielded the same conclusions (e.g., tables 1, A2; figs. 1–6, A1, A2).

Not only are the body sizes of sister species remarkably congruent but individual mammalian orders have a characteristic body size niche (figs. 4–6, A2; table A3). The size of a typical rodent is different from that of a carnivore or of an artiodactyl (1.9 ± 0.59 , 3.6 ± 0.68 , and 4.7 ± 0.65 log units, respectively; table A3), regardless of where it is found. Such patterns are recapitulated on the different continents and across evolutionary time. Although there are quantitative differences among the overall body mass

Figure 4: Mammalian body size patterns for North America, South America, Australia, and Africa. In all cases, the X-axis represents the position in the taxonomic hierarchy; the Y-axis represents log body mass. Values for higher taxonomic levels (e.g., genera, family, order) are computed from the mean of the lower level. *Blue lines* = Artiodactyla on each continent; *red lines* = Carnivora; *orange lines* = Insectivora; and *green lines* = Rodentia. For Australia, we also highlight Diprotodontia (*purple lines*). Note that the segregation of ordinal means and the overall range of body size is very similar for each continent. Comparison with figure A1 in the online edition of the *American Naturalist* suggests that orders in the real data are segregated in a similar fashion to that of the ordered model, but there are a substantial number of overlaps at all levels of the taxonomic hierarchy.



distribution of mammals on each continent, this appears to be largely driven by the unique orders found on each. The moments for most shared orders are statistically indistinguishable (table A3; fig. 5). Such similarities in the moments of individual orders is especially remarkable considering that the three continents share no mammal species in common and have very different geographic settings and geologic histories. Thus a rodent, carnivore, or artiodactyl has the same characteristic body size niche, regardless of which continent is examined (table A3; figs. 4, 5). For example, although the body mass range is narrower in Australia, there is no significant difference in the mean or modal body size of carnivores, regardless of whether they live in North America, South America, Africa, or Australia (table A3).

Within the overall body size distributions, there are some small and interesting differences in the apparent number and locations of submodes. These probably reflect the influence of particular historic events such as the interchange of previously isolated North and South American faunas across the newly formed Isthmus of Panama during the Pliocene (Stehli and Webb 1985; Marquet and Cofre 1999) or the presumed human-caused extinction of the North and South American megafauna at the end of the Pleistocene (Martin and Wright 1967; Alroy 2001). A few other minor differences are worth noting. Africa, which contained far fewer rodents than the other continents (34% of the fauna vs. 68% and 65% for North and South America, respectively), had considerably more insectivores (23% vs. 10% and 1%; table A3). Interestingly, the modal body size of these insectivores was twice as large in Africa as in North America (15 vs. 7 g), and they occupied a wider range of body masses (table A3; figs. 4, 6). Perhaps the greater mode and range of insectivore body size in Africa 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. 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. The flatter

and less modal distribution of body mass in Australia (and the reduced species diversity) may be due in large part to the much reduced land area. Not only is Australia roughly half to one-third the size of the other continents (7,687,000 km² vs. 30,065,000, 17,819,000, and 24,256,000 km² for Africa, South America, and North America, respectively) but much of this is interior desert, further reducing effective land area. Indeed, the overall pattern resembles the much flatter regional distributions found for North and South America in earlier work (Brown and Nicoletto 1991; Marquet and Cofre 1999; Bakker and Kelt 2000). Overall, however, the similarities among continents are far more striking than such small differences (table A3; figs. 4, 5). Moreover, at least in North America, the diversification of mammalian body size that occurred during the Eocene radiation rapidly led to a distribution very close to the modern (fig. 6); this has been maintained over time despite considerable turnover of lineages at all levels from species to orders.

The extremely high heritability of body size we find for most mammalian taxa is recapitulated across disparate geographic regions and taxonomic groups too consistently to be a statistical artifact, but rather, it must reflect a general common mechanism or general rule. This is unlikely to be because of the single overriding influence of phylogeny. A major feature of the distribution of body sizes of mammals is extensive overlap at all levels of the taxonomic hierarchy. Compare, for example, the actual distribution of sizes among taxonomic levels to the perfectly hierarchical model (figs. 4, A1). Despite highly significant differences in the mean, mode, and median body size for the various mammalian orders, there is a great deal of overlap. Although the mean body size for rodents (~2 log units) is more or less invariant across time and space, there are a few much smaller and larger species, and the overall body size range encompasses more than four orders of magnitude (figs. 4, 5; table A3). Such broad ranges are found for most mammalian orders and would be even broader if insular species were considered. The body size of animals on islands long has been known to fluctuate well beyond that found in continental settings (Foster 1964). Thus, despite a characteristic body size

Figure 5: Body size distributions for all mammals and for selected orders on each continent. Moments and other distributional statistics can be obtained from table A3 in the online edition of the *American Naturalist*. The first column represents the combined mammalian biota of North America, South America, and Africa; the second column represents Africa; the third represents South America; and the fourth represents North America. The first row is the total mammal fauna for that region, the second row is rodents, the third row is primates, and the fourth row is carnivores. The fifth column represents the mammalian body size distribution for the continent of Australia. In this instance, the rows represent prominent marsupial orders because of the distinctive fauna found. Note also that the fauna is relatively depauperate; this is at least partially attributable to the much-reduced land area. Our data include only terrestrial nonvolant mammals (see “Material and Methods”); the exclusion of *Chiroptera*, in particular, may bias our interpretations. For a complete faunal and body mass characterization of mammals on these continents that includes both volant and aquatic animals, see Smith et al. 2003.

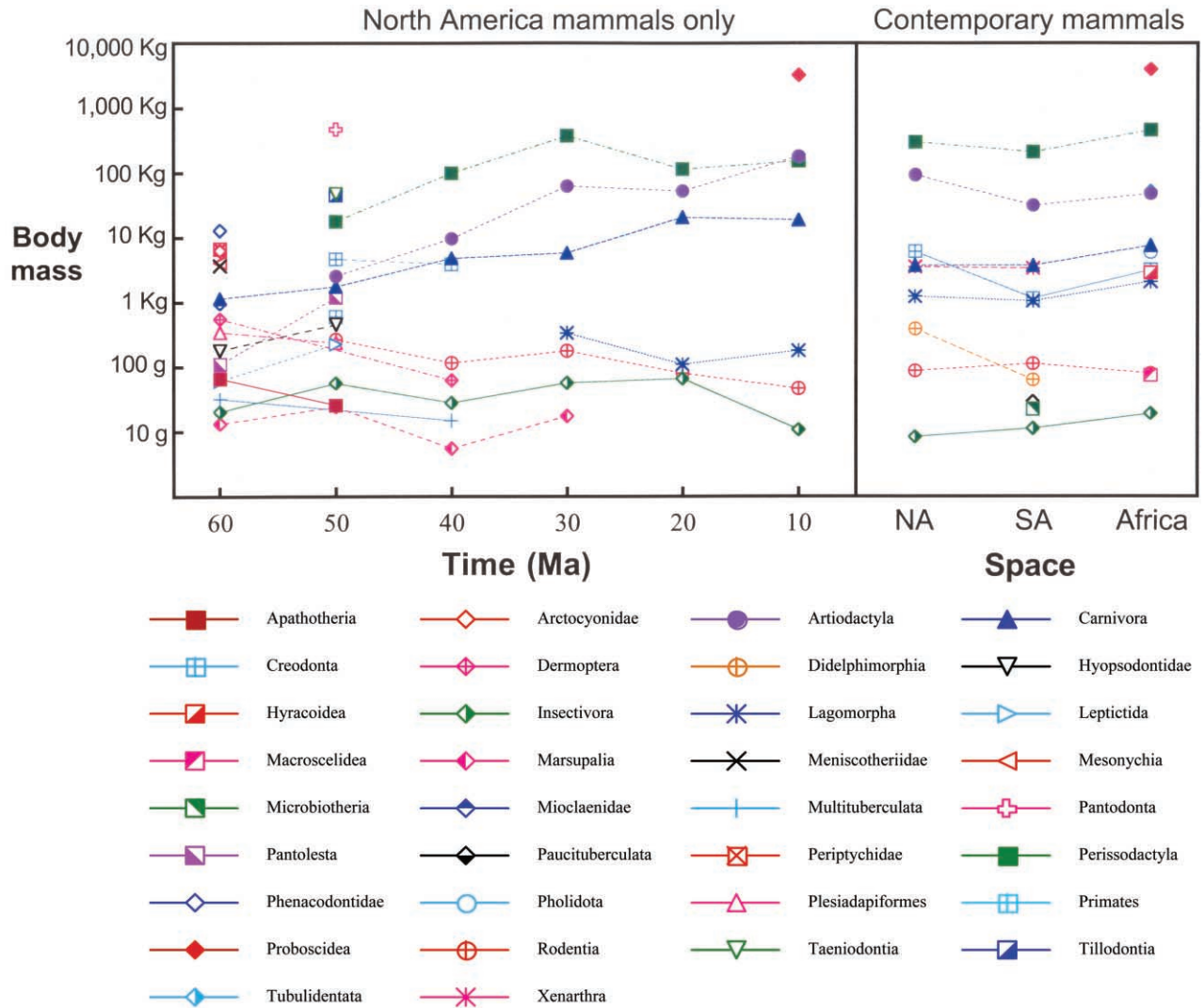


Figure 6: Body mass of mammalian orders and large families over evolutionary time and geographic space. The X-axis represents time on the left portion of the panel (depicted in 10-Ma slices for North America) or continent, depicted on the right portion of the panel; the Y-axis represents logarithmic mean of species within the order or family. Many groups are represented over multiple time slices and/or different continents, but because of high turnover, species composition is very different for each. Nonetheless, ordinal averages are very similar over the last 10 Ma and across geographic space.

niche, mammalian orders clearly do have sufficient evolutionary flexibility to evolve vastly different sizes. In most instances, however, they simply do not.

The general conservatism seen in body size evolution is unexpected, especially given that over evolutionary history, terrestrial mammals have radiated in size over seven orders of magnitude. A number of factors might lead to low levels of body size divergence. These include low levels of genetic variation, insufficient time for evolutionary processes, or a combination of weak directional and/or strong stabilizing selection. Several of these seem highly unlikely

to be sufficiently universal to drive the similarities in mammalian body size patterns. Numerous studies have demonstrated that considerable variation in body size is seen both within populations and across the geographic range (Grant et al. 1976; Grant and Grant 1989; Brown 1995; Smith and Betancourt 1998; Smith et al. 1998; Roy et al. 2000). Furthermore, there are many examples documenting not only that body size is highly heritable but that it has the capability to respond rapidly to directional selection (Falconer 1953, 1973; Rutledge et al. 1973; Grant et al. 1976; Leamy 1988; Grant and Grant 1989; Smith et al.

1995, 1998). The body sizes of elephants and deer, for example, fluctuated by several orders of magnitude within 10,000 years on continental islands isolated by rising sea levels in the terminal Pleistocene (e.g., Lister 1989; Roth 1990). Clearly, body size evolution can occur very rapidly (Lister 1989; Roth 1990; Smith et al. 1995, 1998; Thompson 1998; Simberloff et al. 2000). Thus the notion that there is insufficient underlying genetic variation for selection to act upon or insufficient time for body size divergence seems untenable.

There are a number of reasons why under most circumstances, body size might be subject to low levels of directional selection. If vicariance events have resulted in speciation, for example, the congeneric species will have allopatric geographic ranges and are unlikely to interact ecologically. Consequently there should be little selection for divergence. Selection should be more intense for those species occurring in sympatry. Although there is evidence that coexisting and ecologically similar species differ in body size (Schluter 1988, 2000; Brown and Nicoletto 1991; Holling 1992; Dayan and Simberloff 1994), data have rarely been analyzed in an explicitly evolutionary phylogenetic context (but see Losos 1990, 1996; Giannasi et al. 2000). It is not clear whether most coexisting species are congeneric, for example. Although several studies on mammals and birds have indicated phylogenetic overdispersion (i.e., "repulsion" of closely related species; Bowers and Brown 1982; Graves and Gotelli 1993; Kelt and Brown 1999), others on various plant taxa have found evidence of phylogenetic attraction or clumping (Kelly 1999; Webb 2000). The scale at which the studies are conducted and the mode of dispersal may well influence the level of coexistence observed. Even if species do occur sympatrically and exhibit character displacement, however, it may well involve selection on traits other than body size (Grant and Grant 1989; Schluter 2000). If so, directional selection pressures operating to differentiate the body size of congeners after speciation would be relatively weak unless new environmental or ecological opportunities arise.

The low rates of phenotypic evolution observed (e.g., figs. 1–6) suggest a strong role of stabilizing selection. An earlier study by Lynch (1990) also suggested that stabilizing selection might play a powerful role in mammalian evolution. In a sampling of various mammalian groups, he found the mean rate of morphological change in skull traits to be substantially less than expected (ranging from 3% to 50% of expectations) when compared with a neutral model of evolution. Although his study investigated phenotypic evolution in a variety of different cranial characters, most of these are tightly correlated with body size. His conclusion that stabilizing selection was the predominant evolutionary factor restricting the long-term diver-

sification of mammalian lineages is consistent with our findings.

Stabilizing selection could occur if the modal body size represents a physiological, life-history, or ecological optimum that maximizes fitness in some particular environmental context. If, after speciation events, the congeneric species remain in similar environments with similar selective pressures, stabilizing selection might select for little divergence from the ancestral condition. A recent study suggests that this may well occur; Peterson et al. (1999) found a high conservatism of ecological niches across evolutionary time for a sampling of 37 bird, butterfly, and mammal taxa. The authors attributed the conservatism they found in the ecological characteristics of species to active constraints (i.e., stabilizing selection). Even if competitive pressures are high, they might lead to the species diverging in traits other than body size. Note that many critical life-history characters scale allometrically with body size. Thus major shifts in body size will also result in substantial changes in attributes of morphology, physiology, life history, and ecology (e.g., Weibel 1973; Peters 1983; Calder 1984; Schmidt Nielsen 1984; Charnov 1993; Brown and West 2000), which will alter the realized and fundamental niche dimensions. Extreme variants might have very low fitness and be selected against. It should also be noted that the majority of lineages have been speciating and evolving in densely packed continental faunas (e.g., fig. 4). These faunas contain large numbers of other species of both closely related and more distantly related lineages, and many of these species are of similar body size. There may be selection for similarities in the size of congeneric species because size alterations would increase competitive interactions with other taxa. Certainly, we found very limited diversification in the sizes of congeners, even in the most species-rich genera (fig. 2B, 2C). As a monophyletic lineage speciates to generate multiple descendant species, there is increasing probability that each newly formed species will have relatives of both smaller and larger size. Interactions among such relatives may be one of the factors that constrain size diversification in the lineage as a whole. Thus in most instances there may be strong stabilizing selection to limit the diversification of body size within the group unless a new environment is colonized or the environment changes. Indeed, most examples of rapid or extreme size differentiation have been reported for relatively depauperate insular faunas (Foster 1964; Lister 1989; Roth 1990).

The high similarity of body size found among congeners does not hold for mammals of extremely small size (fig. 1B). Our analysis clearly indicates that this result is not an artifact of sampling or age of the lineage (fig. 2). We believe the lack of body size similarity among congeners may reflect limitations of the ability of these very small

mammals to respond to competition or other environmental pressures. Extremely small body size brings with it a unique set of physiological and life-history constraints. Because of the allometric scaling of many physiological parameters, mammals of small size must spend most of their time foraging to meet their very high mass-specific maintenance costs. This probably explains why many of the very small species are insectivorous, specializing on high-energy food packages. However, five different mammalian orders are represented in the very smallest size class (<18 g; figs. 4, A2; table A1), and larger insectivores do demonstrate heritability of size. Consequently, trophic strategy alone cannot explain the lack of similarity of body size for genera of very small mammals. A more likely explanation is that because most life-history traits scale allometrically with mass (Peters 1983; Calder 1984) and these mammals are at the extreme end of the body mass spectrum, it is difficult for closely related species to diverge in traits other than size. In other words, there is little physiological space to develop novel adaptations to new environments that might lead to speciation. Biomechanical, thermoregulatory, and other constraints on the smallest mammals restrict alterations in body shape that permit ecological specialization in larger species. Given a new and colder ecological niche, for example, small mammals may not be able to increase metabolic rate, insulation, or foraging activities to deal with increased thermoregulatory demands. Instead they may adapt by altering body size. Larger mammals, in contrast, have more evolutionary options when faced with new environmental conditions or opportunities.

The remarkable resemblance of the characteristic body sizes of different mammalian orders over both space and time suggests that they are the outcome of a common set of ecological and evolutionary processes. To some degree, these similarities in the body size niche of taxa across these different continents and across evolutionary time must reflect boundaries imposed by taxonomic affiliation. However, such 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 geographic space and geological time cannot be explained solely in terms of phylogeny. Instead, it has been a complex multivariate process, probably reflecting the interacting influences of numerous mechanisms. Most segments of the body size spectrum are occupied by species representative of multiple genera, families, and orders with distinctively different morphology, physiology, behavior, and ecology (fig. 4). It is hard to imagine how such similar size distributions could be maintained over evolutionary time (fig. 6) except by stabilizing selection to exploit eco-

logical opportunities within the limits of structural and functional allometric constraints. Trophic differences between groups may prevent competition and allow coexistence of species with similar body size. The body size distributions of mammals on continents are emergent properties that are preserved despite or perhaps because of all of the multiple environmental variables and mechanistic processes that affect body size evolution at the level of individual organisms and species populations. Similar emergent patterns of body size distributions have been observed in other organisms in different environmental settings, although some features of the distributions differ from those seen in these mammals (Brown et al. 1993, 1995; Maurer 1998; Marquet and Cofre 1999; Roy et al. 2000). An understanding of these emergent patterns is essential as scientists seek to discover the general laws that underlie the amazing diversity of life.

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Literature Cited

- Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* 280:731–734.
- . 1999. The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. *Systematic Biology* 48:107–118.
- . 2000. New methods for quantifying macroevolutionary patterns and processes. *Paleobiology* 26:707–733.
- . 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292:1893–1896.
- Bakker, V. J., and D. A. Kelt. 2000. Scale-dependent patterns in body size distributions of Neotropical mammals. *Ecology* 81:3530–3547.
- Bininda-Emonds, O. R. P., J. L. Gittleman, and A. Purvis. 1999. Building large trees by combining phylogenetic

- information: a complete phylogeny of the extant carnivora (mammalia). *Biological Reviews of the Cambridge Philosophical Society* 74:143–175.
- Bowers, M. A., and J. H. Brown. 1982. Body size and coexistence in desert rodents: chance or community structure? *Ecology* 63:391–400.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Brown, J. H., and P. F. Nicoletto. 1991. Spatial scaling of species assemblages: body masses of North American land mammals. *American Naturalist* 138:1478–1512.
- Brown, J. H., and G. B. West. 2000. *Scaling in biology*. Oxford University Press, New York.
- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. The evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* 142:573–584.
- Butler, P. M. 1988. Phylogeny of the insectivores. Pages 117–142 in M. J. Benton, ed. *The phylogeny and classification of the tetrapods*. Vol. 2. Mammals. Clarendon, Oxford.
- Calder, W. A. 1984. *Size, function and life history*. Harvard University Press, Cambridge, Mass.
- Carroll, S. B. 2001. Change and necessity: the evolution of morphological complexity and diversity. *Nature* 409:1102–1109.
- Charnov, E. L. 1993. *Life history invariants: some explorations of symmetry in evolutionary ecology*. Oxford University Press, New York.
- Dayan, T., and D. Simberloff. 1994. Character displacement, sexual dimorphism and morphological variation among British and Irish mustelids. *Ecology* 75:1063–1073.
- . 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review* 28:99–124.
- Eisenberg, J. F. 1989. *Mammals of the Neotropics*. Vol. 1. The northern Neotropics: Panama, Columbia, Venezuela, Guyana, Surinam, French Guinea. University of Chicago Press, Chicago.
- Eisenberg, J. F., and K. H. Redford. 1999. *Mammals of the Neotropics*. Vol. 3. The central Neotropics: Ecuador, Peru, Bolivia, Brazil. University of Chicago Press, Chicago.
- Emmons, L. H. 1990. *Neotropical rainforest mammals: a field guide*. University of Chicago Press, Chicago.
- Falconer, D. S. 1953. Selection for large and small size in mice. *Journal of Genetics* 51:470–501.
- . 1973. Replicated selection for body weight in mice. *Genetic Research* 22:291–321.
- . 1989. *Introduction to quantitative genetics*. Longman, London.
- Foster, J. B. 1964. Evolution of mammals on islands. *Nature* 202:234–235.
- Galton, F. 1889. *Natural inheritance*. Macmillan, New York.
- Giannasi, N., R. S. Thorpe, and A. Malhotra. 2000. A phylogenetic analysis of body size evolution in the *Anolis roquet* group (Sauria: Iguanidae): character displacement or size assortment? *Molecular Ecology* 9:193–202.
- Gittleman, J. L., and M. Kot. 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology* 39:227–241.
- Gittleman, J. L., C. G. Anderson, M. Kot, and H. K. Luh. 1996. Comparative tests of evolutionary lability and rates using molecular phylogenies. Pages 289–307 in P. H. Harvey, A. J. Leigh Brown, J. Maynard Smith, and S. Nee, eds. *New uses for new phylogenies*. Oxford University Press, Oxford.
- Gould, S. J. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. *Journal of Paleontology* 62:319–329.
- Grant, B. R., and P. R. Grant. 1989. *Evolutionary dynamics of a natural population: the large cactus finch of the Galápagos*. University of Chicago Press, Chicago.
- Grant, P. R., B. R. Grant, J. N. M. Smith, I. Abbott, and L. K. Abbott. 1976. Darwin's finches: population variation and natural selection. *Proceedings of the National Academy of Sciences of the USA* 73:257–261.
- Graves, G. R., and N. J. Gotelli. 1993. Assembly of avian mixed-species flocks in Amazonia. *Proceedings of the National Academy of Sciences of the USA* 90:1388–1391.
- Haldane, J. B. S. 1928. *Possible worlds and other papers*. Harper, New York.
- Hasler, M. J., J. F. Hasler, and A. V. Nalbandov. 1977. Comparative breeding biology of musk shrews (*Suncus murinus*) from Guam and Madagascar. *Journal of Mammalogy* 58:285–290.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62:447–502.
- Hooker, J. J. 1989. Character polarities in early perissodactyls and their significance for hyracotherium and infraordinal relationships. Pages 79–101 in D. R. Prothero, ed. *The evolution of perissodactyls*. Oxford University Press, New York.
- Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* 238:360–363.
- Jaeger, J. J. 1988. Rodent phylogeny: new data and old problems. Pages 177–200 in M. J. Benton, ed. *The phylogeny and classification of the tetrapods*. Vol. 2. Mammals. Clarendon, Oxford.

- Janis, C. 1993. Victors by default. Pages 169–218 in S. J. Gould, ed. *The book of life*. Norton, New York.
- Jones, K. E., A. Purvis, A. MacLarnon, O. R. P. Bininda-Emonds, and N. B. Simmons. 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biological Reviews* 77:223–259.
- Kappeler, P. M., and E. W. Heymann. 1996. Nonconvergence in the evolution of primate life history and socioecology. *Biological Journal of the Linnean Society* 59: 297–326.
- Kelly, C. K. 1999. On the relationship between function and phylogenetic relatedness: environmental severity and community structure. Abstracts of the XVI International Botanical Congress, St. Louis.
- Kelt, D. A., and J. H. Brown. 1999. Diversification of body sizes: patterns and processes in the assembly of terrestrial mammal faunas. Pages 111–131 in M. L. McKinney and J. A. Drake, eds. *Biodiversity dynamics: turnover of populations, taxa, and communities*. Columbia University Press, New York.
- Kingdon, J. 1982. *East African mammals: an atlas of evolution in Africa*. Vols. 1–3. University of Chicago Press, Chicago.
- Kurten, B., and E. A. Anderson. 1980. *Pleistocene mammals of North America*. Columbia University Press, New York.
- Leamy, L. 1988. Genetic and maternal influences on brain and body size in random breed house mice. *Evolution* 42:42–53.
- Lister, A. M. 1989. Rapid dwarfing of red deer on Jersey in the last interglacial. *Nature* 342:539–542.
- Liu, F. R., M. M. Miyamoto, N. P. Freire, P. Q. Qng, M. R. Tennant, T. S. Young, and K. F. Gugel. 2001. Molecular and morphological supertrees for eutherian (placental) mammals. *Nature* 291:1786–1789.
- Lomolino, M. V. 1985. Body size of mammals on islands: the island rule reexamined. *American Naturalist* 125: 310–316.
- Losos, J. B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. *Evolution* 44: 558–569.
- . 1996. Phylogenetic perspectives on community ecology. *Ecology* 77:1344–1354.
- Lynch, M. 1990. The rate of morphological evolution in mammals from the standpoint of the neutral expectation. *American Naturalist* 136:727–741.
- Lyons, S. K., F. A. Smith, and J. H. Brown. 2004. Of mice, mastodons, and men: human-caused extinctions on four continents. *Evolutionary Ecology Research* 6:339–358.
- Maglio, V. J., and H. B. S. Cooke. 1978. *Evolution of African mammals*. Harvard University Press, Cambridge, Mass.
- 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* 85:299–309.
- Marshall, L. G., J. A. Case, and M. O. Woodburne. 1990. Phylogenetic relationships of the families of marsupials. Pages 433–500 in H. H. Genoways, ed. *Current mammalogy*. Vol. 2. Plenum, New York.
- Martin, P. S., and H. E. Wright, Jr., eds. 1967. *Pleistocene extinctions: the search for a cause*. Yale University Press, New Haven, Conn.
- Martins, E., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* 149:646–667.
- Maurer, B. A. 1998. The evolution of body size in birds. I. Evidence for nonrandom diversification. *Evolutionary Ecology* 12:925–934.
- McShea, D. W. 1994. Mechanism of large scale evolutionary trends. *Evolution* 48:1747–1763.
- Milinkovitch, M. C., A. Meyer, and J. R. Powell. 1994. Phylogeny of all major groups of cetaceans based on DNA sequences from three mitochondrial genes. *Molecular Biology and Evolution* 11:939–948.
- Mones, A. 1986. *Palaeovertebrata Sudamericana. Catalogo sistemático de los vertebrados fosiles de America del Sur. Parte I. Lista preliminar y bibliografía*. Courier Forschungsinstitut Senckenberg 82:1–625.
- Nedbal, M. A., M. W. Allard, and R. L. Honeycutt. 1994. Molecular systematics of hystricognath rodents: evidence from the mitochondrial 12S rRNA gene. *Molecular Phylogenetics and Evolution* 3:206–220.
- Niklas, K. 1994. *Plant allometry: the scaling of form and process*. University of Chicago Press, Chicago.
- Pagel, M., and P. H. Harvey. 1988. Recent developments in the analysis of comparative data. *Quarterly Review of Biology* 62:413–440.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Peterson, A. T., J. Soberon, and V. Sanchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267.
- Purvis, A. 1995. A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London B* 348:405–421.
- Read, A. F., and P. H. Harvey. 1989. Life history differences among the eutherian radiations. *Journal of Zoology (London)* 219:329–353.
- Redford, K. H., and J. F. Eisenberg. 1992. *Mammals of the Neotropics*. Vol. 2. The southern zone: Chile, Argentina, Uruguay, Paraguay. University of Chicago Press, Chicago.
- Roth, V. L. 1990. *Insular dwarf elephants: a case study in*

- body mass estimation and ecological inference. Pages 151–179 in J. Damuth and B. J. MacFadden, eds. *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge University Press, New York.
- Roy, K., D. Jablonski, and K. K. Martien. 2000. Invariant size-frequency distributions along a latitudinal gradient in marine bivalves. *Proceedings of the National Academy of Sciences of the USA* 97:13150–13155.
- Rutledge, J. J., E. J. Eisen, and J. E. Legates. 1973. An experimental evaluation of genetic correlation. *Genetics* 75:709–726.
- SAS Institute. 1989. *SAS/STAT user's guide*, version 6. 4th ed. SAS Institute, Cary, N.C.
- Schluter, D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. *American Naturalist* 131:799–824.
- . 2000. *The ecology of adaptive radiation*. Oxford University Press, Oxford.
- Schmidt-Nielsen, K. 1984. *Scaling: why is animal size so important?* Cambridge University Press, Cambridge.
- Schneider, H., M. P. C. Schneider, I. Sampaio, M. L. Harada, M. Stanhope, J. Czelusniak, and M. Goodman. 1993. Molecular phylogeny of the New World monkeys (Platyrrhini, Primates). *Molecular Phylogenetics and Evolution* 2:225–242.
- Silva, M., and J. A. Downing. 1995. *CRC handbook of mammalian body masses*. CRC, Boca Raton, Fla.
- Simberloff, D., T. Dayan, C. Jones, and G. Ogura. 2000. Rapid character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology* 81:2086–2099.
- Smith, F. A., and J. L. Betancourt. 1998. Response of bushy-tailed woodrats (*Neotoma cinerea*) to late Quaternary climate change in the Colorado Plateau. *Quaternary Research* 50:1–11.
- Smith, F. A., J. L. Betancourt, and J. H. Brown. 1995. Evolution of body size in the woodrat over the past 25,000 years of climate change. *Science* 270:2012–2014.
- Smith, F. A., H. Browning, and U. L. Shepherd. 1998. The influence of climate change on the body mass of woodrats (*Neotoma*) in an arid region of New Mexico, USA. *Ecography* 21:140–148.
- 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* 84:3402.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman, San Francisco.
- Stehli, R. G., and S. D. Webb, eds. 1985. *The great American biotic interchange*. Plenum, New York.
- Sumner, F. B. 1932. Genetic, distributional and evolutionary studies of the subspecies of deer mice (*Peromyscus*). *Biobliographia Genetica* 9:1–106.
- Thompson, J. N. 1998. Rapid evolution as an ecological process. *Trends in Ecology & Evolution* 13:329–332.
- Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist* 156:145–155.
- Weibel, E. R. 1973. Morphometric estimation of pulmonary diffusion capacity. V. Comparative morphometry of alveolar lungs. *Respiratory Physiology* 14:26–43.
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126.
- . 1999. The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* 284:1677–1679.
- Wilson, D. E., and D. M. Reeder. 1993. *Mammal species of the world: a taxonomic and geographic reference*. 2d ed. Smithsonian Institution, Washington, D.C.
- Wyss, A. R., and J. J. Flynn. 1993. A phylogenetic analysis and definition of the Carnivora. Pages 32–52 in F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds. *Mammal phylogeny: placentals*. Springer, New York.

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