

Higher origination and extinction rates in larger mammals

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Do large mammals evolve faster than small mammals or vice versa? Because the answer to this question contributes to our understanding of how life-history affects long-term and large-scale evolutionary patterns, and how microevolutionary rates scale-up to macroevolutionary rates, it has received much attention. A satisfactory or consistent answer to this question is lacking, however. Here, we take a fresh look at this problem using a large fossil dataset of mammals from the Neogene of the Old World (NOW). Controlling for sampling biases, calculating per capita origination and extinction rates of boundary-crossers and estimating survival probabilities using capture-mark-recapture (CMR) methods, we found the recurring pattern that large mammal genera and species have higher origination and extinction rates, and therefore shorter durations. This pattern is surprising in the light of molecular studies, which show that smaller animals, with their shorter generation times and higher metabolic rates, have greater absolute rates of evolution. However, higher molecular rates do not necessarily translate to higher taxon rates because both the biotic and physical environments interact with phenotypic variation, in part fueled by mutations, to affect origination and extinction rates. To explain the observed pattern, we propose that the ability to evolve and maintain behavior such as hibernation, torpor and burrowing, collectively termed “sleep-or-hide” (SLOH) behavior, serves as a means of environmental buffering during expected and unexpected environmental change. SLOH behavior is more common in some small mammals, and, as a result, SLOH small mammals contribute to higher average survivorship and lower origination probabilities among small mammals.

body size | environmental buffering | metabolism | Neogene mammals | turnover

Evolution operates at different scales of time and levels of the biological hierarchy (1). Body size covaries with many individual and species level traits (2), each of which could influence the tempo of evolution at population, species and clade levels. Multiple studies have shown that smaller sized mammals have higher molecular rates of evolution in absolute time, possibly because of a generation time effect and/or metabolic rate effect (3–8). Higher molecular rates may translate to higher rates of phenotypic changes (9 but see 10, 11) and a greater chance of reproductive isolation, which could ultimately lead to higher speciation rates (12) and higher rates of pseudoextinction, which could be observed as higher extinction rates among fossil taxa. As such, small mammals could be expected to have higher origination and extinction rates as observed in the fossil record. However, empirical studies on historical extinctions show that large mammals are at higher risk of extinction and have been selectively removed (13–17), as is also indicated by the Pleistocene megafauna extinction literature (18, 19), even though body size *per se* may not always be a good predictor of extinction risk (20–22). Neither molecular studies nor research on historical extinctions and extinction in the shallow fossil record gives us direct insight into the distribution of taxon durations and long-term

turnover rates. Previous studies show mixed results on mammal size-biased selectivity. Three possible scenarios have been described, namely, as no size bias (23, 24), greater survivorship in large mammals versus small (25, 26), and greater survivorship in small mammals versus large (27, 28). However, little is known about mammal body size biases in origination rates in the fossil record. The uncertainty in both the simple existence of a body size bias in origination and extinction rates, as well as the direction in which the bias should manifest itself, is considerable. On average, compared within groups, species with larger body sizes often have wider geographic ranges (24, 29), need greater patch sizes (30), have smaller population sizes/lower densities/abundances (31), have longer generation times (32), have lower fecundity (33), have lower specific production rates (34), and have longer individual life spans and lower metabolic rates (35). These traits potentially push survivorship and the propensity to generate new species and genera in opposing directions: larger mammals have wider geographic ranges and potentially greater dispersal abilities that could lower their extinction risk (36). Conversely, the longer generation times and smaller population sizes of larger mammals might increase extinction risk (37). Similarly, the smaller effective population size of larger mammals may confer higher speciation and origination rates, but, simultaneously, their ability to disperse and encourage gene flow may dampen these rates.

Here, we use a large Neogene Old World (NOW) fossil mammal dataset (38) to study whether there are body size biases in taxon durations, survivorship, and originations. Common problems encountered in studying fossil lineages are the heterogeneous quality of localities and the uncertain endpoints of taxon durations. In addition, although taphonomic differences among mammals of different body sizes have long been recognized (39, 40), the bias introduced into preservation rates has not been incorporated in analyses in a comprehensive fashion. We embrace these issues and clearly demonstrate, using various analytical approaches, that large mammals have both higher extinction and origination rates and therefore a duration distribution that has a more truncated right tail.

Results and Discussion

Among mammal genera with shorter durations, there is a predominance of large mammals (Artiodactyla, Carnivora, Creodonta,

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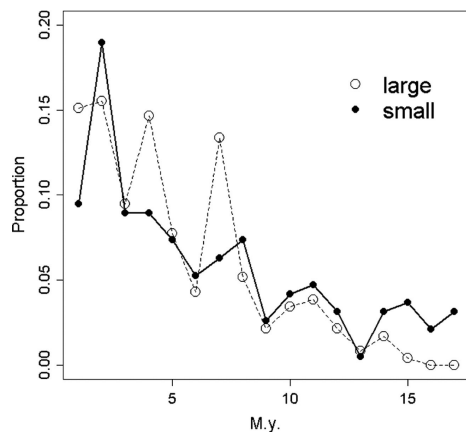


Fig. 1. Histogram of durations of extinct small and large mammal genera. This histogram represents the full dataset (All); for subsets, see Fig. S1. Proportions are calculated for small (●) and large (○) mammals separately. One-million-year bins are plotted.

Hyracoidea, Perissodactyla, Primates, Proboscidea, and Tubulidentata) whereas, among those with longer durations, there is an excess of small mammals (Insectivora, Rodentia, and Lagomorpha) (Fig. 1 and supporting information (SI) Fig. S1). Mean and median durations of large and small mammal genera reflect the same tendency: small genera have greater mean and median durations than large ones (Kolmogorov–Smirnov test, $P < 0.05$, Mann–Whitney U test < 0.05 ; Table S1 in Dataset S1). At species level, the same difference is present in duration means, although it is not statistically significant (Table S1 in Dataset S1). This difference in durations could be due to only a lower rate of extinction, but we find that large mammal genera have both higher per capita rates of origination and extinction than small mammals (Table 1 and Table S2 in Dataset S1; Mann–Whitney U test < 0.05). The differences in extinction rates are greater than in origination rates, in general (Table S2 in Dataset S1). Using a capture-mark-recapture (CMR) approach, we conclude similarly that large animals have comparatively lower survivorship (Table S3 in Dataset S1). The best models in each case from CMR analyses always include a body size effect, and the weights for these top models are high (Table S3 in Dataset S1), regardless of the sub-setting or temporal binning of the data. The estimates for body size effect, and their lower confidence limits, are positive (Table 2), indicating that large mammals survive with a lower probability. Species results are statistically weaker or insignificant, because species occurrences are sparse, but neverthe-

Table 1. Per capita rates of origination and extinction

Rates	Data subsets	Large	Small	M–W	N
p	All	0.40	0.25	0.008	18
	5_occ	0.23	0.13	0.003	17
	5_taxa	0.35	0.27	0.094	18
	10_occ_10_taxa	0.17	0.16	0.078	17
q	All	0.30	0.15	0.103	18
	5_occ	0.35	0.15	0.059	17
	5_taxa	0.23	0.13	0.103	18
	10_occ_10_taxa	0.34	0.13	0.045	17

Mean per capita rates of origination, p , and extinction, q , per million years for large and small mammal genera. All, the entire dataset; 5_occ, data subset where only genera with at least five occurrences were included; 5_taxa, subset where only localities with at least five genera were included 10_occ_10_taxa, subset where first all genera with fewer than 10 occurrences were excluded and then localities with fewer than 10 genera excluded. M–W, P values for paired, two-tailed Mann–Whitney U tests. N , number of 1-M.y. time bins for which comparisons were possible. See Table S2 in Dataset S1 for alternative binning schemes.

less point in the same direction (CMR species results not presented).

Large mammal genera from NOW (Artiodactyla, Carnivora, Creodonta, Hyracoidea, Perissodactyla, Primates, Proboscidea, and Tubulidentata), for which we have body mass estimates via a nearest living relative approach, truly have greater body mass (Fig. 2; Kolmogorov–Smirnov test $P < 0.0001$) compared with small mammals (Insectivora, Rodentia, and Lagomorpha). Unfortunately, because the duration distributions of these genera are based on truncated durations, we cannot distinguish their duration distribution from that of small mammals for which we have similar body mass estimates (Kolmogorov–Smirnov test $P = 0.43$). Body size is indeed a general predictor of mammal taxon durations (this study) even though there are certainly short-duration small and long-duration large mammal species and genera (see SI Text for a discussion).

How much of this detected difference is due to preservation differences? Small and large mammals have different modes of preservation and are often collected in the field and processed in the laboratory with different methods (25, 41). Specifically, large mammals are often preferentially preserved and recorded (39); therefore, they should have greater apparent durations. Despite the prediction of this preservation bias, we find that large mammals have on average shorter durations. However, taxonomic practices could have an influence in the opposite direction. For example, large mammal species might be preferentially described as new (e.g., more “splitters” among large mammal researchers), which could potentially bias large mammal durations toward being shorter. Unfortunately, no available data allow us to address such potential factors. We were, however, able to model body size as a covariate in preservation rate and found that its effect is inconsistent (Table 2). In cases where body size had an effect on preservation rate, the effect of body size on survivorship remained strong (Table 2). In other words, large mammals may have a somewhat higher preservation rate, but their survival probability is lower than that of small mammals even after accounting for differential preservation.

Why do our results differ from other mammalian body size turnover rate studies mentioned in the introduction? Muñoz-Durán (23) and Viranta (24) found no size bias in survivorship, but their studies involved only carnivores and these are all considered large mammals in our analyses; therefore, there is no direct contradiction (see SI Text for a discussion on carnivores). Van Valen (26) demonstrated that large mammal taxa have a longer half life than mammals in general in a semi-global genus dataset, but mammal taxonomy and chronology have improved over time. An independent lower latitude fossil mammal dataset from Miocene deposits in Pakistan, known as the Siwaliks (25, 41), also shows opposing results. The Siwaliks dataset has a broad taxonomic coverage, but a more limited temporal and geographic coverage. Also, differences in collecting strategies not taken into account could have played a part in opposite conclusions. A real biological signal may also be present: the Siwaliks assemblages represent a subtropical fauna and differ from NOW taxa, which were derived from a largely temperate fauna. The disadvantages of being a large mammal may not be felt under conditions of a more dependable (tropical or subtropical) environment. Consequently, the effects of a shorter generation time and species competition (42) as local small mammal diversity increases could lead to more rapid turnover of small mammals in the (sub)tropics (43).

Although shorter generation times and higher metabolic rates of small mammals may increase molecular rates of evolution (8, 11), and even if we were to assume that molecular changes translate substantially to phenotypic changes (12), these shorter-term, generational changes do not seem to translate to higher turnover rates as we have shown here (but see ref. 44). The study of evolutionary rates should therefore embrace different levels of the biological hierarchy. We emphasize that this discrepancy does not imply

Table 2. Body size effects on survivorship and preservation

Bin data subsets	Estimate	1-M.y. bins				1.5-M.y. bins				2-M.y. bins			
		Beta	SD	L	U	Beta	SD	L	U	Beta	SD	L	U
All	Φ	0.664	0.181	0.309	1.018	0.600	0.170	0.267	0.932	1.208	0.000	1.208	1.208
5_occ	Φ	0.783	0.191	0.409	1.157	0.678	0.161	0.363	0.993	1.931	0.000	1.931	1.931
	pr	-0.449	0.211	-0.864	-0.035	-0.434	0.244	-0.913	0.045	-0.542	0.260	-1.052	-0.031
5_taxa	Φ	0.824	0.233	0.368	1.281	0.669	0.218	0.243	1.096	0.817	0.304	0.220	1.413
	pr	-0.473	0.212	-0.889	-0.058	-0.544	0.296	-1.124	0.036	-0.685	0.405	-1.478	0.108
10_occ.10_taxa	Φ	0.969	0.280	0.420	1.518	0.617	0.252	0.123	1.111	NA	NA	NA	NA

Group effect for each of the best models from the four data subsets, using 1-, 1.5-, and 2-M.y. bins. Estimates presented are survivorship (Φ) and preservation (pr). Beta, estimates for body size effect; SD, standard deviations; L, lower of the 95% confidence interval; U, upper of the 95% confidence interval.

micro- and macroevolution discontinuity, but that using different observational scales and units reveals basal and emergent processes in turn.

Small mammals have on average lower turnover rates at both species and genus levels, even though noisier species data did not allow us to infer species level results with statistical confidence. We take this result one step further and present a hypothesis that to our knowledge has never been analyzed: it is not just being smaller *per se* that allows greater survivorship (many small mammals also have short species and genus durations) (Fig. 1 and Fig. S1). Rather, a greater proportion of small mammals may be more apt at hiding (e.g., in burrows or tree holes) or going into low metabolic rate modes (e.g., hibernation and torpor). We call such behavior “sleep-or-hide” (SLOH). Taxa that demonstrate the ability to buffer themselves from environmental stress in this manner are here termed SLOH taxa.

We used living species to infer the presence/absence of SLOH behavior in fossil genera. Of the 50 large NOW mammal genera for which we have the nearest living relative estimates, 15 exhibit SLOH behavior whereas, for 67 small NOW mammal genera (i.e., genera from the orders Insectivora, Lagomorpha, and Rodentia), 41 exhibit SLOH behavior (see Table S4 in Dataset S1). This bias is significant (χ^2 test $P = 0.0001$).

More genera inferred to have SLOH behavior in our dataset have smaller body mass estimates (Fig. 3; Kolmogorov–Smirnov test $P < 0.001$). There is also a group of small mammals that does not display SLOH behavior (Fig. 3). Therefore, some, but not all, small mammals may be better buffered against environmental changes than larger mammals.

As discussed in more detail in *SI Text*, there is good evidence that the longest-lived small mammal genera have SLOH traits, as inferred from their nearest living relatives. Thus, for the most

inclusive dataset (All) we find in the longest living 16-million year (M.y.) class a mole, two gliding squirrels, and two dormice. In the 15-M.y. class, there is a shrew, a hedgehog, a ground squirrel, a hamster, and a burrowing field mouse. The 14-M.y. class comprises two shrews, a mole, a gliding arboreal squirrel, and a burrowing mole rat. Apart from two eomyid rodents with unknown lifestyles, all genera in these highest range classes are likely to exhibit one or more SLOH traits. The sole large mammal in these duration classes is the tapir, genus *Tapirus* (extinct in the study area and therefore included in the analysis).

Body masses of large mammals increased over the Neogene (Fig. S2; see also ref. 45), and this temporal trend corresponds to a decrease in the ability to sleep and/or hide (Fig. S2). In contrast, there are no such trends over the Neogene for small mammals (Fig. S2). Incidentally, this body size constraint on SLOH behavior could explain an old paradox: the European Miocene–Pliocene boundary is well defined by a turnover event in the large mammal fauna but not that of small mammals (46).

We interpret the patterns in our data to indicate that the ability of a species or genus to shield itself from environmental fluctuations lowers turnover rates, and that the ability to “sleep-or-hide” is constrained by body size (47). We suggest that SLOH genera are less extinction prone and experience less selective pressure to evolve to cope with environmental change. Whether species are seasonal or facultative in the hibernation–torpor continuum (48), this behavior is associated with decreased food resources, lower ambient temperatures, and lowered oxygen availability (49). Because this behavior is in part plastic (48, 50–52), species that display it are expected to cope better with (un)expected climate variation. It is typical for mammals to take shelter in burrows, holes, or caves,

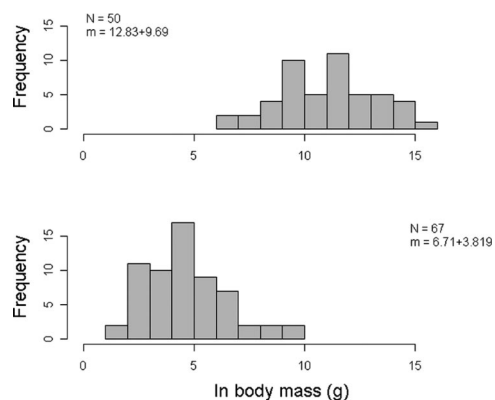


Fig. 2. Histograms of ln body mass of NOW mammal genera designated large (Upper) and small (Lower). Body masses are inferred by using a nearest relative approach. N , sample size; m , mean natural log (ln) body mass (in grams).

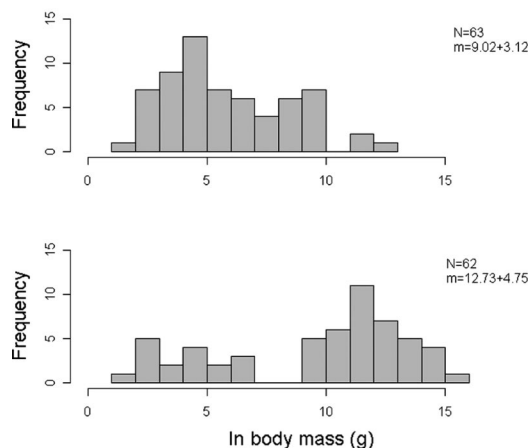


Fig. 3. Histograms of ln body mass of SLOH (Upper) and non-SLOH (Lower) genera. N , sample size; m , mean ln body mass (in grams). See Fig. S3 for an alternative plot of this figure.

during hibernation or torpor, in part to maintain a more constant ambient environment. In fact, burrowing could have evolved as an adaptation to deteriorating conditions (53, 54), in combination with the exploitation of underground resources. In addition to providing a more constant ambient environment, such hiding places can also double as refuges from predators (17, 55, 56), including human hunters (21).

Climate and environment both have a large part to play in the evolutionary theater, even though the play must also depend on life-history and biotic interactions. Which taxa survive may be strongly influenced by the number and scale of climate reversals (57). However, in a similar environmental backdrop (Neogene of Europe), large mammals survive at lower rates than small mammals. Large mammals suffer from compound disadvantages. They have more deleterious mutations (37), smaller population sizes (31), and longer generation times (32) and are, in addition, probably constrained by their size from being apt at hiding or shutting down or lowering their metabolic rates temporarily. They may also require more energy to survive during periods of environmental stress (58, 59). However, we show that some small mammals are at an advantage because of “intrinsic traits,” in contrast to claims that small mammal extinctions are driven only by environmental factors (16). But it is not just bad news for large mammals: they enjoy higher origination rates, and therefore their overall diversity is maintained. Even though community energy use is independent of body size (60, 61), large and small mammals, with their different specific production rates and life styles (34), respond differently to the same general environment. Paleobiological analyses (this study), combined with analyses clarifying how life history affects evolutionary and ecological patterns (34) inform us with greater confidence which kinds of species are more vulnerable to climatic fluctuations and trends, not the least of which are seen in the current climate crisis.

Materials and Methods

Data. The data we used are species occurrences of Neogene Old World land mammals from the NOW database (38) accessed on June 26, 2007. These data are based on published accounts of species occurrences at named sites (localities), vetted for taxonomic inconsistencies. We exclude localities east of 60°E, localities in Afro-Arabian countries, for the purpose of including only European Neogene localities for which we have greater confidence in both age estimates of localities and taxonomic identifications of samples. The occurrence data we used include specimens unidentified at the species level (i.e., with the suffixes sp., cf., and indet.), but any discussion of species results reflects only species that are fully identified. Our resulting dataset covers the longitudes 9.13°W to 58.9°E and latitudes 30.86°N to 55.0°N. Volant and marine mammals were excluded, but all trophic levels are represented.

Locality ages in the NOW database are recorded as minimum and maximum age estimates based on various combinations of direct dates (e.g., radiometric) and time units (62–66). In our analyses, locality ages are the means of minimum and maximum age estimates. However, we remove all localities with maximum minus minimum ages greater than the duration of the MN-unit into which the mean age falls, according to the chronology of Steininger *et al.* (62).

We have used both the full dataset as described in the previous paragraphs (All) and various subsets of it in our analyses. In the subset 5.occ, we include only genera that appear at least five times in the data, in which case we lose some localities that are potentially taxon rich. Conversely, in 5.taxa, we exclude localities that have fewer than five genera. Therefore, some genera could have been removed from analyses simply by association with those poorer localities. Similarly, 10.occ.10.taxa is the data subset where, first, only genera that appear at least 10 times in the data are retained, and then those sites with at least 10 genera. We ran analogous analyses for species but do not present all results for economy and clarity.

Durations. For the calculation and comparisons of untruncated taxon durations (in Fig. 1, Fig. S1, and Table 1), we used the following approach to remove potentially extant taxa in our fossil data. We first excluded taxa that appear at localities that are 0.5 M.y. old and younger and then further excluded taxa known to be living today (see SLOH) within the geographic bounds of the NOW data we are using. This is a highly conservative approach to removing extant or very recently extinct taxa. However, less conservative approaches (e.g., doing only the

second sweep of exclusion) do not change results. Note that the analyses described in the next sections do not require any removal of extant taxa because one-side truncation of stratigraphic ranges is not a problem in rate calculations, as it is in duration calculations.

Per Capita Rates. For each data subset, we tabulated whether a genus was recorded as present or absent during time bins that span 1, 1.5, or 2 M.y. These alternative binning schemes were done to check for the robustness of our results with respect to the variability in the uncertainty of locality ages. If a genus was absent during one or more time bins, but was present in some time bin before and after those absences, it was assumed to have survived those time intervals. We calculated per capita extinction (q) and origination (p) rates (67) for large and small mammals separately in each dataset, where

$$p = \ln(N_t/N_b)/\Delta t,$$

$$q = \ln(N_b/N_{bt})/\Delta t$$

and N_{bt} is the number of taxa that cross both the earlier (bottom) and the later (top) boundary of a time bin, N_t is the number of genera that cross only the later of the time bins, N_b the number that cross only the earlier boundary of the time bins, and Δt is the width of the time bins, following ref. 67. We use per capita rates, based on boundary crossers, because they are relatively insensitive to secular trends in the quality of preservation (67). Even though the observed first and last occurrences of taxa may be temporally quite far removed from the true time of origination and extinction, even in densely sampled datasets (68), there is a strong positive correlation between the ranks of observed ranges and estimates of true durations (see ref. 69).

CMR Estimates. Capture-mark-recapture (CMR) methods have many powerful applications in ecology (70, 71) and are gradually finding their way into the paleobiological literature (70–72). Our purpose of employing CMR methods is to estimate both survivorship and preservation probabilities with the aim of investigating the effect of body size on both probabilities. By using a CMR approach, we also control for differences in preservation among large and small mammals. We compared time-varying estimates of survival (Φ) and preservation (pr) probabilities with either no body size effect, or additive or multiplicative effects of body size using a model selection approach (73) (see *S1 Text* for more details).

Body Size Groups. Body size estimates for individual genera are not available for a substantial portion of fossil taxa in the NOW database. Therefore, we assigned to each genus one of two size classes, based on their taxonomic identity. All genera belonging to the orders Insectivora, Rodentia, and Lagomorpha are designated “small.” All remaining genera are regarded as “large,” namely Artiodactyla, Carnivora, Creodonta, Hyracoidea, Perissodactyla, Primates and Proboscidea, and Tubulidentata (74). In the absence of body size estimates for a large proportion of species in NOW, we justify our use of this coarse classification as follows. Bimodality in the body size distribution of mammals (26, 75, 76) has existed and intensified since the Eocene (45, 77). Moreover, body sizes are constrained by phylogeny with mammalian taxa having characteristic sizes over both space and time (78, 79). In addition, we used a nearest living relative approach to estimate mean body masses for the genera in the NOW database where possible (see next section for details).

SLOH. We used MammalBase, a database of living mammal attributes, based on refs. 80–83, compiled by one of us (K.L.), to extract SLOH information on extant species. SLOH attributes for genera used in this article are attached in Table S4 in Dataset S1 but further information is available on request. We coded all known extant species for SLOH behavior according to whether they (i) are hibernators, (ii) go into torpor, (iii) can be dormant, (iv) can go into aestivation mode, (v) make or use burrows or are fossorial, (vi) make or use tunnels or chambers, (vii) live in tree holes, or (viii) are cave dwellers. If one of these eight nonmutually exclusive traits is present for a given species, we coded it as 1 for its SLOH value and 0 if none was observed (Table S4 in Dataset S1). However, for data analyses, we treated the absence of mention of these traits as zeros instead of “NA” as coded, because of the common practice of not noting absent traits. If a NOW genus has any living species for which any one of the SLOH attributes is tabulated as present, we assign a SLOH value of “1” to that NOW genus and therefore to all of the NOW species that are members of the genus (nearest living relative approach). Additionally, one of us (L.F.) manually checked the entries described above and presented in Table S4 in Dataset S1, to ensure the quality of the data. L.F. provided alternative coding, and we show results based on amended assignments in Table S4 in

Dataset S1. These amendments, however, do not change our qualitative results or general conclusions.

Body Mass Estimates. With reference to the previous sections, for NOW genera with living species for which body masses are known from MammalBase, we similarly calculated the mean body mass from these living species and used these as mean body mass estimates for these genera. To supplement body mass data from MammalBase, we used body mass data compiled by two National Center for

Ecological Analysis and Synthesis (NCEAS) working groups (ref. 84 and J. Damuth, personal communication).

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