

SPATIAL SCALING OF SPECIES COMPOSITION: BODY MASSES OF NORTH AMERICAN LAND MAMMALS

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Abstract.—We describe the nonrandom assembly of the North American terrestrial mammalian fauna based on body size and spatial scale. The frequency distribution of body masses among species for the entire continental fauna was highly modal and right skewed, even on a logarithmic scale; the median size of the 465 species was approximately 45 g. In contrast, comparable frequency distributions for 24 small patches of relatively homogeneous habitat were essentially uniform, with approximately equal numbers of species in each logarithmic size class; the median sizes of the 19–37 species ranged from approximately 100 to 2,500 g. Frequency distributions for 21 biomes (large regions of relatively similar vegetation) were intermediate between the continental and local assemblages. This pattern of assembly indicates that species of modal size (20–250 g) tend not to coexist in local habitat patches and they replace each other more frequently from habitat to habitat across the landscape than species of relatively large or small size. We hypothesize that three mechanisms are necessary and possibly sufficient to produce this result: competitive exclusion of species of similar size within local habitats, differential extinction of species of large size with small geographic ranges, and greater specialization of modal-sized species owing to energetic and dietary constraints.

The diversity and composition of biotas vary with spatial scale. The increase in species richness with sample area has been quantified by species-area relationships for nonisolated sites within continents, as well as for islands or insular habitat patches and continents of varying sizes (see, e.g., MacArthur and Wilson 1967; Flessa 1975; Schoener 1976; Connor and McCoy 1979; Brown and Gibson 1983; Brown 1986). Here, we address the question of whether there are other changes in the composition of the biota as species diversity increases with increasing spatial scale.

Because different processes affect biotic composition on different scales (see, e.g., Orians 1980; Ricklefs 1987), we would expect these processes to result in predictable changes in the attributes of species. On the largest scales, entire continents or large geographic regions within continents, species-level processes such as colonization, extinction, and speciation affect biotic composition. On the smallest scales, within small patches of homogeneous habitat, ecological interactions of species with each other and with the abiotic environment determine which combinations of species coexist. It is also on these small scales that microevolutionary processes of natural selection and genetic drift operate within populations. On intermediate scales, both macroscopic and microscopic processes cause changes in species composition across the landscape. However, processes

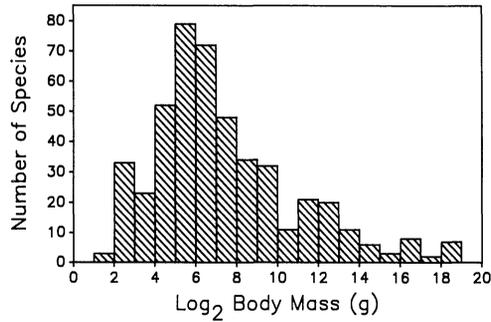


FIG. 1.—Frequency distribution, on a \log_2 scale, of the body masses of the 465 species of terrestrial North American mammals. Note the characteristic modal, right-skewed shape.

operating on disparate scales are partially coupled. Macroscopic biogeographic and evolutionary processes affect microscopic community structure because local ecological communities are assembled from continental and regional species pools. Conversely, microscopic ecological and evolutionary processes affect the composition of continental and regional assemblages because large-scale biotas reflect the cumulative effects of phenomena that occur in many local communities.

In this article we use the distribution of body sizes among species of North American land mammals to assess one aspect of variation in faunal composition with spatial scale. Body size is an easily measured variable that is closely correlated with many aspects of morphology, physiology, behavior, and ecology through allometric relations (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Zeveloff and Boyce 1988). In 1959, Hutchinson and MacArthur called attention to the distribution of body sizes among species of North American mammals (fig. 1). On a logarithmic scale, this distribution is highly modal and skewed toward larger body sizes. Qualitatively similar distributions have since been found for a wide range of organisms, from birds and insects (May 1978, 1988; Morse et al. 1988) to bacteria (Bonner 1988).

We characterize the variation in the distributions of body sizes among species with respect to spatial scale by comparing the frequency distributions for three scales: the entire North American continent, regional biomes, and local habitat patches. We reject the null hypothesis that the sizes of mammals co-occurring on successively smaller spatial scales are random subsamples of the larger species pools. We propose mechanistic hypotheses to account for the observed pattern of faunal assemblage.

METHODS

We compiled species lists (App. A) of terrestrial North American mammals for three different spatial scales: (1) the entire North American continent, including Mexico, (2) 21 biomes as defined and mapped by Dasman (1975), and (3) 24 small patches of relatively homogeneous habitat. The North American species list was

taken from Hall (1981) and supplemented with Mexican species from Ramirez-Pulido et al. (1986). Species lists for the biomes were compiled by using the range maps in Hall (1981) to determine the occurrence of species in the biomes mapped by Dasman (1975). Species lists for the local habitats were obtained from the literature or from colleagues who contributed unpublished data from intensive field studies. We tried to ensure that the local habitats represented a small area (usually 10–1,000 ha) of uniform geology and vegetation and that the faunal list included all species that utilized the habitat at the time of colonization by European humans. The analyses included all species of native mammals except bats, pinnipeds, cetaceans, and the sea otter.

A single value of body mass was assigned to each species wherever it occurred; we ignored intraspecific geographic variation. The body masses were obtained from field guides (Burt and Grossenheider 1976; Whitaker 1980), from G. Ceballos (personal communication) for most Mexican species, and, in the few cases where masses were unavailable, from estimation based on comparisons with closely related species of similar head and body length.

The analysis focused on the frequency distributions of species in logarithmic (\log_2 ; see App. B for size categories) body-size categories. We used \log_2 intervals because most previous analyses have been based on log-transformed data and because base 2 divides the fauna into a convenient number of categories (see, e.g., Preston 1962). Using logarithmic size categories makes our analyses insensitive to small errors in assigning body masses to species (such as may be caused by intraspecific geographic variation).

The distributions of body masses among species for biomes and local habitats were compared with null models that assumed that species were assembled at random from appropriate larger-scale species pools. Each of the 21 biome distributions was compared with the North American distribution by drawing at random 500 times from the continental species pool the same number of species as occurred in that biome. The median was calculated for each of the 500 simulations; the number of simulated medians out of 500 was compared with the observed value to evaluate the null hypothesis that the biome was a random subsample of the continental species pool. A similar procedure was used to compare the distributions for 24 local habitats and 24 simulations, each consisting of 500 random draws from the biome distributions in which each of those habitats was located.

Inspection suggested that the North American distribution was highly modal and that the distributions for biomes and local habitat patches became progressively more uniform. We quantified this change in shape by comparing all distributions to a log-uniform distribution, with the same range as the North American distribution, by using the Kolmogorov-Smirnov D_n statistic and test.

If the distributions of body sizes change with spatial scale, there must be a differential replacement of certain size classes between biomes and especially between local habitats. In other words, different size classes should show different degrees of beta diversity. There are two ways species can change status from absent to present (or vice versa) between habitats. A species may be replaced because the border of its geographic range has been crossed. Alternatively, a

TABLE 1
SUMMARY STATISTICS FOR FREQUENCY DISTRIBUTIONS OF LOG_2 OF BODY MASSES (IN GRAMS) FOR
MAMMALS OF NORTH AMERICA AND 21 NORTH AMERICAN BIOMES

Biome Number	Region	N	Median	Minimum	Maximum	Interquartile Range	Standard Skewness
All	North America	464	6.4	1.6	18.9	4.1	9.2
1	Sitkan	46	10.2	2.3	18.9	7.8	.4
2	Oregonian	77	8.1	2.8	18.9	6.5	1.9
3	Yukon taiga	46	10.1	1.6	18.8	8.9	.3
4	Canadian taiga	72	8.0	1.6	18.9	8.4	1.4
5	Eastern forest	74	8.4	1.6	18.9	7.2	1.3
6	Austroriparian	59	8.4	1.6	18.9	7.6	1.2
7	Californian	88	7.0	2.6	18.9	6.3	2.8
8	Sonoran	102	7.6	2.6	18.9	7.1	2.5
9	Chihuahuan	113	7.3	2.3	18.9	6.4	2.9
10	Tamaulipan	66	10.0	2.3	18.7	7.7	.3
11	Great Basin	95	8.1	1.6	18.9	6.4	2.3
12	Alaskan tundra	37	10.8	2.3	18.8	8.5	.0
13	Canadian tundra	38	10.6	2.3	18.8	8.6	.4
14	Grasslands	115	8.5	2.3	18.9	7.1	1.7
15	Rocky Mountains	110	7.6	1.6	18.9	6.6	2.3
16	Sierra-Cascade	108	7.1	2.3	18.9	6.4	2.8
17	Madrean-Cordilleran	182	7.1	2.3	18.9	6.2	3.4
18	Campechean	95	8.2	2.3	18.2	6.4	1.3
19	Guerreran	119	7.6	2.3	18.2	5.9	2.4
20	Sinaloan	84	7.6	2.6	17.0	7.0	2.0
21	Yucatecan	51	11.6	2.8	18.2	5.4	- .5
Biome mean		82.2	8.6	2.2	18.7	7.0	1.5

species with specialized habitat requirements may not occur in some of the habitat types within its geographic range. For each of the 24 local habitats, we compiled two frequency distributions of body sizes, one containing those species in the continental species pool whose geographic ranges did not include the habitat and the other containing those species in the continental pool whose geographic range did include the site but that did not occur in that habitat. Then we summed each kind of list with redundancy (counting each species repeatedly, as many times as it occurred) to determine the overall shapes of the distributions for species exhibiting the two kinds of replacement between habitats. For most habitats this was straightforward, because the authors of the local species lists included information on the occurrence of species in the other habitat types within that local area. In three cases, these local lists were not available and we used other published sources to determine which species had geographic ranges that included the site but were found in adjacent habitats.

RESULTS

The frequency distributions of body masses of North American terrestrial mammals varied with the spatial scale of the sample: the medians and interquartile ranges increased and the skewness decreased from continent to biome to local habitat patch (tables 1 and 2). The distribution for the entire continental fauna

TABLE 2

SUMMARY STATISTICS FOR FREQUENCY DISTRIBUTIONS OF LOG₂ OF BODY MASSES (IN GRAMS) FOR NORTH AMERICAN MAMMALS IN 24 LOCAL PATCHES OF UNIFORM HABITAT

Local Habitat Patch Number	Locality	Habitat Type	Biome	N	Median	Minimum	Maximum	Interquartile Range	Standard Skewness	Sources
1	White Sands, N.Mex.	Chihuahuan desert	9	34	8.4	3.2	16.8	5.8	.7	Anonymous 1987
2	Bernalillo Co., N. Mex.	Riparian forest	9	31	12.0	2.6	18.9	6.9	-.5	Hink et al. 1984
3	Deep Canyon, Calif.	Pine forest	8	18	9.7	5.1	16.8	6.9	.6	Ryan 1968
4	Deep Canyon, Calif.	Pinon/Juniper	8	23	9.8	2.6	16.8	8.7	.1	Ryan 1968
5	Deep Canyon, Calif.	Agave/Ocotillo	8	26	8.6	2.6	16.8	8.1	.8	Ryan 1968
6	Cochise Co., Ariz.	Chihuahuan desert	9	32	7.6	3.2	16.8	8.3	1.0	J. H. Brown, personal communication
7	Barge Canal, Fla.	Longleaf pine	6	19	7.6	5.1	25.7	16.7	4.5	Anonymous 1976
8	Barge Canal, Fla.	Scrub oak	6	22	10.7	2.3	17.1	7.7	.0	Anonymous 1976
9	Barge Canal, Fla.	Pine flatwoods	6	18	10.8	1.6	17.1	7.7	-.3	Anonymous 1976
10	Chamela, Jalisco, Mexico	Deciduous forest	19	27	12.0	4.8	16.8	5.3	-.5	Ceballos and Miranda 1986
11	Chamela, Jalisco, Mexico	Evergreen forest	19	28	11.8	4.8	16.8	6.8	-.1	Ceballos and Miranda 1986
12	Green Mountains, Vt.	Spruce/Fir	5	34	10.1	2.3	18.9	7.9	.1	J.F. Merritt, personal communication
13	Ligomier Valley, Pa.	Deciduous forest	5	30	8.8	1.6	18.9	8.8	.5	J.F. Merritt, personal communication
14	Cook Co., Minn.	Aspen/Birch	4	22	8.9	2.3	17.4	8.6	.3	Timm 1975
15	Cook Co., Minn.	White pine	4	25	7.6	2.3	17.4	8.4	.7	Timm 1975
16	Animas Mountains, N. Mex.	Oak forest	17	28	12.0	2.6	18.5	7.7	-.8	Cook 1986
17	Sagehen, Calif.	Jeffrey pine	16	29	9.4	2.8	18.9	8.2	.6	Morrison et al.
18	Cascade Mountains, Oreg.	Alpine tundra	16	29	8.4	2.8	18.9	9.9	.6	E.R. Brown 1985
19	Cascade Mountains, Oreg.	Sage	16	36	8.1	2.6	18.5	8.2	1.0	E.R. Brown 1985
20	Cascade Mountains, Oreg.	Ponderosa pine	16	37	10.4	4.0	18.9	7.9	.2	E.R. Brown 1985
21	Lac Qui Parle Co., Minn.	Upland prairie	14	23	11.0	2.3	18.9	10.4	.0	E. Birney and G. Nordquist, personal communication
22	Washington Co., Minn.	Shrub swamp	4	29	10.8	2.3	17.1	8.4	-.2	E. Birney and G. Nordquist, personal communication
23	Norman Co., Minn.	Willow swamp	14	32	11.2	2.3	18.8	8.6	-.1	E. Birney and G. Nordquist, personal communication
24	Konza Prairie, Kans.	Tallgrass prairie	14	31	8.5	2.3	18.9	10.7	.3	Finck et al. 1986
Habitat mean				27.6	9.8	3.8	17.3	8.4	.4	

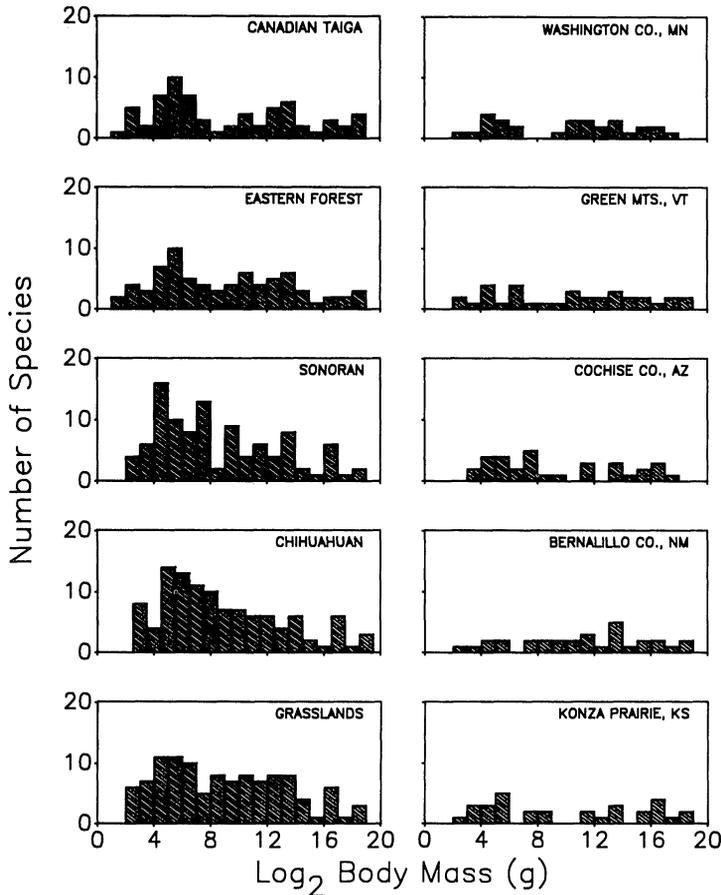


FIG. 2.—Frequency distributions, on a \log_2 scale, of the body masses of terrestrial mammals inhabiting five biomes and five local patches of uniform habitat within those biomes. Note that the biome distributions are all highly modal, but the habitat distributions are all nearly uniform on the logarithmic scale.

was highly modal and significantly right skewed; the mode was in size class 5, approximately 45 g (fig. 1). In contrast, the distributions for all 24 local habitats had an approximately equal number of species in each logarithmic size category (fig. 2); these distributions were all statistically indistinguishable from log-uniform distributions (table 3). The distributions for the biomes were intermediate between those for the continent and those for the local habitats (fig. 2); nine of the 21 biomes did not differ significantly from log-uniform distributions (table 3).

Neither the biomes nor the local habitats were random samples of the species pools on the next larger scale, continent and biomes, respectively. All 21 biome distributions had medians significantly ($P < .05$; <25 of 500 simulations) larger than the North American distribution. Nine of the 24 local habitat patches had medians significantly larger than the simulated medians ($P < .05$), and an addi-

TABLE 3

COMPARISONS OF THE DISTRIBUTIONS OF BODY SIZES FOR NORTH AMERICA, 21 BIOMES, AND 24 LOCAL HABITAT PATCHES WITH A LOG-UNIFORM DISTRIBUTION, USING THE KOLMOGOROV-SMIRNOV TEST

	<i>Dn</i>	<i>P</i> value	
North America	.32	.0000	
Biome:			
Sitkan	.10	.9999	
Oregonian	.16	.0464	
Yukon taiga	.11	.9992	
Canadian taiga	.16	.0618	
Eastern forest	.13	.1889	
Austroriparian	.14	.2009	
Californian	.23	.0001	
Sonoran	.21	.0001	
Chihuahuan	.22	.0001	
Tamaulipan	.20	.4693	
Great Basin	.16	.0116	
Alaskan tundra	.08	1.0000	
Canadian tundra	.11	.9999	
Grasslands	.15	.0128	
Rocky Mountains	.17	.0034	
Sierra-Cascade	.20	.0003	
Madrean-Cordilleran	.20	.0001	
Campechean	.21	.0001	
Guerreran	.22	.0001	
Sinaloan	.18	.0079	
Yucatecan	.16	.1626	
	Habitat	<i>Dn</i>	<i>P</i> value
Locality:			
White Sands, N.Mex.	Chihuahuan desert	.18	.2078
Bernalillo Co., N.Mex.	Riparian forest	.12	.9999
Deep Canyon, Calif.	Pine forest	.13	.9999
Deep Canyon, Calif.	Piñon/Juniper	.16	.9999
Deep Canyon, Calif.	Agave/Ocotillo	.17	.4057
Cochise Co., Ariz.	Chihuahuan desert	.21	.1157
Barge Canal, Fla.	Longleaf pine	.19	.5303
Barge Canal, Fla.	Scrub oak	.13	.9996
Barge Canal, Fla.	Pine flatwoods	.13	.9999
Chamela, Jalisco, Mexico	Deciduous forest	.24	.0876
Chamela, Jalisco, Mexico	Evergreen forest	.19	.2611
Green Mountains, Vt.	Spruce/Fir	.07	1.0000
Ligonier Valley, Pa.	Deciduous forest	.14	.9991
Cook Co., Minn.	Aspen/Birch	.15	.9998
Cook Co., Minn.	White pine	.18	.4121
Animas Mountains, N.Mex.	Oak forest	.16	.4658
Sagehen, Calif.	Jeffrey pine	.12	.9999
Cascade Mountains, Oreg.	Alpine tundra	.17	.4053
Cascade Mountains, Oreg.	Sage	.13	.5224
Cascade Mountains, Oreg.	Ponderosa pine	.08	1.0000
Lac Qui Parle Co., Minn.	Upland prairie	.09	1.0000
Washington Co., Minn.	Shrub swamp	.10	.9999
Norman Co., Minn.	Willow swamp	.11	.9999
Konza Prairie, Kans.	Tallgrass prairie	.19	.2009

NOTE.—The North American and biome distributions were compared with a log-uniform distribution with the same range as the observed North American distribution, and the local habitats were compared to a log-uniform distribution with the same range as the biome in which they occurred. For each comparison the Kolmogorov-Smirnov *Dn* statistic and the probability value are given.

TABLE 4

RESULTS OF SIMULATIONS TO EVALUATE THE NULL HYPOTHESIS THAT THE BODY-SIZE DISTRIBUTIONS FOR EACH OF THE 24 LOCAL HABITATS ARE A RANDOM SUBSET OF THE BIOME POOL IN WHICH THAT HABITAT IS LOCATED

HABITAT	MEDIAN		
	Observed	Simulated	Proportion of Simulations That Are Less than Observed Value
White Sands, N.Mex.	8.4	7.29	.088
Bernalillo Co., N.Mex.	12.0	7.54	.001
Deep Canyon, Calif.	9.7	7.38	.096
Deep Canyon, Calif.	9.8	7.46	.048
Deep Canyon, Calif.	8.6	7.29	.156
Cochise Co., Ariz.	7.6	7.09	.386
Barge Canal, Fla.	7.6	7.12	.736
Barge Canal, Fla.	10.7	8.61	.060
Barge Canal, Fla.	10.8	8.59	.090
Chamela, Jalisco, Mexico	12.0	7.78	.001
Chamela, Jalisco, Mexico	11.8	7.77	.001
Green Mountains, Vt.	10.1	7.72	.068
Ligonier Valley, Pa.	8.8	8.80	.384
Cook Co., Minn.	8.9	7.23	.382
Cook Co., Minn.	7.6	6.69	.432
Animas Mountains, N.Mex.	12.0	8.38	.004
Sagehen, Calif.	9.4	7.16	.002
Cascade Mountains, Oreg.	8.4	6.99	.168
Cascade Mountains, Oreg.	8.1	6.99	.168
Cascade Mountains, Oreg.	10.4	7.35	.001
Lac Qui Parle Co., Minn.	11.0	8.42	.058
Washington Co., Minn.	10.8	7.36	.004
Norman Co., Minn.	11.2	8.53	.001
Konza Prairie, Kans.	8.5	7.70	.238

NOTE.—The probability of failing to reject each null hypothesis is given as the proportion of the 500 simulations that are less than the observed value for medians.

tional six patches were marginally significantly larger ($P < .10$) than the random draws from the biome in which they were located (table 4). The medians for the local habitat patches were all significantly larger than the medians of random draws from the North American distribution.

The only way to account for the progressive flattening of the frequency distributions from continental to biome to local scales is by high spatial replacement of species in the modal size classes. This is reflected in the limited habitat distributions and small geographic ranges of these species compared to their larger relatives. The vast majority of species in the smaller size categories (less than class 12, approximately 1 kg) occurred in four or fewer biomes, whereas the majority of species in the larger size categories occurred in eight or more biomes (fig. 3). An even clearer pattern is apparent for the areas of geographic ranges: a substantial proportion of the species in the smaller size categories (less than class 13) had ranges of less than 100,000 km², whereas all species in the larger size classes had ranges that exceeded this area (fig. 4).

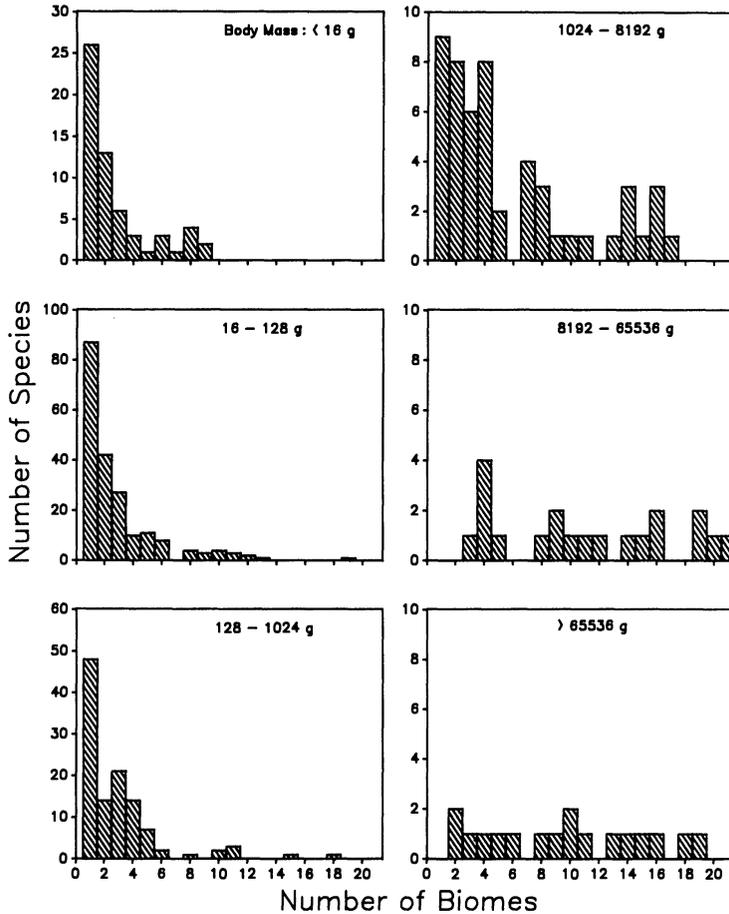


FIG. 3.—Frequency distributions of species in different body-size classes according to the numbers of biomes where they occur. Note that species of small size tend to occur in few biome types, whereas the majority of species in the larger size classes inhabit many biomes.

The composition of species may vary among habitats across the landscape for two reasons: because these species have limited geographic ranges or because they do not occur in all the habitats within their geographic ranges. It is of interest to assess the contributions of these two phenomena to the replacement of different-sized species among local habitats. For each local habitat, we determined the identity and body mass of those species in the continental species pool that were absent because they either had a geographic range that did not encompass the site or had a geographic range that included the site but did not occur in that habitat. These are illustrated in figure 5, which shows the frequency distributions of body masses of the species in these two categories summed with redundancy for the 24 local habitats. Note the general similarity in these distributions, although there were proportionately more medium-sized species (classes

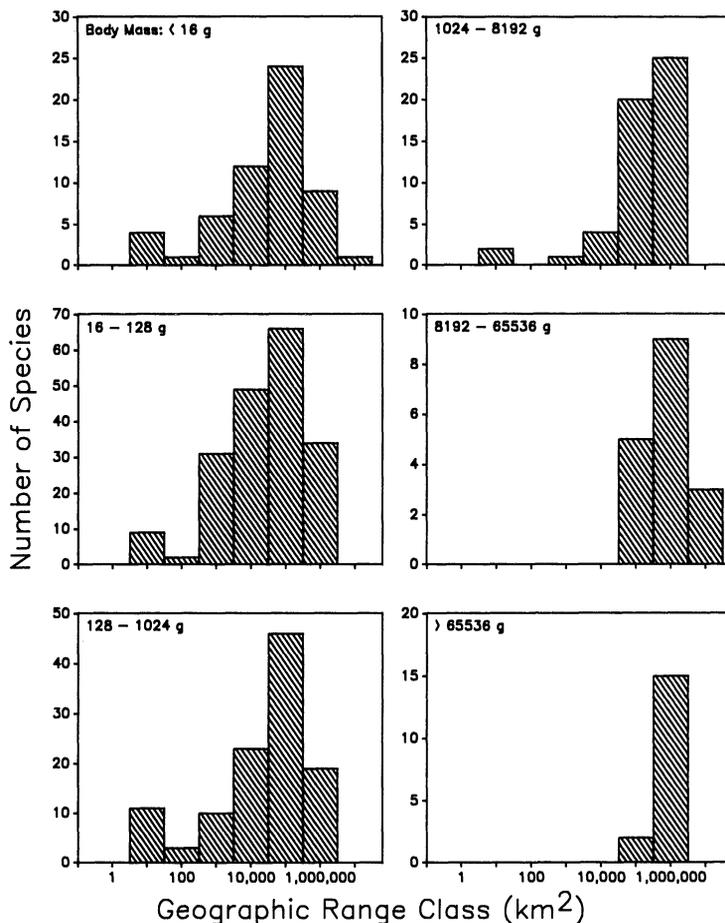


FIG. 4.—Frequency distributions of species in different body-size classes according to the areas of their geographic ranges (measured by planimetry from maps in Hall 1981). Note that many species of small size have restricted geographic ranges, whereas most species of large size are distributed over large areas.

9–13) in category 2. Species in the modal size classes replaced each other more rapidly across the landscape both because they had more restricted geographic ranges and because they occurred in a smaller proportion of habitat types within their geographic ranges.

DISCUSSION

Patterns

We have shown what appears to be a general pattern of spatial scaling of North American terrestrial mammalian assemblages with respect to body size. The distribution of body masses for the continent as a whole is highly modal and skewed

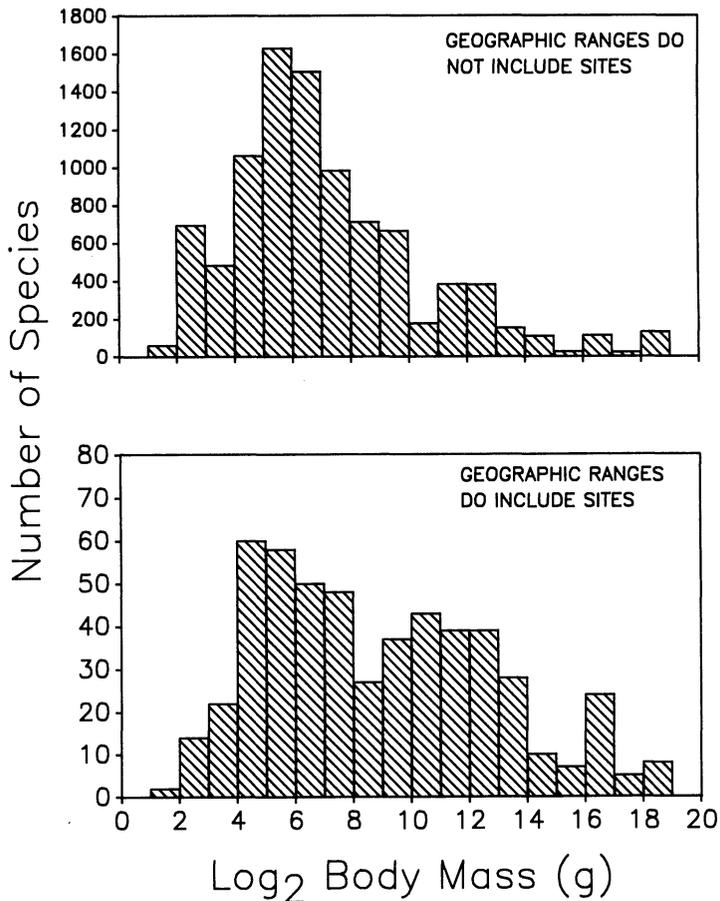


FIG. 5.—Frequency distributions of body masses summed with redundancy (see text) for the two classes of species that did not occur in the 24 local habitat patches: those whose geographic ranges did not include the local sample sites (*top*) and those whose geographic ranges did encompass the sites even though they did not occur in the habitats sampled (*bottom*). Note that both distributions are modal and right skewed.

toward larger size classes (fig. 1). The frequency distributions for small patches of homogeneous habitat have ranges of body sizes similar to those of the North American distribution, but they contain an approximately equal number of species in each logarithmic size class (fig. 2). The distributions for biomes, which are intermediate in area and habitat diversity between the continent and the local habitats, are intermediate in shape between the North American and the habitat distributions. These patterns characterize the composition of the mammalian faunas on these scales before the impact of European humans. Hunting, trapping, habitat changes, and other human impacts within the last three centuries have caused the local extirpation of a few species; human introductions of alien species have resulted in the colonization of some additional species. These recent changes

in species composition were not sufficient, however, to change the shapes of the above distributions to any substantial extent.

The North American mammalian fauna experienced additional changes in the period 500–20,000 yr ago when catastrophic extinctions occurred (Martin and Klein 1984). Although the causes of these losses are hotly debated, humans may have played a substantial role. It is clear that large species suffered more extinctions (Martin 1984; Webb 1984). These extinctions were not sufficient, however, to affect the qualitative patterns reported here. Despite the number of species and genera that were lost, the frequency distribution of body masses for North American fauna prior to the Quaternary extinctions still has a mode and right skew similar to the distribution for the contemporary fauna (R. Rusler, personal communication). Similarly, the addition of species known or presumed to have become extinct within the last 20,000 yr to the local habitats would have extended the range to larger size categories in some cases but would not have substantially altered the shape of the frequency distributions.

The shape of the continental distribution, first emphasized by Hutchinson and MacArthur (1959), appears to be typical of the frequency distributions of body sizes of species in diverse taxa from large geographic regions (May 1978, 1988; Bonner 1988). An explanation for this pattern in mammals, and perhaps in other organisms, must take into account the changes in the frequency distributions with spatial scale. The continental mammalian fauna is not simply the sum of species assemblages on smaller spatial scales, and the faunas of local habitats and biomes are not just random subsamples of the species pools on large spatial scales. Species near the modal size of approximately 45 g replace each other frequently between habitats and biomes, whereas species of large size tend to have large geographic ranges and to occur in a large proportion of the habitats (figs. 3 and 4).

Hypotheses

We offer the following hypotheses to explain this pattern: (1) competitive exclusion tends to prevent local coexistence of similar-sized species with similar resource requirements, (2) differential extinction of species of large size with small geographic ranges tends to limit the number of large species in the continental fauna, and (3) allometric energetic constraints cause modal-sized species to be more specialized in their use of resources than larger species. We develop each of these hypotheses in more detail below.

Competitive exclusion among similar-sized species.—Since the faunas of local habitats contain fewer modal-sized species than random samples of assemblages from larger spatial scales, it appears that some local process prevents coexistence of species of similar size. Competitive exclusion is the most likely process to have this effect. If such competition occurs, however, its impact should be limited to those species that share requirements for the same limited resources. Competitive exclusion should occur within but not between feeding guilds. There is substantial evidence for interspecific competition among species of mammals and other organisms with similar diets (see, e.g., Hutchinson 1959; McNab 1963; Rosenzweig 1966; MacArthur 1972; Brown 1975, 1987; Pacala and Roughgarden

1982, 1985; Brown and Munger 1985; Grant 1986). In at least some of these cases, competition appears to account for the tendency of local communities to be composed of species that are more different in body size than expected from random assemblages drawn from appropriate species pools (see, e.g., Schoener 1970, 1984; Brown 1973; Simberloff and Boecklen 1981; Bowers and Brown 1982; Brown and Bowers 1985; Hopf and Brown 1986). It is hypothesized that the log-uniform distributions on the scale of habitats reflect the fact that local assemblages are composed of multiple guilds, each of which tends to have its own log-uniform distribution. For example, if mammals are divided into two very general trophic groups, herbivores and carnivores, most habitats contain representatives from each group that vary in size from less than 20 g to more than 100 kg.

Large species with small geographic ranges have high extinction probabilities.—The fact that large species exhibit low beta diversity (low replacement between habitats and geographic regions) suggests that some large-scale process prevents the accumulation of high diversity of large mammals in the continental fauna. We hypothesize that this process is the selective extinction of species with large body sizes and small geographic ranges. Individuals of large size have large resource requirements, and as a result they require large home ranges and occur at low population densities (McNab 1963; Schoener 1968; Parra 1978; Harestad and Bunnell 1979; Damuth 1981; Peters 1983; Peters and Raelson 1984). As a consequence, species of large size with small geographic ranges have small total population sizes and should be differentially susceptible to extinction (MacArthur and Wilson 1967; Brown 1981; Pimm et al. 1988; Schoener and Spiller 1988). If extinction is caused exclusively by demographic variation (in the absence of major environmental change), critical population sizes for persistence are very small, and even small geographic ranges would often contain sufficient individuals to avoid extinction. If, on the other hand, extinction is caused by environmental variation, even relatively large, dispersed populations may be at risk (Goodman 1987).

We hypothesize that environmental changes have been a major cause of mammalian extinctions and that these changes have differentially affected the species in each size class with the smallest geographic ranges. The observation that the minimum size of geographic ranges of large species is larger than that of modal-sized species (Brown 1981; Rapoport 1982; Brown and Maurer 1987, 1989; see also fig. 4) is consistent with this hypothesis, as is the observation that mammals and other organisms of large size have been differentially susceptible to historical perturbations that caused mass extinctions (Martin and Klein 1984; Webb 1984).

Large mammals may also have lower speciation rates than their smaller relatives. Large species tend to have greater vagility and broader environmental tolerances, and these should result in less isolation and genetic differentiation of populations and in lower speciation rates than in small species. While lower speciation rates might contribute to the low diversity of large mammals in the continental fauna, they are not sufficient to account for the failure to observe large species with small geographic ranges.

Specialization of modal-sized species.—A correlate of body size that is related to both of the above hypotheses is the apparently greater specialization of modal-sized species. Not only does the greatest number of mammalian species occur in the size range of 20–250 g, but species within this size range exhibit greater turnover among habitats and on the average have smaller geographic ranges (figs. 3, 4). This suggests that modal-sized species are more frequently limited by variation in the physical environment, the presence of other organisms, or both processes than their larger relatives. We hypothesize that this specialization is not simply a consequence of geographic and habitat distribution (in which case the above arguments would be circular) but is caused by allometric constraints on physiology and energetics.

It is well-known that energetic and basic nutrient requirements (D) of individuals scale as a fractional exponent of body mass (M) as $M^{0.67}$ to $M^{0.75}$ (Peters 1983; Calder 1984). Although the following qualitative argument does not depend on the precise value of the exponent, we will assume that the daily energy demand of free-living mammals scales as

$$D = c_1 M^{0.75}, \quad (1)$$

where c_1 is a constant (Nagy 1987). The rate of food intake in a variety of mammals also scales as $M^{0.75}$ (Calder 1984). However, larger animals have larger and longer alimentary tracts; in both herbivorous and carnivorous mammals gut capacity (A) scales as approximately

$$A = c_2 M^{1.0}, \quad (2)$$

where c_2 is another constant (Calder 1984). As a consequence, larger animals retain food in the gut for a longer period; turnover time (T) for gut contents scales as approximately

$$T = c_3 M^{0.25}, \quad (3)$$

where c_3 is another constant (Calder 1984). This enables larger animals to ingest poorer-quality food and, by subjecting it to digestion for a longer period, still to extract sufficient energy and nutrients to meet their requirements. Thus, diet quality scales inversely and digestive efficiency scales directly with body size.

The food quality (Q) necessary to meet requirements can be predicted from the ratio of metabolic demand to gut capacity; it should scale as

$$Q = D/A = c_4 M^{-0.25}, \quad (4)$$

where c_4 is another constant. The best data to evaluate this prediction are for ruminant mammals (Hoppe 1977; Sibly 1981; du Toit and Owen-Smith 1989). The predicted value of -0.25 is very close to those (-0.20 to -0.27) estimated by McNaughton and Georgiadis (1986). We also used data on 14 species of African ruminants from Hoppe (1977; cited in Sibly 1981) to obtain another estimate of the scaling exponent for food quality. We performed a regression of the reciprocal of reticulo-rumen contents divided by metabolic demand against body mass and obtained an exponent of -0.351 ± 0.088 .

We hypothesize that these physiological constraints on food quality force smaller animals to specialize in higher-quality foods and to restrict their foraging to habitats where suitable foods are available in sufficient supply. Even small omnivorous species should be subject to these allometric relations and should restrict their diets to foods of high energetic and nutritional value. Other constraints of body size, such as those on reproductive and life-history traits (see, e.g., Eisenberg 1981; Peters 1983; Calder 1984), increase the nutritional demands on smaller organisms and tend to reinforce the selection to specialize on foods and habitats. Another mechanism must be hypothesized to account for the small number of species (and the low population densities of these species) in the smaller-than-modal classes (see Brown and Maurer 1987, 1989; Dial and Marzluff 1988).

The specialization hypothesis developed here is not independent of the competitive-exclusion and differential-extinction hypotheses presented above. Rather, the nutritional constraints and the resulting specialization provide another level of explanation for the pervasive effects of body size on resource use, habitat selection, population regulation, and distributional limits that ultimately determine small-scale species interactions and large-scale species dynamics.

Allocation of Food and Space among Species

Regardless of whether the above hypotheses are necessary and sufficient to explain the empirical patterns, the spatial scaling of the body-size distributions has important implications for the allocation of food and space among species and hence for the assembly of continental biotas. First, the nature of ecological communities depends on the spatial scale of study. The larger and more heterogeneous the area sampled (and these will tend to be correlated), the more species composition will reflect beta diversity (replacement of species between habitats) relative to alpha diversity (number of coexisting species within a habitat).

Furthermore, not only the number of species but also the kinds of species that actually and potentially interact vary with spatial scale. The limited number of species that coexist in small patches of relatively homogeneous habitat tend to be of different sizes. Because of the energetic constraints outlined above, this will tend to result in coexisting species' using different food resources or using the same resources in different ways. Many of the coexisting species of similar size are in different trophic guilds. In terrestrial mammals, carnivores and herbivores span virtually the entire range of body sizes. Although species in the same guilds may coexist locally and compete for food (especially if they are of different body sizes), often the most severe competition will be among species (of similar sizes) that rarely encounter each other because they occur in adjacent but largely nonoverlapping habitats and geographic regions.

The spatial scaling of body size emphasizes the importance of beta diversity (Cody 1975; Wilson and Shmida 1984). The high frequency of species in the modal size classes on the biome or continental scale reflects the frequent replacement of these species among local habitats. This turnover can be of two types. On the one hand, it may reflect crossing the borders of geographic ranges. On the other

hand, it may reflect the fact that species do not occur in all habitats in their geographic ranges. The distribution of body sizes of species in the former category (fig. 5, *top*) is virtually identical in shape to the North American distribution. The species in the latter category (fig. 5, *bottom*) also exhibit a highly modal body-size distribution but are composed of relatively more representatives in size classes 9–13 (500 g–16 kg), many of which appear to be omnivores with relatively large geographic ranges.

Generality

Since the present analyses are exclusively of data for North American terrestrial mammals, it is reasonable to ask how general the results are. Of course it would be desirable to obtain and analyze comparable data for other groups of organisms in other geographic regions. Until this is done, we can make two comments.

First, the right-skewed distribution for the North American mammal fauna is typical of the shapes of frequency distributions of body-size measurements for many other taxa from large geographic areas. For example, May (1978, 1988), Bonner (1988), Morse et al. (1988), and Brown and Maurer (1989) present examples of qualitatively similar size distributions for a wide variety of organisms from bacteria to insects to birds. In addition, Rusler (1987) examined frequency distributions of body masses among species and genera of mammals on different continents. She found similar right-skewed distributions for all the larger continents with diverse faunas. We cannot claim that these biotas exhibit the same pattern of spatial scaling within continents without analyses of data for smaller scales; but it seems unlikely that there would be so much similarity in the large-scale patterns unless the underlying mechanisms and small-scale patterns were also similar.

Second, none of the mechanisms that we have proposed above to account for the patterns in North American mammals is inherently specific either to mammals or to the North American continent. Allometric scaling of morphological and physiological variables with body size exhibits similar exponents in a wide variety of animals, including vertebrates and invertebrates, endotherms and ectotherms (Peters 1983; Calder 1984). The relationship of body size to population density, area of geographic range, dietary specialization, and other attributes of species that affect the assembly of both local communities and continental biotas appears to be similar in the organisms that have been studied to date (see data on beetles, birds, and mammals in Brown and Maurer [1987, 1989] and Morse et al. [1988]). The generality of these relationships makes us optimistic that both the patterns of spatial scaling and the mechanistic processes that produce them are also general.

The constraints on the body sizes of species that occur together on different spatial scales can be thought of as one important component of the rules for assembling continental biotas. Although complete assembly rules would be based on other variables in addition to body size, it is clear that size, and traits that are correlated with size, profoundly affects the composition of species assemblages (see also Cody 1975; Diamond 1975; Brown 1981; Brown and Maurer 1987, 1989;

Dial and Märzluff 1988). Because of its pervasive influence on physiology, behavior, and ecology, body size influences the coexistence of species in local habitats, the turnover of species across the landscape, and the colonization, speciation, and extinction of species on continental scales.

Additional assembly rules will be required to account for differences in biotas among continents and between continents and islands. The importance of body size is also seen in the divergence of insular populations from their mainland relatives (see, e.g., for mammals, Foster 1964; Lomolino 1985) and in the systematic variation in the frequency distribution of size among species or genera in continental faunas as a function of the area of the land mass (see, e.g., Brown 1986; Rusler 1987; see also Van Valen 1973).

Implications for Conservation

The rules for assembling species on different spatial scales also have important implications for the maintenance of diversity and for the disassembly of biotas during environmental perturbations. Such disassembly has occurred naturally in the past, most dramatically during episodic mass extinctions (Martin and Klein 1984; Jablonski 1986; Raup 1986). At present, such disassembly is occurring in response to the multiple effects of the growing human population (Wilson 1988). Losses of species during past mass extinctions and in response to the impacts of modern humans are nonrandom with respect to body size and other attributes of species (see, e.g., Diamond 1984; Martin 1984; Webb 1984). For example, of the species known to have disappeared during the last three centuries from the 24 local habitats that we studied, 11 of 13 are larger than 2 kg and seven are larger than 35 kg. From the patterns of faunal assembly and these kinds of data on known extinctions, it should be possible to predict which species will be most vulnerable to perturbations (Arita et al. 1990).

Most current conservation strategies focus on efforts to preserve individual endangered species and threatened habitats. These procedures, by themselves, will be inadequate to prevent wholesale extinctions caused by human activities. It is estimated that between 5 and 30 million species of organisms currently inhabit the earth (Erwin 1983; May 1988; Wilson 1988). It will be impossible to identify which ones are endangered, much less to develop recovery plans for them, on a species-by-species basis. It will be almost equally difficult to inventory all kinds of habitats.

Rules for the assembly and disassembly of biotas suggest alternatives to present approaches to conservation biology. The statistical patterns of biotic composition on different spatial scales provide a basis for assessing vulnerability to extinction on the basis of body size and other variables, such as area of geographic range (e.g., see Brown and Maurer 1987, 1989; Pimm et al. 1988; Arita et al. 1990). Not only can these assessments identify classes of species that may be vulnerable, they can point to the spatial scales and habitat types that warrant attention. For example, reserves of different sizes, dispersions, and habitats will be differentially effective in enhancing the survival of different species, depending on their body sizes and other ecologically relevant attributes. In addition, body size and other

easily measured variables provide a way of initially assessing the ecological roles of species. The patterns of species replacement within and between large areas, such as biomes and continents, suggest that there is considerable complementarity in these roles. As human impacts inevitably increase and native species inevitably become extinct, the only way to restore lost diversity and ecological functions will be through introduction of alien species. Assembly rules can be used to identify candidate species for introduction to fill missing ecological roles. For example, Janzen (1982) has advocated the use of feral livestock to replace seed dispersal, browsing, and grazing roles of large native mammals that have been extirpated from tropical reserves.

CONCLUSIONS

We conclude that processes operating over a wide range of spatial scales—from interspecific interactions that affect coexistence within local habitats to colonization, speciation, and extinction events that affect the distribution of species over the continent—interact to determine the composition of the biota at all scales, from local to continental (Cody 1975; Orians 1980; Brown 1981; Rapoport 1982; Ricklefs 1987; Brown and Maurer 1987, 1989). All of these processes are reflected in the body sizes of co-occurring species, because of the pervasive influence of size on many aspects of physiology, behavior, and ecology. Both the microscopic perspectives of physiological, population, and community ecology and of microevolution and the macroscopic perspectives of biogeography and macroevolution are required if we are to understand completely the composition of biotas on any spatial scale.

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APPENDIX A

TABLE A1

LIST OF SPECIES, THEIR BODY MASSES, AND THE BIOMES AND LOCAL HABITATS IN WHICH THEY OCCUR

Genus and Species	Mass (g)	Biomes	Local Habitats
<i>Agouti paca</i>	8,200	17,18,19,21	
<i>Alces alces</i>	457,000	1,3,4,5,11,12,13,14,15,16	12,23
<i>Allouatta apliata</i>	7,280	17,18,19	
<i>A. pigra</i>	7,000	17,18,21	
<i>Alpox lagopus</i>	3,000	3,4,12,13	
<i>Ammospermophilus harrisi</i>	150	8,17	6
<i>A. interpres</i>	156	9	
<i>A. leucurus</i>	156	7,8,9,11,15,16,20	4,5
<i>A. nelsoni</i>	120	7	
<i>Antillocapra americana</i>	68,000	7,8,9,10,11,14,15,16,17,20	1,6,19,21,24
<i>Aplodontia rufa</i>	950	2,16	
<i>Ateles geoffroyi</i>	7,500	17,18,19,21	
<i>Batomys musculus</i>	9	17,18,19,20	
<i>B. taylori</i>	9	6,10,14,17,18,20	16
<i>Bassariscus astutus</i>	1,400	2,6,7,8,9,10,11,14,15,16,17,18,19,20	1,3,4,5,10,16
<i>B. sumichrasti</i>	1,400	17,18,19,21	
<i>Bison bison</i>	422,000	3,4,5,6,9,10,11,14,15,16	24
<i>Blarina brevicauda</i>	22	4,5,6,14	7,8,9,12,13,14,15,22,23,24
<i>B. telmalestes</i>	22	6	
<i>Cabassus centrali</i>	800	17,19	
<i>Caluromys derbianus</i>	500	17,18	
<i>Canis lupus</i>	43,000	1,2,3,4,5,7,8,9,10,11,12,13,14,15,16,17,19,20	2,6,12,13,14,15,16,17,19,20,21,22,23,24
<i>C. latrans</i>	16,000	1,2,3,4,5,6,7,8,9,10,11,12,14,15,16,17,18,19,20	1,2,3,4,5,6,10,11,16,17,18,19,20,21,22,23,24
<i>C. rufus</i>	29,100	5,6,14	
<i>Castor canadensis</i>	24,000	1,2,3,4,5,6,7,8,9,10,11,13,14,15,16,17	2,12,14,19,20,22,23
<i>Cervus elaphus</i>	500,000	1,2,4,5,6,7,8,9,11,14,15,16,17	2,12,13,17,18,20,21,24
<i>Chironectes minimus</i>	750	17,18,19	
<i>Clethrionomys californicus</i>	29	2,16	
<i>C. gapperi</i>	29	1,2,4,5,9,11,13,14,15,16,17	12,13,14,15,22,23
<i>C. rutilus</i>	29	1,3,4,12,13,15	
<i>Coendu mexicanus</i>	5,000	17,18,19,21	
<i>Condylura cristata</i>	53	4,5,6	14,22,23

<i>Conepatus leuconotus</i>					1
<i>C. mesoleucus</i>	3,500	10,14,18			10,11,16
<i>C. semistriatus</i>	4,500	8,9,10,14,17,19,20			
<i>Cryptotis goldmani</i>	3,500	18,21			
<i>C. goodwini</i>	8	17,19			
<i>C. magna</i>	7	19			
<i>C. mexicana</i>	7	17			
<i>C. mexicana</i>	7	17,18,19			
<i>C. nigrescens</i>	7	18,19,21			
<i>C. parva</i>	5	5,6,9,10,14,17,18,19			7,8,9,24
<i>Cyclopes dydactylus</i>	300	17,18,19			
<i>Cynomys gunnisoni</i>	900	8,9,15			
<i>C. leucurus</i>	900	11			
<i>C. ludovicianus</i>	1,200	9,14,17			1
<i>C. mexicanus</i>	900	9			
<i>C. parvidens</i>	900	11,15			
<i>Dama hemionus</i>	118,100	1,2,3,4,7,8,9,10,11,14,15,16,17,20			1,2,6,16,17,18,19,20,21,24
<i>D. virginia</i>	106,850	2,4,5,6,8,9,10,11,14,15,16,17,18,19,20,21			3,4,5,7,8,9,10,11,12,13,16,20,22,23,24
<i>Dasyprocta mexicana</i>	5,000	18			
<i>D. punctata</i>	4,000	17,18,19,21			
<i>Dasypus novemcinctus</i>	7,000	6,10,14,17,18,19,20,21			7,8,10,11
<i>Dicrostonyx groenlandicus</i>	57	3,4,12,13			
<i>D. hudsonius</i>	57	13			
<i>Didelphis marsupialis</i>	3,000	10,17,18,19,21			10,11
<i>D. virginiana</i>	3,000	2,5,6,7,8,9,10,14,15,17,18,19,20,21			7,8,9,13,22,23
<i>Dipodomys agilis</i>	77	7,8			4
<i>D. deserti</i>	138	8,11			
<i>D. elator</i>	72	14			
<i>D. elephantiinus</i>	72	7			
<i>D. gravipes</i>	92	7			
<i>D. heermanni</i>	72	2,7,16			
<i>D. ingens</i>	156	7			
<i>D. merriami</i>	47	8,9,11,16,17,20			1,4,6
<i>D. microps</i>	65	8,11,16			
<i>D. nelsoni</i>	100	9			
<i>D. nitratoides</i>	42	7			
<i>D. ordii</i>	72	8,9,10,11,14,15,16,17			1,6,19
<i>D. panamintinus</i>	57	7,11			
<i>D. peninsularis</i>	47	8			
<i>D. phillipsii</i>	41	17			
<i>D. spectabilis</i>	132	8,9,15,17			1,6

TABLE A1 (Continued)

Genus and Species	Mass (g)	Biomes	Local Habitats
<i>D. stephensi</i>	56	7	
<i>D. venustus</i>	72	7	
<i>Eira barbara</i>	5,000	17,18,19,21	
<i>Erethizon dorsatum</i>	13,000	1,2,3,4,5,7,8,9,10,11,12,13,14,15,16,17	1,2,6,12,13,14,15,16,17,19,20
<i>Felis concolor</i>	110,000	1,2,3,4,5,6,7,8,9,10,11,14,15,16,17,18,19,20,21	1,2,3,4,5,6,7,8,10,11,13,16,17,18,19,20,21,22,23,24
<i>F. onca</i>	113,000	6,8,9,10,14,17,18,19,20,21	10,11
<i>F. pardalis</i>	12,000	6,8,10,14,17,18,19,20,21	10,11
<i>F. wiedii</i>	5,000	10,14,17,18,19,20,21	10,11
<i>F. yagouaroundi</i>	9,000	8,10,14,17,18,19,20,21	10,11
<i>Galictis vittata</i>	3,000	17,18,19,21	10,11
<i>Geomys arenarius</i>	354	9	1
<i>G. bursarius</i>	354	5,6,9,14	20,24
<i>G. colonus</i>	165	6	
<i>G. fontanelus</i>	165	6	
<i>G. personatus</i>	397	14	
<i>G. pinetis</i>	165	6	7,8
<i>G. tropicalis</i>	350	10	
<i>Glaucomys sabrinus</i>	85	1,2,4,5,7,11,14,15,16	7,12,14,15,20
<i>G. volans</i>	85	5,6,14,17,18	12,13
<i>Gulo gulo</i>	20,000	1,2,3,4,5,7,11,12,13,14,15,16	12,14,15,18,20
<i>Habromys chinanteco</i>	40	18	
<i>H. lepturus</i>	85	17,18	
<i>H. lophurus</i>	40	19	
<i>H. simulatus</i>	40	18	
<i>Heteromys desmarestianus</i>	85	17,18,19,21	
<i>H. gaumeri</i>	70	18,21	
<i>H. goldmani</i>	85	19	
<i>H. lepturus</i>	40	17,18	
<i>H. longicaudatus</i>	85	19	
<i>H. nelsoni</i>	70	18	
<i>H. temporalis</i>	85	18	
<i>Hodomys alleni</i>	220	19,20	
<i>Homo sapiens</i>	55,000	1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,21	3,4,5,6,7,8,9,12,13,14,15,16,17,19,21,22,23,24
<i>Lagurus curtatus</i>	28	7,11,14,15,16	19

<i>Lemmus trimucronatus</i>	90	1,3,4,12,13,15	
<i>Lepus alleni</i>	3,600	8,20	
<i>L. americanus</i>	1,148	3,4,5,12,14,15,16,17	12,14,15,17,22,23
<i>L. arcticus</i>	4,750	13	
<i>L. californicus</i>	3,100	2,7,8,9,10,11,14,15,16,17,20	1,4,5,6,16,19,20
<i>L. callotis</i>	3,000	9,17	
<i>L. flavigularis</i>	3,000	19	
<i>L. othus</i>	4,250	12	
<i>L. townsendi</i>	3,450	11,14,15,16	19,21,24
<i>Liomys irroratus</i>	50	9,10,14,17,18,19	
<i>L. pictus</i>	65	8,17,18,19,20	10,11
<i>L. salvini</i>	57	19	
<i>L. spectabilis</i>	65	19	2,19,20,23
<i>Lutra canadensis</i>	11,000	1,2,3,4,5,6,7,8,9,11,12,13,14,15,16,17	
<i>L. longicaudus</i>	11,000	17,18,19,20,21	
<i>Lynx canadensis</i>	12,000	1,2,3,4,5,11,12,13,15,16	12,14,15,19,22,23
<i>L. rufus</i>	15,000	2,4,5,6,7,8,9,10,11,14,15,16,17,19,20	1,2,3,4,5,6,8,9,12,13,16,17,18,19,20,22,23,24
<i>Marmosa canescens</i>	60	17,18,19,20	10,11
<i>M. mexicana</i>	130	17,18,19,21	
<i>Marmota caligata</i>	6,300	1,2,3,12,16	
<i>M. flaviventris</i>	3,350	7,11,15,16	17,19
<i>M. monax</i>	4,200	1,3,4,5,6,14,15	13
<i>M. olympus</i>	6,300	2	
<i>M. Vancouverensis</i>	6,300	1,2	
<i>Maries americana</i>	1,060	1,2,3,4,5,11,12,13,14,15,16	12,15,18
<i>M. pennanti</i>	4,800	1,2,4,5,7,11,13,14,15,16	12,15
<i>Mazama americana</i>	25,000	17,18,19,21	
<i>Megadontomys thomasi</i>	80	17,18,19	
<i>Megasorex gigas</i>	20	20	
<i>Mephitis macroura</i>	2,700	8,9,10,17,18,19,20	
<i>M. mephitis</i>	4,000	2,4,5,6,7,8,9,10,11,13,14,15,16,17	10,11
<i>Microdipodops megacephalus</i>	14	11,16	1,2,4,6,8,9,12,13,16,21,22,23,24
<i>M. pallidus</i>	14	16	
<i>Microsorex hoyi</i>	3	3,4,5,14,15	
<i>Microtus californicus</i>	80	2,7,8,16	13
<i>M. canicaudus</i>	72	2	
<i>M. chrotorrhinus</i>	35	4,5	15
<i>M. guatemalensis</i>	42	17	
<i>M. longicaudus</i>	55	1,2,3,7,8,9,11,14,15,16,17	17,18,19,20
<i>M. ludovicianus</i>	35	6	

TABLE A1 (Continued)

Genus and Species	Mass (g)	Biomes	Local Habitats
<i>M. mexicanus</i>	42	8,9,10,15,17,19	
<i>M. miturus</i>	41	3,12	19
<i>M. montanus</i>	72	11,14,15,16,17	18
<i>M. oaxacensis</i>	42	17	
<i>M. ochrogaster</i>	40	4,5,6,14	21,24
<i>M. oconomus</i>	53	3,4,12,13	
<i>M. oregoni</i>	23	2,16	
<i>M. pennsylvanicus</i>	71	1,3,4,5,6,9,11,12,13,14,15,16,17	14,15,21,22,23
<i>M. pinetorum</i>	32	5,6,14	13
<i>M. quasiater</i>	40	18	
<i>M. richardsoni</i>	85	11,15,16	18
<i>M. townsendi</i>	72	1,2	
<i>M. umbrosus</i>	42	17	
<i>M. xanthognathus</i>	142	3,4,15	
<i>Mustela erminea</i>	114	1,2,3,4,5,9,11,12,13,14,15,16	12,14,15,22,23
<i>M. frenata</i>	340	1,2,4,5,6,7,8,9,10,11,14,15,16,17,18,19,20,21	1,2,3,6,7,8,11,12,13,17,18,19,20,21
<i>M. nigripes</i>	584	8,9,14,15,17	18
<i>M. nivalis</i>	45	1,3,4,5,12,13,14,15	13,20,22,23,24
<i>M. vison</i>	1,350	1,2,3,4,5,6,7,9,11,12,13,14,15,16	2,14,15,19,20,22,23
<i>Myrmecophaga tridactyla</i>	32,000	17,18,19,21	
<i>Napeozapus insignis</i>	22	4,5	12,13,15
<i>Nasua nasua</i>	9,000	8,9,10,14,17,18,19,20,21	10,11,16
<i>Nelsonia neotomodon</i>	80	19	
<i>Neofiber alleni</i>	213	6	
<i>Neotoma albigula</i>	198	8,9,14,15,17,20	1,4,5,16
<i>N. alleni</i>	200	19,20	10
<i>N. augustopalata</i>	198	10	
<i>N. cinerea</i>	300	1,2,3,8,9,11,15,16	17,18,19,20
<i>N. devia</i>	200	8	
<i>N. floridana</i>	328	5,6,14	24
<i>N. fuscipes</i>	267	2,7,8,16	
<i>N. goldmani</i>	198	9	
<i>N. lepida</i>	200	7,8,11,15	3,5
<i>N. mexicana</i>	185	8,9,15,17,19,20	1,16

<i>N. micropus</i>	310	9, 10, 14, 17	1
<i>N. nelsoni</i>	198	18	
<i>N. palatina</i>	198	19	
<i>N. phenax</i>	198	20	
<i>N. stephensi</i>	200	9, 15, 17	
	40	17	
<i>Neotomodon alstoni</i>	10	2	
<i>Neurotrichus gibbsii</i>	6	7, 8, 9, 10, 14, 15, 17, 20	2, 4, 5, 16
<i>Nothosorex crawfordi</i>	6	19	
<i>N. gigas</i>	60	17, 18, 19, 20	11
<i>Nyctomys sumichrasti</i>	118	3, 4	
<i>Ochotona collaris</i>	118	1, 11, 15, 16	18
<i>O. princeps</i>	1,800	1, 2, 4, 5, 6, 8, 9, 11, 12, 13, 14, 15, 16, 17	2, 19, 22, 23
<i>Ondatra zibethicus</i>	30	9, 19	
<i>Oryzomys arenicola</i>	30	8, 9, 10, 11, 14, 15, 16, 17	1, 6, 19, 21
<i>O. leucogaster</i>	30	7, 8, 9, 10, 11, 16, 17, 20	1, 6
<i>O. torridus</i>	91,000	1, 3, 11, 15, 16	18
<i>Oreamnos americanus</i>	500	19	
<i>Orthogeomys cuniculus</i>	500	19	
<i>O. grandis</i>	500	19	
<i>O. hispidus</i>	500	17, 18, 21	
<i>O. lanius</i>	500	18	
<i>Oryzomys alfaroi</i>	80	17, 18, 19	
<i>O. caudatus</i>	50	17	
<i>O. couesi</i>	80	18, 21	
<i>O. fulgens</i>	80	9	
<i>O. fulvescens</i>	80	17, 18, 19, 20, 21	
<i>O. melanotis</i>	50	17, 18, 19, 20, 21	
<i>O. palustris</i>	54	5, 6, 10, 14, 17, 19, 20	11
<i>Osgoodomys banderanus</i>	50	19	
<i>Otonyctomys hatti</i>	40	18, 21	
<i>Otolytomys phyllotis</i>	64	17, 18, 19, 21	
<i>Ovibus moschatus</i>	286,000	12, 13	
<i>Ovis canadensis</i>	91,000	7, 8, 9, 11, 14, 15, 16, 17	4, 5, 18, 20
<i>O. dalli</i>	73,100	3, 12, 15	
<i>Pappogeomys alcorni</i>	150	19	
<i>P. bulleri</i>	150	19, 20	
<i>P. castanops</i>	330	9, 10, 14	1, 2, 11
<i>P. fumosus</i>	150	19	
<i>P. gymnurus</i>	600	19	
<i>P. merriami</i>	600	17, 18, 19	

TABLE A1 (Continued)

Genus and Species	Mass (g)	Biomes	Local Habitats
<i>P. neglectus</i>	150		
<i>P. tylorhynchus</i>	600		
<i>P. zinzeri</i>	150		
<i>Parascalops breweri</i>	52	4,5	
<i>Perognathus alticola</i>	24	8	
<i>P. amplus</i>	9	8	
<i>P. apache</i>	10	9,15	
<i>P. arenarius</i>	23	8,20	
<i>P. artus</i>	23	20	
<i>P. baileyi</i>	21	8,17,20	
<i>P. californicus</i>	23	7	
<i>P. dalquesti</i>	14	20	
<i>P. fallax</i>	21	7,8	4,5
<i>P. fasciatus</i>	9	14,15	
<i>P. flavescens</i>	11	9,14,15	
<i>P. flavus</i>	9	8,9,10,14,15,17	1,6,21,24
<i>P. formosus</i>	24	8,11	
<i>P. goldmani</i>	23	8,20	
<i>P. hispidus</i>	47	8,9,10,14,17	2,6,24
<i>P. hooperi</i>	36	10	
<i>P. inornatus</i>	13	7	
<i>P. intermedius</i>	18	8,9	
<i>P. lineatus</i>	23	9	
<i>P. longimembris</i>	9	7,8,11,16	4,5
<i>P. merriami</i>	8	14	
<i>P. nelsoni</i>	17	9,17	
<i>P. parvus</i>	24	11,15,16	17,19,20
<i>P. penicillatus</i>	23	8,9,17	1,6
<i>P. pernix</i>	17	20	
<i>P. spinatus</i>	24	8,20	5
<i>P. xanthonotus</i>	24	7	
<i>Peromyscus atwateri</i>	29	14	
<i>P. aztecus</i>	40	18	
<i>P. banderanus</i>	60	19,20	

<i>P. boyllii</i>	36	2,7,8,9,10,11,14,15,16,17,19	4,5,16
<i>P. bullatus</i>	40	18	
<i>P. californicus</i>	38	2,7,8	3
<i>P. crinitus</i>	20	7,8,9,11,15	5,19
<i>P. difficilis</i>	32	9,14,15,17	
<i>P. eremicus</i>	40	7,8,9,10,17,20	1,5,6
<i>P. eva</i>	22	20	
<i>P. evidens</i>	40	19	7,8,9
<i>P. floridanus</i>	29	6	
<i>P. furvus</i>	33	17	
<i>P. gossypinus</i>	33	5,6	7,8,9
<i>P. grandis</i>	71	17	
<i>P. guatemalensis</i>	40	17,19	
<i>P. gymnotis</i>	40	19	
<i>P. leucopus</i>	20	5,6,8,9,10,14,17,18,19,21	2,12,13,22,23,24
<i>P. maniculatus</i>	35	1,2,3,4,5,6,7,8,9,10,11,13,14,15,16,17,18,19,20	1,2,3,4,5,6,12,13,14,15,17,18,19,20,21,24
<i>P. megalops</i>	71	19	
<i>P. mekisturus</i>	60	18	
<i>P. melanocarpus</i>	60	17	
<i>P. melanophrys</i>	40	9,17,19	
<i>P. melanotis</i>	30	9,17	
<i>P. melanurus</i>	40	19	
<i>P. merriami</i>	40	8,20	
<i>P. mexicanus</i>	75	17,18,19	8,9
<i>P. nuttalli</i>	25	5,6	
<i>P. ochraverter</i>	40	10	
<i>P. pectoralis</i>	39	9,10,17	
<i>P. perfulvus</i>	40	19,20	10,11
<i>P. polionotus</i>	12	6	7,8
<i>P. polius</i>	40	9,17	
<i>P. simulus</i>	40	20	
<i>P. spicilegus</i>	36	17	
<i>P. thomasi</i>	75	17,18,19	
<i>P. truei</i>	37	2,7,8,9,11,14,15,16,17,20	3,4,17,19
<i>P. winkelmani</i>	40	20	
<i>P. yucatanicus</i>	40	18,21	
<i>P. zarhinchus</i>	40	17	
<i>Phenacomys albipes</i>	23	2	
<i>P. intermedius</i>	28	1,2,4,7,11,15,16	17,18
<i>P. longicaudus</i>	36	2	

TABLE A1 (Continued)

Genus and Species	Mass (g)	Biomes	Local Habitats
<i>P. silvicola</i>	36		
<i>Philander opossum</i>	500	10,17,18,19,21	
<i>Potos flavus</i>	5,000	17,18,19,21	
<i>Procyon lotor</i>	7,000	1,4,5,6,7,8,9,10,11,14,15,16,17,18,19,20,21	2,7,8,9,10,11,12,13,22,23
<i>P. pygmeus</i>	2,500	21	
<i>Rangifer tarandus</i>	169,000	3,4,5,12,13,15	12,14,15
<i>Reithrodontomys burti</i>	20	8,20	
<i>R. chrysopsis</i>	19	17,19	
<i>R. fulvescens</i>	28	6,8,9,10,14,17,18,19,20	
<i>R. gracilis</i>	20	17,18,20,21	6,10,11
<i>R. hirsutus</i>	20	19	
<i>R. humulis</i>	13	5,6	7
<i>R. megalotis</i>	15	2,7,8,9,11,14,15,16,17	1,2,6,19,21,24
<i>R. mexicanus</i>	19	17,18,19	
<i>R. microdon</i>	20	17,19	
<i>R. montanus</i>	9	8,9,14,17	24
<i>R. raviventris</i>	15	7	
<i>R. sumichrasti</i>	19	17,19	
<i>R. tenuirostris</i>	20	19	
<i>Rheomys mexicanus</i>	40	19	
<i>R. thomasi</i>	40	19	
<i>Romerolagus diazi</i>	477	17	
<i>Scalopus anthony</i>	100	8	
<i>S. aquaticus</i>	140	5,6,14	8,9
<i>Scapanus latimanus</i>	140	2,7,8,16	3,17
<i>S. orarius</i>	56	2,11,16	18,20
<i>S. townsendi</i>	140	2	
<i>Sciurus aberti</i>	900	8,9,15,17	
<i>S. alleni</i>	750	10	
<i>S. arizonensis</i>	700	8,17	
<i>S. aureogaster</i>	690	17,18,19	
<i>S. carolinensis</i>	555	2,4,5,6,14	9,12,13
<i>S. colliciae</i>	498	20	10,11
<i>S. deppei</i>	225	17,18,19,21	
<i>S. griseus</i>	681	7,8,16	17,20

<i>S. kaibabensis</i>	900	8	
<i>S. nayaritensis</i>	498	17	
<i>S. niger</i>	1,000	4,5,6,10,14	7,9
<i>S. oculatus</i>	750	17	
<i>S. variegatoides</i>	498	17,19	
<i>S. yucatanensis</i>	225	18,21	
<i>Scotinomys teguina</i>	15	17	
<i>Sigmodon alleni</i>	120	19	
<i>S. arizonae</i>	198	8,20	
<i>S. fulviventor</i>	120	8,9,17	
<i>S. hispidus</i>	198	5,6,8,9,10,14,17,18,19,21	1,2,6,7,8,9,24
<i>S. leucotis</i>	120	17	
<i>S. mascotensis</i>	120	19,20	10
<i>S. minimus</i>	120	9,17	
<i>S. ochrognatus</i>	112	9,17	16
<i>Sorex alaskanus</i>	14	1	
<i>S. arcticus</i>	9	2,3,4,5,12,13,14	14,15,23
<i>S. arizonae</i>	7	17	
<i>S. bendii</i>	16	2	18,20
<i>S. cinereus</i>	5	1,3,4,5,12,13,14,15	12,13,14,15,21,22,23
<i>S. dispar</i>	6	4,5	12,13
<i>S. emarginatus</i>	7	17	
<i>S. fumeus</i>	8	4,5	12,13
<i>S. gaspensis</i>	5	4	
<i>S. juncensis</i>	7	7	
<i>S. longirostris</i>	3	5,6	
<i>S. lyelli</i>	5	16	7,9
<i>S. macrodon</i>	7	18	
<i>S. merriami</i>	6	8,9,11,15,16,17	19
<i>S. milleri</i>	7	9,10,17	
<i>S. monticolus</i>	7	8,9,17	
<i>S. nanus</i>	7	8,9,11,14,15	
<i>S. oreopolus</i>	7	17	
<i>S. ornatus</i>	7	7	
<i>S. palustris</i>	14	3,4,5,8,11,13,14,15,16	22,23
<i>S. preblei</i>	3	11,15	
<i>S. saussurei</i>	6	9,17	
<i>S. sclateri</i>	7	18	
<i>S. sitzodon</i>	7	17	
<i>S. tenellus</i>	7	11,16	

TABLE A1 (Continued)

Genus and Species	Mass (g)	Biomes	Local Habitats
<i>S. trigonirostris</i>	7	16	
<i>S. trowbridgii</i>	8	2,7,16	17
<i>S. vagrans</i>	7	1,2,3,4,9,12,14,15,17	17,18,20
<i>S. ventralis</i>	7	17	
<i>S. veraeapacis</i>	7	17	
<i>Spermophilus adocetus</i>	125	19	
<i>S. annulatus</i>	500	20	
<i>S. armatus</i>	355	11,15	
<i>S. atricapillus</i>	275	20	
<i>S. beecheyi</i>	738	2,7,8,16	3,4,5,17
<i>S. beldingi</i>	284	11,16	17
<i>S. brunneus</i>	300	11	
<i>S. columbianus</i>	576	11,15	18,20
<i>S. franklini</i>	600	4,5,14	22,23
<i>S. lateralis</i>	223	2,7,11,15,16	17,18,19,20
<i>S. madrensis</i>	275	17	
<i>S. mexicanus</i>	340	9,10,14,17	
<i>S. parryi</i>	700	3,4,12,13,15	
<i>S. perotensis</i>	140	18	
<i>S. richardsonii</i>	419	11,14,15	21
<i>S. saturatus</i>	223	16	
<i>S. spilosoma</i>	125	8,9,10,14,15,17	1,6
<i>S. tereticaudus</i>	145	7,8,20	
<i>S. townsendii</i>	226	11,16	19
<i>S. tridecemlineatus</i>	160	4,5,9,14,15	21,24
<i>S. variegatus</i>	817	8,9,10,11,14,15,17,18,19,20,21	2,16
<i>S. washingtoni</i>	218	11	
<i>Spilogale gracilis</i>	900	7,11	4,5,16
<i>S. putorius</i>	900	2,5,6,8,9,10,11,14,15,16,17,18,19,20,21	20
<i>S. pygmaea</i>	320	19,20	10,11
<i>Sybilagus aquaticus</i>	2,150	5,6,14	
<i>S. audubonii</i>	1,013	1,2,7,8,9,10,11,14,15,16,17,20	1,2,6
<i>S. bachmani</i>	843	2,7,8,20	5,19,20
<i>S. brasiliensis</i>	950	17,18,19	

<i>S. cunicularius</i>	3,000	17,19,20	10
<i>S. floridanus</i>	1,800	4,5,6,8,9,10,14,17,21	8,16
<i>S. griseus</i>	964	2,7	19
<i>S. idahoensis</i>	35	11,16	
<i>S. insonus</i>	3,000	19	8
<i>S. nuttalli</i>	855	11,15,16	12,13
<i>S. palustris</i>	1,600	6	
<i>S. transitionalis</i>	1,048	5	
<i>Synaptomyis borealis</i>	29	3,4,12,13,15,16	15,22,23,24
<i>S. cooperi</i>	36	4,5,14	
<i>Tamandua mexicana</i>	6,000	17,18,19,21	
<i>Tamias alpinus</i>	39	7	
<i>T. amoenus</i>	51	1,7,11,15,16	17,20
<i>T. bulleri</i>	100	20	
<i>T. cinereicollis</i>	71	17	
<i>T. dorsalis</i>	85	8,11,15,17,20	16
<i>T. durangae</i>	85	17	
<i>T. merriami</i>	113	7,8	3
<i>T. minimus</i>	50	3,4,5,7,8,9,11,13,14,15,16	19
<i>T. obscurus</i>	100	7	
<i>T. ochrogenys</i>	75	2	
<i>T. palmeri</i>	75	8	
<i>T. panamintinus</i>	54	7,16	
<i>T. quadrimaculatus</i>	85	7,16	
<i>T. quadrivittatus</i>	71	9,15	
<i>T. ruficaudus</i>	60	11,15	
<i>T. senex</i>	75	2,7,16	
<i>T. siskiyou</i>	75	2	
<i>T. sonomae</i>	75	2	
<i>T. speciosus</i>	67	7,16	
<i>T. striatus</i>	103	4,5,6,14	12,13,14,15
<i>T. townsendii</i>	75	2,16	
<i>T. umbrinus</i>	71	11,15	
<i>Tamiasciurus douglasii</i>	225	1,2,7,16	
<i>T. hudsonicus</i>	196	1,4,5,8,9,11,12,13,14,15	12,13,14,15,20
<i>Tapirus bairdii</i>	300,000	17,18,19,21	
<i>Taxidea taxus</i>	10,000	2,4,5,7,8,9,10,11,14,15,16,17,20	1,2,4,5,6,17,18,19,20,21,24
<i>Tayassu pecari</i>	60,000	17,18,19	
<i>T. tajacu</i>	30,000	8,9,10,14,17,18,19,20,21	6,10,11,16
<i>Thalartctos maritimi</i>	382,500	12,13	

TABLE A1 (Continued)

Genus and Species	Mass (g)	Biomes	Local Habitats
<i>Thomomys baileyi</i>	100	9	
<i>T. bottae</i>	130	8,9,16,17	2,3,4,5,6
<i>T. mazama</i>	75	2,16	
<i>T. merriami</i>	113	7	
<i>T. monticola</i>	80	7,16	17
<i>T. talpoides</i>	100	4,11,14,15,16	18,19,20
<i>T. umbrinus</i>	130	2,7,8,9,11,15,16,17,19,20	16,19
<i>Tylomys bullaris</i>	280	17	
<i>T. nudicaudus</i>	280	17,18,19	
<i>T. tumbalensis</i>	280	18	
<i>Urocyon cinereoargenteus</i>	4,000	2,4,5,6,7,8,9,10,11,14,15,16,17,18,19,20,21	1,2,3,4,5,7,8,9,10,11,12,13,16,22,23
<i>Ursus americanus</i>	140,000	1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,20	2,8,9,12,13,14,15,16,17,18,20,22,23,24
<i>U. arctos</i>	363,000	1,2,3,4,7,8,9,10,11,12,13,14,15,16,17	2,16,17,18,19,20
<i>Vulpes macrotis</i>	3,200	7,8,9,17,20	1,6
<i>V. velox</i>	2,000	7,8,9,11,14,15,16,17,20	20,21
<i>V. vulpes</i>	5,000	1,2,3,4,5,6,7,8,9,11,12,13,14,15,16,17	14,15,21,22,23,24
<i>Xenomys nelsoni</i>	130	19,20	10,11
<i>Zapus hudsonius</i>	18	1,3,4,5,6,12,14,15	2,22,23,24
<i>Z. princeps</i>	28	2,4,7,8,9,11,14,15,16	18,20
<i>Z. trinitatus</i>	28	2,16	
<i>Zygoeomys trichopus</i>	500	20	

NOTE.—See tables 1 and 2 for the keys to the numbers used to designate biomes and local habitats, respectively.

APPENDIX B

TABLE B1

LOG₂ BODY-SIZE CLASSES FOR NORTH AMERICAN MAMMALS, AND THE MINIMUM, MIDPOINT, AND MAXIMUM BODY MASS IN EACH CLASS

SIZE CLASS	MASS (g)		
	Minimum	Midpoint	Maximum
1	1	1.4	1.9
2	2	2.8	3.9
3	4	5.7	7.9
4	8	11.3	15.9
5	16	22.6	31.9
6	32	45.3	63.9
7	64	90.5	127.9
8	128	181	255.9
9	256	362	511.9
10	512	724	1,023.9
11	1,024	1,448	2,047.9
12	2,048	2,896	4,095.9
13	4,096	5,793	8,191.9
14	8,192	11,585	16,383.9
15	16,384	23,170	32,767.9
16	32,768	46,341	65,535.9
17	65,536	92,682	131,071.9
18	131,072	185,364	262,143.9
19	262,144	370,728	524,287.9
20	524,288	741,455	10,485,503

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