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Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use

JOHN DAMUTH

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560, U.S.A.

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Global regressions of ecological population densities on body mass for mammals and for terrestrial animals as a whole show that local population energy-use is approximately independent of adult body mass—over a body mass range spanning more than 11 orders of magnitude. This independence is represented by the slope of the regressions approximating −0.75, the reciprocal of the way that individual metabolic requirements scale with body mass. The pattern still holds for mammalian primary consumers when the data are broken down by geographic area, by broad habitat-type and by individual community. Slopes for mammalian secondary consumers are also not statistically distinguishable from −0.75. For any given body mass temperate herbivores maintain on average population densities of 1.5 to 2.0 times those of tropical ones, though slopes do not differ. Terrestrial animals of all sizes exhibit approximately the same range of population energy-use values. These results agree with those reported for population energy-budgets. It is suggested that rough independence of body mass and the energy-use of local populations is a widespread rule of animal ecology and community structure.

KEY WORDS:—population density – allometry — energy flow – body mass – energy budget – mammals – terrestrial animals – aquatic animals – metabolism.

CONTENTS

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INTRODUCTION

Among animal species, a large number of physiological and ecological characteristics can be related to body mass by an equation of the form $X = aM^b$, where M is body mass, X the characteristic of interest, and a and b are constants (e.g. Kleiber, 1932; Hemmingsen, 1950, 1960; McNab, 1963; Jarman, 1974; Jerison, 1973; Blueweiss, Fox, Kudzma *et al.*, 1978; Damuth, 1981a, 1981b; Eisenberg, 1981; McMahon & Bonner, 1983; Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1984). The exponent, b, is also the slope of the line expressing the linear relationship between the log-transformed variables: $\log(X) = \log(a) + b[\log(M)]$.

Large animals are typically less abundant locally than are small animals (b is negative). For herbivorous mammals, it has been shown that population density decreases with body mass according to an interspecific allometric relation, the exponent of which is approximately the negative of the exponent by which metabolic rates increase with body mass (Damuth, 1981a). The amount of energy used by the local population of a particular species is its population density multiplied by individual metabolic requirements. Relating this quantity to body mass involves summing the exponents of the density and metabolic-rate relations, which cancel for mammalian primary consumers (Damuth, 1981a):

$$[\text{Energy-use}] \propto M^{[b \text{ for density}] + [b \text{ for metabolism}]} \simeq M^0 = 1.$$

This means that the amount of trophic energy used by the local population of any herbivore species is essentially independent of its body mass. Further, it was shown that this global relationship also roughly characterizes that found within local communities (Damuth, 1981a; in press). Approximate independence of body mass and population energy-use will be the case in any group of species where the exponent for population density scaling is approximately equal to the negative of that for individual metabolic requirements.

Subsequent work has attempted to characterize population density scaling in other groups of animals, and to examine the scaling in herbivorous mammals in more detail (Gittleman, 1983; Peters, 1983; Peters & Wassenberg, 1983; MacMahon & Bonner, 1983; Peters & Raelson, 1984; Robinson & Redford, 1986; Brown & Maurer, 1986; Juanes, 1986). While describing some relationships of interest, none of these studies (except that of Robinson & Redford) have been strictly comparable to that of Damuth (1981a). This is because the studies have either mixed dietary categories (Gittleman), mixed metabolic types (i.e. endothermy and ectothermy; Peters & Wassenberg; MacMahon & Bonner), used crude (rather than ecological) densities (Peters *et al.*), used seasonal (rather than year-round) densities (Brown & Maurer, Juanes), used a small body-size range (Brown & Maurer, Juanes), or used a small sample size for some groups (Robinson & Redford, in part). The present contribution reports analyses based upon ecological densities for 467 species of mammals and for 200 species of other vertebrate and invertebrate taxa, which constitute the largest and most extensive data set used to date (see Appendix).

MATERIALS AND METHODS

Data sources and analytical techniques

I collected dietary information, mean adult body-mass, and population density data from the published literature (see Appendix). For the mammals, data were obtained from approximately 115 journals surveyed completely for the years 1950–1979 (if applicable), and from the numerous books. Coverage since 1979 is not as comprehensive. The data represent the contents of over 600 articles, mostly primary literature. The mammal data include only terrestrial, non-volant mammal species. For poikilothermic vertebrates and for invertebrates, the data are taken from approximately 130 articles spanning the same time period. The data on poikilothermic organisms are not intended to represent a complete literature review, but are considered to be representative for the groups included.

Birds were not included because many species migrate over long distances, and most reports in the literature are of breeding densities only (e.g. Brown & Maurer, 1986; Juanes, 1986). It is therefore difficult to obtain from the literature estimates of population density that are comparable to those available for other animals.

Dietary information for mammals was obtained from the same sources as were the density and body-mass data, and from general works dealing with mammalian natural history (Burt & Grossenheider, 1964; Van Den Brink, 1968; Collins, 1973; Hunsaker, 1977; Haltenorth & Diller, 1977). Non-mammals have not been analysed here by dietary groupings.

Body masses are mean adult values, based upon the mean of both sexes if there is size dimorphism. Where only a range of values was available, I used the midpoint of the range to approximate a mean value. For some invertebrate species that exhibit indeterminate growth biomass values were given over a growing season; I thus had available densities at different body sizes. In such cases I used the geometric (rather than the arithmetic) mean for both body mass and density, because there was commonly an allometric relationship between these variables for such species. Otherwise, vertebrates and invertebrates were treated in the same way.

Population density for each species is the mean value over all of the localities for which densities were reported for that species. When there was more than one locality for a species, within-locality means were calculated first (by year, if appropriate), then the mean of means over all localities (this prevents bias caused by there being different numbers of censuses of the same population). The data are thus time-averaged over whatever length of time the original studies covered (in the majority of cases at least 1 year—especially for small mammals); for species known to 'cycle' (e.g. many microtine rodents) the densities are averaged over at least one cycle. This requirement was relaxed for many invertebrate species for which there were no data on densities over a dormant season. I excluded reports of outbreaks or population crashes, most island populations of mainland species, and other work likely to be recording unusual situations. I accepted data based on most methods current researchers employ, but excluded relative measures and most reports based upon kill-trapping, unless it was clear that the total number of individuals had been removed and/or that migration had been negligible. In all cases I attempted to take into account the comments of the authors concerning the reliability and comparative value of their own estimates.

'Ecological' densities refer to those over the area of habitat actually used by the animals, as opposed to 'crude' densities, which report the number of individuals occupying some arbitrarily-chosen area, only part of which the animals under study may occupy (frequently a total park area, or a political or administrative district). While of importance in conservation practice, crude densities are obviously not suitable for ecological comparisons among species. Many references explicitly reported ecological densities. However, for many species the detailed patterns of habitat-use are not well-known. Nevertheless, most authors expressed some awareness of the degree to which their study organisms occupied or traversed the area sampled, and it was therefore possible to distinguish those data that in all probability constituted or closely approximated ecological densities from those that did not. I cannot claim that every one of the data points is a bona fide ecological density, but every effort was made to achieve this, and extremely misleading crude densities have been excluded by this means. (The reference lists in the Appendix occasionally include some papers containing unreliable or otherwise inappropriate data that nevertheless gave useful comparative information, but the listed values are based only upon reliable data.)

I transformed the data to logarithms, and used standard linear regression techniques for statistical analysis. Over the range of body masses studied, error in the estimation of body mass for individual species is relatively small and has a negligible effect upon the regression coefficients. Felsenstein (1985) has cautioned that a degree of unrecognized statistical dependence among the data values will cause an overestimation of the degrees of freedom involved in statistical hypothesis-testing. In a large and diverse data set such as this one this effect will ordinarily be minor; however, it is not possible to guarantee that the data values reported in the literature are distributed completely independently with regard to all relevant variables. Thus, the 'real' standard errors of the regression statistics reported here may be somewhat larger than the listed values.

Dietary groupings

It is expected that diet will have an effect upon population density values. This is not only because of the trophic 'pyramid' (Elton, 1927), but also because different types of foods may typically be present in different abundances, and the qualities of different foods may impose different ecological or physiological limitations on their potential for exploitation by particular consumers. Furthermore, dietary differences are related to differences in levels of basal metabolism in mammals (McNab, 1986a), and these differences in energetics may influence ecological variables, including population density. It would be ideal to compare in a single regression only those mammals that differ in body size but that have identical diets. However, too fine a division of dietary categories is not practical in such an analysis. This is because diet itself is related to body mass (Bell, 1970; Jarman, 1974; Clutton-Brock & Harvey, 1977; Eisenberg, 1981), and variation in population density for a given body mass is typically such that a range of body mass of at least three orders of magnitude is required for density regressions to be statistically meaningful (Damuth, 1981a). Therefore, the mammal data have been grouped into rather broad dietary divisions. 'Primary consumers' include all species that obtain a majority of their yearly energy requirements from plant material. This grouping thus includes a number of rodent species that are often classified as 'omnivorous' (e.g. Landry, 1970). Such species frequently consume animal matter opportunistically, particularly in the season of highest insect abundance, but the rest of the year they depend primarily on plant foods (e.g. for *Peromyscus* see Whittaker, 1966; Flake, 1973; Meserve, 1976). Rodent species known to be insectivorous specialists (e.g. *Onychomys, Rhinosciurus*) have been included among the 'invertebrate-consumers'. Invertebrate-consumers include specialist insectivores of all sizes, but this is a somewhat heterogeneous grouping, since the larger species are almost all myrmecophagous, as opposed to the more generalized insectivory of the smaller species. Vertebrate-consumers have been separated from invertebrate-consumers because the body-mass range differs between the two groupings, and because the latter were observed to have, on average, higher densities. A regression calculated on the combined data would reflect these differences as well as the relationship of interest.

ALLOMETRY OF METABOLIC REQUIREMENTS

It has long been known that basal and standard metabolic rates of homeothermic, poikilothermic and unicellular organisms scale as body mass raised to the 0.75 power (Kleiber, 1932; Hemmingsen, 1950, 1960). Recently McNab (1986a, b) has shown that much of the variation in mammalian basal rates not explained by size can be explained by differences in diet. (Of course, the actual causal factors responsible for this correlation may be other, unknown characteristics with which diet and phylogenetic relationships are correlated; e.g. Elgar & Harvey, in press.) Grazing mammals and those feeding on vertebrate flesh exhibit high rates of basal metabolism, and those feeding on invertebrates, fruit and leaves exhibit low rates. However, within the dietary groupings used in this study, basal rates for primary consumers and for vertebrate-consumers still scale with b equal to approximately 0.75 (Table 1).

Invertebrate-consumers as a group exhibit a significantly lower slope. At small body-sizes eutherian mammals elevate their metabolic rates in order to maintain endothermy, but marsupials do not (McNab, 1983, 1986b). Even with the eutherians of less than 100 g removed from the analysis, the slope is less than 0.75 (0.60). Myrmecophagous mammals, which make up most of the large invertebrate-consumers, encounter particular problems in energy acquisition at large size owing to the nature of their food source, and this may be in part

Table 1. Mammalian metabolic-rate scaling

Trophic group	Slope	S.E.	Intercept	r	N
Primary consumers	0.72	0.012	0.59	0.98	200
Invertebrate-consumers	0.55	0.030	0.93	0.91	78
Invertebrate-consumers, excluding eutherians < 100 g	0.60	0.044	0.78	0.88	56
Vertebrate-consumers	0.74	0.042	0.61	0.97	23

Regressions are for $\log_{10}$ metabolic rate (O_2 consumption in $cm^3\ h^{-1}$) regressed on $\log_{10}$ body mass (g). The data are combined from Hayssen & Lacy (1985) and McNab (1986), and include only the terrestrial, non-volant therian mammal species. S.E. = standard error of the slope; r = correlation coefficient; N = sample size (number of species).

responsible for the difference in scaling in this somewhat heterogeneous grouping (McNab, 1984).

Metabolic rates of active, free-ranging mammals in nature are much less well known. Available evidence indicates that active metabolic rates roughly parallel basal rates, varying between approximately 1.5 to 3.0 times basal values at all body sizes (Brody, 1945; Chew & Chew, 1970; Mullen, 1971; Mullen & Chew, 1973; McKay, 1973; Moen, 1973; Gessaman, 1973; King, 1974; Schreiber, 1978; Nagy & Milton, 1979; Damuth, 1982; Peters, 1983; Nagy, 1987). A similar range is reported for poikilothermic organisms (Peters, 1983). Thus, metabolic requirements in nature can be considered for most purposes to scale approximately as mass to the 0.75 power (see also Farlow, 1976, for metabolic requirements of captive vertebrates). Furthermore, since assimilation efficiency is independent of body size (Kleiber, 1975; Peters, 1983), the scalding of metabolic requirements also represents the scalding of energy-consumption in nature.

ALLOMETRY OF POPULATION DENSITY

Mammals—primary consumers

For the set of mammalian primary consumers, population density scales as body mass to the −0.73 power (Table 2, Fig. 1). This value is statistically indistinguishable from −0.75, and agrees with previous results (Damuth, 1981a). Table 3 shows the data broken down by geographic region and by broad habitat-type. Choice of categories was limited by the need to have both a large enough sample size and a sufficiently large body-mass range for the regressions to be meaningful. There are no statistically significant differences in slope among any of the appropriate comparisons (analysis of covariance and *t*-tests, all $P > 0.05$), and none of the slopes are significantly different from −0.75. (Robinson & Redford, 1986, reported a somewhat shallower slope in their comparable sample of Neotropical herbivores.) However, there are differences in the elevations of the lines: tropical species, in both open and forest habitats, have significantly lower population densities than do their non-tropical counterparts (as Peters & Raelson, 1984, found for a sample of herbivore crude

Table 2. Population density regressed on body mass for mammals

Trophic group	Slope	S.E.	Intercept	r	N
Primary consumers	−0.73	0.024	4.15	−0.84	368
Invertebrate-consumers	−0.81	0.082	3.65	−0.82	50
Invertebrate-consumers, excluding eutherians < 100 g	−0.76	0.124	3.38	−0.79	25
Vertebrate-consumers	−0.96	0.106	3.47	−0.82	42
All mammals	−0.78	0.027	4.06	−0.80	467

Regressions are for $\log_{10}$ population density (number of individuals per km^2) regressed on $\log_{10}$ body mass (g). Symbols and abbreviations as in Table 1.

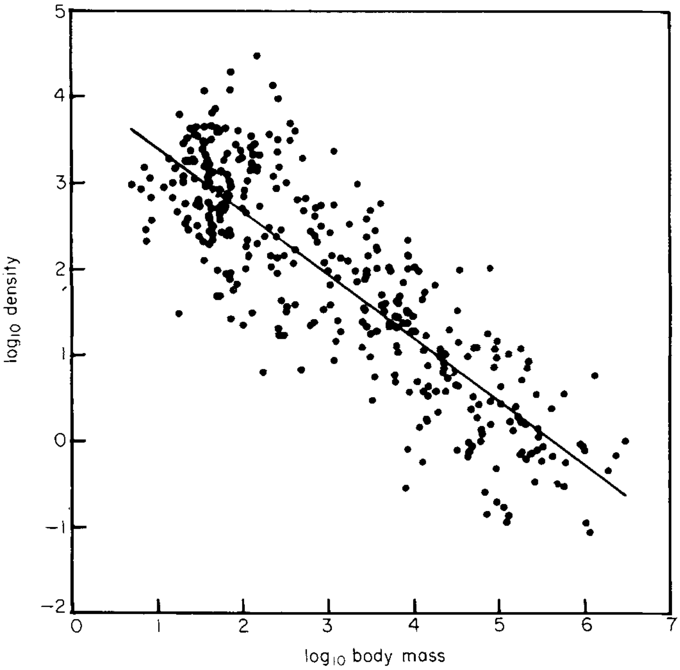

Figure 1. Population density regressed on body mass for mammalian primary consumers. Each point represents one species. Data in the Appendix. Regression equation in Table 2.

densities). The average temperate herbivore maintains a population density approximately 1.5 to 2.0 times that of a tropical herbivore of the same size. Because in this sample the body-size range is the same for both tropical and non-tropical species, the global regression exhibits a similar slope to that of the subsets, in spite of this difference between tropical and non-tropical densities.

Table 3. Mammmalian primary-consumer regressions, by geography and habitat-type

Grouping	Slope	S.E.	Intercept	r	N
Geography					
Tropics	−0.73	0.031	4.08	−0.85	203
Non-tropics	−0.79	0.051	4.51	−0.84	97
North America	−0.75	0.057	4.33	−0.82	84
East Africa	−0.73	0.056	4.13	−0.85	68
South & Central America (tropics)	−0.70	0.086	4.06	−0.80	40
Habitat					
Grasslands & Savanna	−0.80	0.039	4.46	−0.88	124
Tropical	−0.76	0.043	4.20	−0.89	83
Non-tropical	−0.78	0.100	4.62	−0.78	41
Forests	−0.72	0.035	4.14	−0.85	165
Tropical	−0.67	0.047	3.91	−0.80	120
Non-tropical	−0.72	0.060	4.31	−0.88	45

Regressions are of $\log_{10}$ population density (number of individuals per km^2) regressed on $\log_{10}$ body mass (g). Species from desert areas in both the tropics and temperate zones were excluded from these calculations. Symbols and abbreviations as in Table 1.

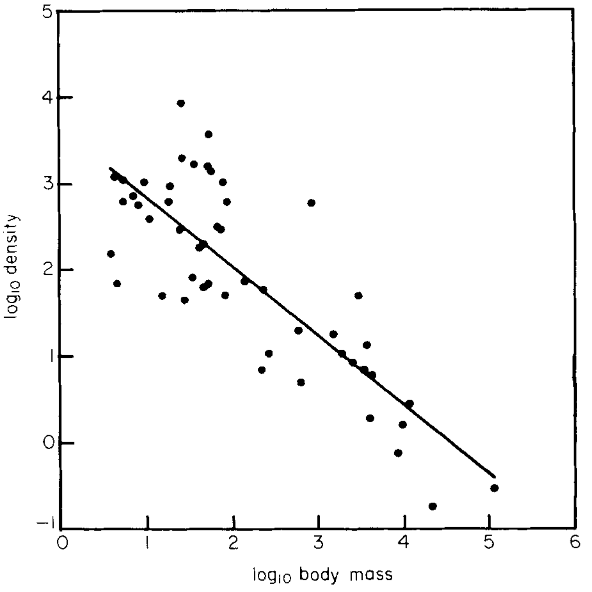

Figure 2. Population density regressed on body mass for mammalian insect-consumers. Each point represents one species. Data in the Appendix. Regression equation in Table 2.

Mammals—secondary consumers

The slopes for invertebrate-consumers and vertebrate-consumers are not significantly different from that for herbivores ($P > 0.40$ and $P > 0.05$, respectively), nor are they different from -0.75 (Table 2, Figs 2–3). The elevations of the secondary-consumer lines are lower than that for primary

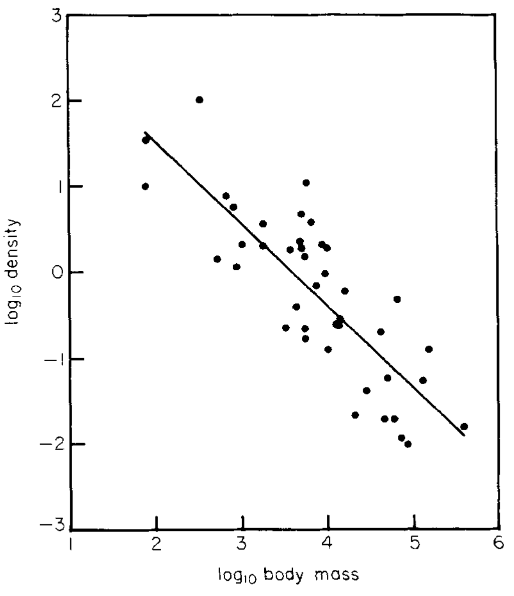

Figure 3. Population density regressed on body mass for mammalian vertebrate-consumers. Each point represents one species. Data in the Appendix. Regression equation in Table 2.

Table 4. Population density regressed on body mass for the Animalia

Grouping	Slope	S.E.	Intercept	r	N
All Animalia	−1.05	0.015	5.11	−0.94	667
Aquatic animals	−0.87	0.036	6.11	−0.90	140
Terrestrial animals	−0.95	0.018	4.68	−0.92	527
Terrestrial animals, adjusted for metabolism	−0.76	0.018	3.98	−0.88	527

Regressions are of $\log_{10}$ population density (number of individuals per km^2) regressed on $\log_{10}$ body mass (g). Symbols and abbreviations as in Table 1. For adjustment for metabolism, see text.

consumers. The secondary consumer data sets have not been broken down further for analysis because of the small sample size within each geographic and habitat category.

When small eutherians are removed from the invertebrate-consumer regression the slope drops from −0.81 to −0.76. This means that the small

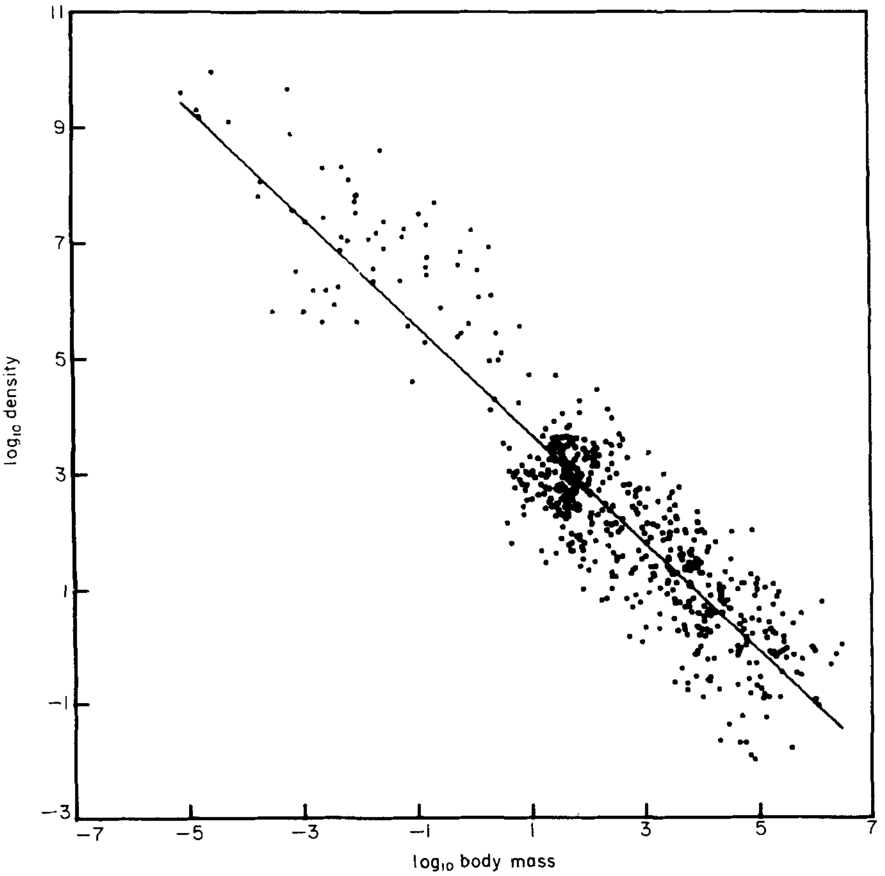

Figure 4. Population density regressed on body mass for terrestrial animals (unmodified data). Each point represents one species. Data in the Appendix. Regression equation in Table 4.

insectivores that exhibit high metabolic rates are also exhibiting high population densities, which is somewhat unexpected (see discussion).

Terrestrial animals

Adding data on terrestrial invertebrates and poikilothermic vertebrates to the data for mammals yields a regression for terrestrial organisms. All trophic levels and dietary types have been combined for this analysis. The slope (−0.95) is significantly steeper than −0.75, as Peters & Wassenberg (1983) reported for a similar regression (Table 4, Fig. 4). However, in such regressions (including that of Fig. 4) poikilothermic ectotherms and homeothermic endotherms have been included in the same analysis. Homeothermic individuals use energy at a rate that is approximately 30 times that of poikilotherms of the same size (Hemmingsen, 1950, 1960; Peters, 1983). Thus, in this data set, differences in population density for a given size do not necessarily directly reflect corresponding differences in population energy-use. We can crudely correct for this difference in metabolic level by dividing all poikilothermic population densities by a factor of 30. Each data point will then be comparable in the way that it represents rate of energy-use. The resulting regression exhibits a slope of −0.76, showing that in the terrestrial biota energy use is independent of body mass over 11 orders of magnitude (Table 4, Fig. 5).

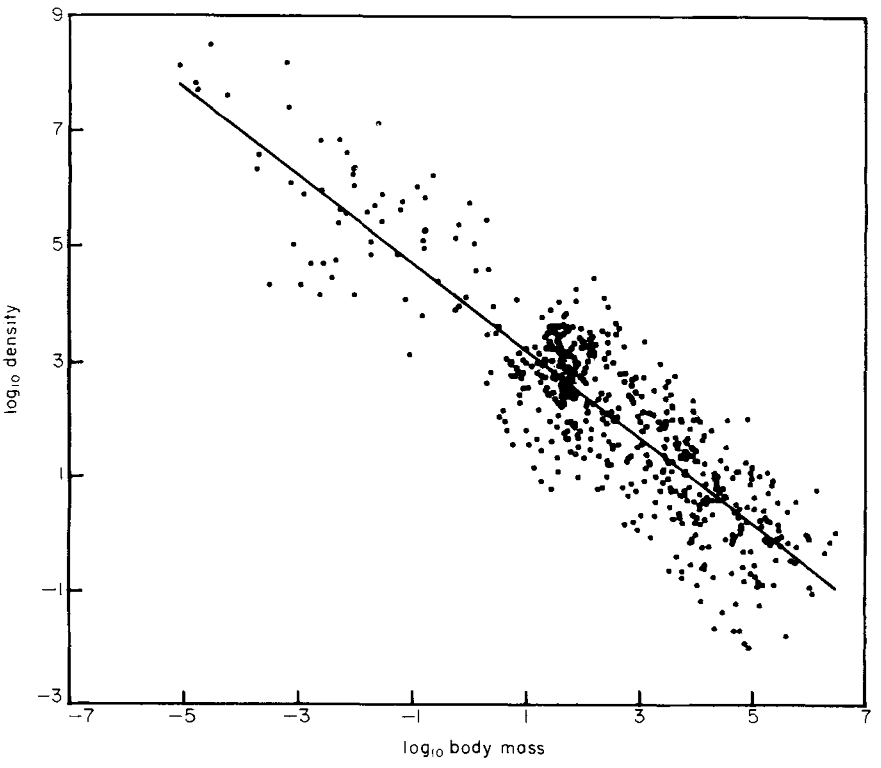

Figure 5. Population density regressed on body mass for terrestrial animals (corrected for metabolic level; see text). Each point represents one species. Data in the Appendix. Regression equation in Table 4.

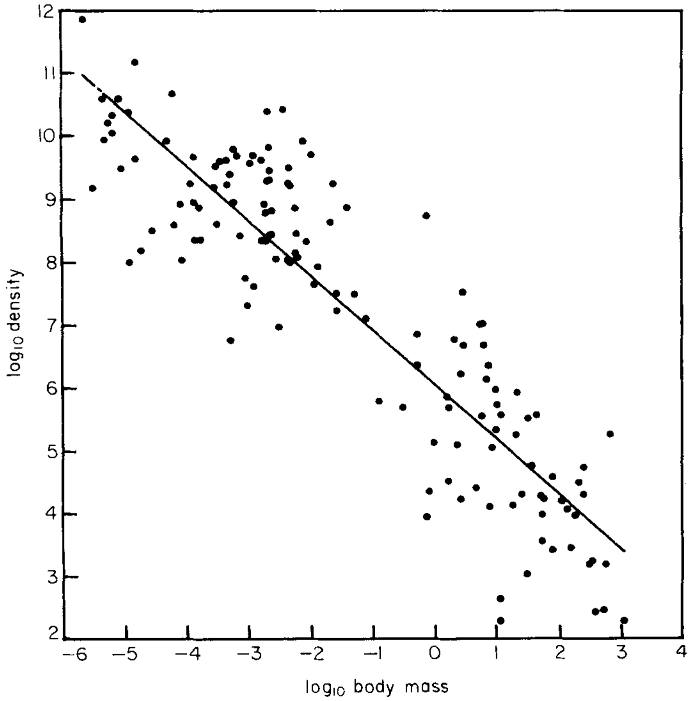

Figure 6. Population density regressed on body mass for aquatic animals. Each point represents one species. Data in the Appendix. Regression equation in Table 4.

Aquatic animals

All aquatic organisms in the data set are poikilothermic ectotherms, and so can be compared directly. The slope (−0.87) is significantly steeper than −0.75 (Table 4, Fig. 6).

ALLOMETRY OF ENERGY BUDGETS

The independence of body mass and energy-use can be examined directly through the scaling of energy-budgets. Odum (1971) and Ricklefs (1973) have suggested that population energy budgets of different-sized species are often very similar. Humphreys (1981) has compiled estimates of yearly population energy budgets for 89 non-avian animal species. For both aquatic and terrestrial

Table 5. Regressions of population assimilation-rate on body mass

Grouping	Slope	Intercept	r	N
Terrestrial animals	0.072	−0.278	0.15	63
Aquatic animals	−0.058	1.97	−0.18	26
All combined	−0.080	1.16	−0.15	89

Data consist of all non-avian data reported per species in Humphreys (1981). Assimilation rate is in kcal m^{-2} year, body mass in grams. None of the slopes are significantly different from 0 ($P > 0.10$). Symbols and abbreviations as in Table 1.

organisms the slopes of the regressions of population assimilation-rate on body mass are approximately zero (Table 5).

DISCUSSION

Population density decreases approximately as body mass to the -0.75 power among mammalian primary and secondary consumers, and among terrestrial organisms as a whole (when adjusted for differences in metabolic level). There is thus a reciprocal relationship between the scaling of population density and that of individual metabolic requirements (which scale approximately as body mass to the $+0.75$ power). This strongly suggests that within a trophic level or dietary category local population energy-use is independent of body mass. This interpretation is in agreement with the scaling of population energy budgets among both aquatic and terrestrial animals, where no relationship is observed between body mass and population assimilation rate. Thus, on an ecological time scale, no terrestrial organism has an overall advantage in obtaining energy solely as a result of its size.

These relationships hold over body-mass ranges of from 3 to 11 orders of magnitude. On a smaller scale, size differences among close competitors or guild members may have an effect on competitive or evolutionary success (e.g. Morse, 1974; Roughgarden, 1983; Persson, 1985; Pregill, 1986; Brown & Maurer, 1986; Martin, 1986). This is not a contradiction, as Brown & Maurer (1986) assert, but rather a contrast involving processes of different scope that probably act on different time scales. It may usually be to a species' advantage, relative to its fellow guild members, to be the largest member of its guild, but at the same time it may be no advantage to belong to a guild of large rather than small species. For example, within a guild of ungulates it may be advantageous to be large enough to displace members of other guild-species from resources. But the overall scaling relationships analysed here show that the population energy-use of the largest, most successful ungulate species of this guild will not on average exceed that of the most successful member of a guild of rodents (or herbivorous insects). We should not be surprised that the combined effects of the many and diverse factors moulding community structure and faunal diversity give rise to different patterns and relationships at different scales of observation. At the scale of comparison discussed here body mass has no effect upon the level of energy-consumption or energetic dominance attained by a local population.

A possible exception occurs among insectivorous mammals. While among most insectivorous mammals population density scales approximately as body mass to the -0.75 power, small eutherians exhibit both unusually high metabolic rates and high population densities. Their populations thus appear to be using energy at a high rate. It may be significant that the highest population densities attained by small primary consumer species are among grazing microtines, which also have high metabolic rates (McNab, 1980, 1986a). Ordinarily, one would expect that higher individual metabolic rates would reduce the average population density that could be maintained by a species. If McNab (1980, 1986a, 1986b) is correct in arguing that in eutherians higher basal metabolic rates lead to higher rates of growth and population increase, it may be that these small insectivores are able to recover rapidly from population lows, and thus maintain high average densities. Alternatively, it may be that the prevalence of daily torpor in many small mammal species (McNab, 1983) or other size-dependent differences in activity levels cause extrapolations from measured metabolic rates to overestimate actual daily metabolic intake for the smallest forms.

Another exception may be aquatic organisms, where population density scaling would suggest that there is a slight energetic advantage to small size. However, the 26 population assimilation-rates for aquatic species show no such relationship. One explanation for this discrepancy may be that density estimates for freshwater plankton (the small end of the sample) and for fish (the large end) may not be comparable, because of differences in estimation techniques. Also, the assumption that active metabolic rates scale parallel to standard rates, based largely upon data for medium-sized and large terrestrial species, may not be strictly applicable in the case of all aquatic organisms.

Not only is average population energy-use conserved across body size, but inspection of the figures reveals that the range of variation about the regression line is approximately the same at all body masses. Terrestrial animals as different in size and ecological characteristics as elephants and phytophagous insects exhibit the same range of population energy-consumption values. This suggests that the limits to the levels of energy-use that a species may evolve to attain are set to a large degree by biological interactions among species in evolutionary time (Damuth, in press).

Since population density and energy-use data are derived from local populations, the patterns revealed in these global regressions also imply that similar patterns should be observed in local communities; this has been found to be true in a sample of various herbivorous mammal communities (Damuth, 1981a, in press). Thus, available evidence shows that on a number of different scales approximate independence of body mass and local population energy-consumption is an extremely widespread ecological regularity.

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APPENDIX: POPULATION DENSITY AND BODY MASS DATA

Species	Mass (g)	References	Density	References
MAMMALS—Primary consumers				
Primates:				
Alouatta caraya	7250	123	25	486
Alouatta palliata	6550	123	51	181, 185
Alouatta seniculus	7250	123	74	181, 486
Aotus trivirgatus	960	123	100	714
Ateles belzebuth	6000	123	13.5	181
Ateles geoffroyi	6000	123	45	181
Avahi laniger	1070	39	150	111, 562
Callicebus moloch	680	123	255	181
Callicebus torquatus	1200	181	15	361
Callithrix jacchus	241	182	900	181
Cebus albifrons	2520	147, 181	37	147
Cebus capucinus	2600	123, 124, 181	80	26, 181
Cebus olivaceous	2600	123	35	183
Cercocebus albigena	8000	123	33	106, 685, 686
Cercocebus galeritus	6000	123	45	124, 550
Cercopithecus aethiops	4050	123	53	160, 165, 240, 273, 636, 637, 638
Cercopithecus ascanius	3550	123	108	639
Cercopithecus campbelli	3600	123	20	68
Cercopithecus cephus	3500	123	20	243, 550
Cercopithecus mitis	4500	123	42	123, 124
Cercopithecus neglectus	4350	123	34	123, 124
Cercopithecus nictitans	4950	123	22.5	550
Cercopithecus pogonias	2700	123	22.5	550
Cheirogaleus intermedius	177	39	250	109
Colobus badius	8150	123	230	123, 124
Colobus guereza	9850	123	112	166, 360, 725
Colobus satanas	9500	124	30	124
Erythrocebus patas	7800	124	0.3	124
Euoticus elegantulus	300	109, 124	17.5	109
Galago alleni	260	109, 124	17.5	109
Gorilla gorilla	127000	123	1.8	124
Hylobates agilis	5900	123	5.1	124

Appendix (*cont.*)

Species	Mass (g)	References	Density	References
Primates (*cont.*)				
Hylobates klossi	5800	123	30	124
Hylobates lar	5800	123	6.2	445
Hylobates muelleri (= *moloch*)	6100	123	22	705
Indri indri	12 500	123	12	540, 541
Lepilemur mustelinus	600	123	288	111
Lemur catta	2700	123	250	562
Lemur fulvus	2100	123	1030	643, 656
Lemur mongoz	1700	39, 124	350	562
Macaca fascicularis	5000	123	25	124, 425, 445, 622, 705
Macaca mulatta	7850	123	35	294, 485
Macaca nemestrina	9100	123	20	124, 425, 445
Macaca sinica	5150	123	100	124
Microcebus coquereli	385	526	121	525, 526
Microcebus murinus	725	526	215	525, 526
Miopithecus talapoin	1250	123	26.2	242
Pan paniscus	22 700	534	4	384
Pan troglodytes	45 000	123	2.5	124
Papio anubis	19 500	123	10.3	116, 165, 261, 285, 578, 675
Papio cynocephalus	17 500	123	4	124
Papio hamadryas	13 900	123	1.8	382
Papio papio	19 500	123	12.5	172
Papio ursinus	18 600	123	2.3	124, 145
Perodicticus potto	1150	109	9	108, 109
Phaner furcifer	425	276	675	525
Pithecia pithecia	1024	182	40	181
Pongo pygmaeus	53 000	123	2	424, 425
Presbytis aygula	6250	123	29	124, 425
Presbytis entellus	12 800	123	57	124
Presbytis cristatus	8350	123	150	123
Presbytis johni	8150	123	107	123
Presbytis melalophos	6300	123	42	123, 445, 622
Presbytis obscurus	8350	123	33	123, 445, 622
Presbytis rubicunda	6300	123	11.4	705
Presbytis senex	8150	123	154	124
Propithecus verreauxi	3600	123	175	562
Saguinus midas	315	123	33	726
Saguinus oedipus	600	181	23	181
Saimiri sciureus	665	123	25	181
Saimiri oerstedi	665	123	25	181
Symphalangus syndactylus	10 700	123	5.2	117, 425, 445, 622
Theropithecus gelada	17 100	123	69.5	164, 165
Artiodactyla:				
Adenota kob	83 400	261, 327, 396, 495	7.76	66, 67, 194, 198, 208, 245, 261
Aepyceros melampus	52 400	160, 300, 301, 327, 386, 463, 495, 568, 681, 727	13.1	66, 67, 141, 142, 160, 223, 224, 265, 293, 298, 326, 368, 386, 404, 463, 569, 609, 626
Alcelaphus buselaphus	158 000	261, 327, 495, 681, 727	2.06	57, 66, 160, 223, 224, 261, 265, 293, 368, 386, 404, 576, 609, 631, 675

Species	Mass (g)	References	Density	References
Alces alces	403 000	93, 226, 593, 674	0.72	4, 74, 199, 319, 335, 343, 367, 374, 468, 518, 532, 535, 603, 728
Ammodorcas clarkei	31 000	327	0.83	597
Antidorcas marsupialis	31 800	144, 327, 495, 681, 727	4.65	144, 440
Antilocapra americana	46 500	93	0.93	40, 82, 85, 271, 511, 730
Antilope cervicapra	29 800	184, 260	4.8	184
Axis axis	48 100	184, 294	13	184, 294, 465
Axis porcinus	31 000	184	35	184
Bison bison	551 000	93, 274	0.32	235, 236
Bison bonasus	850 000	674	1.0	64, 373, 374
Blastocerus dichotomus	125 000	683	0.146	591
Bos banteng	263 000	184	0.85	184, 305, 528
Bos gaurus	568 000	184	0.61	184, 353, 465
Boselaphus tragocamelus	149 000	184	2.7	184
Bubalus bubalis	274 000	184	1.2	184, 528, 669
Capra hircus	75 000	674	3.1	89, 589, 590
Capra waalie	100 000	164	4.6	164
Capreolus capreolus	21 700	674, 683	8.6	4, 64, 89, 374, 549
Cephalophus natalensis	14 000	327	8.0	153
Cephalophus rufilatus	12 500	327	4.0	675
Cervus canadensis	310 000	93	0.93	306, 366, 423, 730
Cervus elaphus	175 000	674, 683	5.48	37, 62, 64, 89, 107, 365, 374, 415, 416, 489, 549, 628
Cervus duvauceli	170 000	184	12.7	184, 303, 587
Cervus unicolor	138 000	184	1.42	184, 305, 465, 528
Connochaetes taurinus	203 000	160, 299, 301, 327, 386, 397, 495, 568, 681, 727	7.59	66, 69, 153, 160, 223, 224, 293, 298, 492, 521, 569, 631, 682
Damaliscus dorcas	70 000	327, 681, 727	18.8	144, 171
Damaliscus lunatus	122 000	327, 681, 727	11.0	66, 67, 261, 265, 293, 368, 463, 609, 626 630, 631
Gazella granti	58 800	327, 386, 495, 681	1.06	57, 66, 223, 224, 293, 386, 404, 576, 631
Gazella thomsoni	21 000	326, 396, 495, 681	6.64	57, 66, 223, 224, 293, 631, 651
Giraffa camelopardalis	912 000	386, 681, 727	0.937	57, 66, 67, 139, 179, 198, 222, 223, 224, 265, 293, 298, 386, 402, 404, 493, 576, 609, 631, 675

Appendix (*cont.*)

Species	Mass (g)	References	Density	References
Artiodactyla (*cont.*)				
Hippotragus equinus	225 000	160, 261, 327, 495, 681	0.774	67, 160, 198, 261, 368, 537, 569, 626, 675
Hippotragus niger	197 000	160, 327, 495, 681	0.66	160
Hyemoschus aquaticus	13 300	162	17.9	162
Kobus defassa	211 000	160, 261, 327, 397, 495, 681	9.11	66, 67, 160, 192, 194, 208, 223, 224, 261, 265, 293, 385, 463, 609, 625, 626
Kobus ellipsiprymus	194 000	295, 327, 463, 681	1.69	66, 67, 295, 298, 386, 404, 675
Kobus leche	90 600	13, 47, 327, 495, 568, 569, 681	15.5	13, 47, 569, 586
Kobus vardoni	69 300	17, 160, 327, 568, 681	0.15	160
Lama guanacoe	89 000	458	0.51	225
Litocranius walleri	42 000	327, 397, 495	1.03	404, 729
Madoqua kirkii	4940	327, 663, 681	111	293, 386, 663
Mazama americana	20 000	182	10	183
Muntiacus muntjak	14 200	184	3.53	36, 184, 294, 528, 529
Odocoileus hemionus	89 300	93, 730	10	50, 118, 180, 279, 306, 423, 594, 649, 650, 730
Odocoileus virginianus	85 100	93	12.6	6, 100, 132, 190, 218, 275, 319, 343, 378, 389, 417, 433, 451, 502, 658, 672
Oreotragus oreotragus	14 300	164, 327, 495, 681	4.6	66, 164, 293
Oryx gazella	167 000	327, 495	0.75	404, 631
Ourebia ourebi	13 600	160, 261, 327, 463, 495, 501, 568, 681	1.9	67, 160, 261, 293, 368, 446, 463, 464, 501, 569, 626, 675
Ovibos moschatus	250 000	93, 311, 700	0.36	206, 228, 311, 453, 454, 455, 624
Ovis canadensis	75 900	93, 246	1.68	84, 246, 401, 604
Pelea capreolus	24 000	327, 494, 501	5.71	144, 446, 501
Phacochoerus aethiopicus	60 900	160, 261, 301, 386, 397, 463, 568, 681, 727	1.30	66, 67, 69, 153, 160, 193, 194, 198, 208, 223, 224, 261, 293, 298, 386, 404, 463, 626, 675
Potamochoerus porcus	65 700	160, 568, 681, 727	0.27	66, 153, 160

Species	Mass (g)	References	Density	References
Rangifer tarandus	100000	87, 93, 260, 414	2.88	27, 227, 238, 288, 292, 324, 340, 349, 400, 414, 453, 454, 455, 503, 509, 513, 560, 602, 610, 659, 676, 699
Raphicerus campestris	12300	327, 495	0.60	66, 153, 293
Raphicerus sharpei	8210	160, 327, 568, 681	0.85	160
Redunca arundinum	59400	160, 327, 495, 568, 681, 727	1.46	69, 160, 569
Redunca fulvorufula	28000	327, 495, 681, 727	6.69	317, 318, 501
Redunca redunca	43500	261, 327, 495	0.81	66, 67, 198, 208, 261, 293, 304, 368, 463, 626, 675
Saiga tatarica	42500	674	0.80	28
Sus scrofa	55300	184, 294, 305, 674	2.84	4, 184, 287, 294, 529, 536, 549
Sylvicapra grimmia	11300	160, 164, 261, 327, 350, 357, 495, 568, 681	1.53	66, 67, 153, 160, 164, 261, 293, 357, 626, 675
Syncerus caffer	544000	160, 261, 327, 386, 463, 495, 568, 681	3.81	66, 67, 69, 160, 192, 195, 208, 261, 293, 326, 348, 403, 404, 463, 493, 533, 576, 626, 631, 651
Taurotragus oryx	453000	160, 327, 386, 463, 495, 568, 681, 727	0.345	57, 66, 67, 160, 223, 224, 265, 293, 404, 463, 493, 569, 576, 609, 626, 631, 651, 670
Tayassu tajacu	21700	93, 683	7.46	52, 191, 601, 723
Tragelaphus angasi	90600	301, 327, 727	0.209	153
Tragelaphus imberbis	110000	327, 386, 397, 681	0.182	386, 404
Tragelaphus scriptus	40800	160, 164, 301, 327, 495, 568, 681, 707	10.3	14, 67, 160, 164, 192, 208, 261, 293, 323, 675
Tragelaphus spekei	74800	327, 495, 681	110	505
Tragelaphus strepsiceros	171000	160, 326, 327, 495, 681, 706, 727	1.79	66, 153, 160, 298, 326, 569
Tragulus memmina	3200	184	3.1	184
Vicugna vicugna	47500	458	3.5	370, 458
Perissodactyla:				
Ceratotherium simum	2220000	204, 727	0.74	67, 69, 204, 680

Appendix (*cont.*)

Species	Mass (g)	References	Density	References
Perissodactyla (*cont.*)				
Diceros bicornis	952 000	301, 386, 681	0.84	66, 69, 255, 256, 293, 300, 326, 386, 404, 431, 473, 493, 577, 631, 651, 675, 697
Dicerorhinus sumatrensis	1 120 000	184	0.093	459, 635
Equus burchelli	259 000	160, 301, 386, 463, 568, 681, 727	3.74	66, 67, 69, 160, 179, 223, 224, 293, 298, 404, 463, 493, 569, 576, 626, 630, 631, 651
Equus grevyi	390 000	159, 396	2.57	630, 631
Equus zebra	270 000	159	1.5	336
Rhinoceros unicornis	1 255 000	184	6.27	184
Rhinoceros sondaicus	997 000	184	0.12	184, 305
Tapirus bairdii	300 000	185	0.63	660
Tapirus terrestris	175 000	182	0.8	183
Proboscidea:				
Elephas maximus	1 810 000	184	0.49	184, 351, 352, 353, 465, 472, 529
Loxodonta africana	2 860 000	160, 293, 386, 523, 681	1.09	7, 66, 67, 86, 95, 103, 160, 179, 192, 193, 198, 207, 208, 254, 261, 293, 326, 404, 493, 533, 538, 576, 618, 631, 651, 675, 692, 693, 708
Hyracoidea:				
Dendrohyrax validus	2430	358	25.6	383
Lagomorpha:				
Lepus americanus	1360	93	141	5, 10, 154, 156, 355, 713
Lepus californicus	2420	93, 263	13.0	115, 216, 266, 289, 730
Lepus capensis	3030	96, 187, 398, 674	9.97	555
Lepus nigricollis	2710	184	101	184
Lepus timidus	3020	219, 674	18.6	219, 691
Lepus townsendi	3400	93	5.84	216, 730
Ochotona princeps	154	93, 341, 434	558	75, 88, 452
Oryctolagus cuniculus	1640	398, 674	131	170, 712
Sylvilagus auduboni	854	93, 115, 260, 296	35.4	115, 209, 216, 730
Sylvilagus bachmani	692	93	544	131
Sylvilagus floridanus	1130	93, 260	588	575, 667
Sylvilagus nuttalli	1020	93	68.8	422
Rodentia:				
Acomys subspinosus	22	732	3450	563
Aethomys hindei	146	500	1590	500
Aethomys namaquensis	42	557, 647	3300	563
Agouti paca	8200	182	25	183
Akodon olivaceus	29.1	233, 497	3626	233, 515

Species	Mass (g)	References	Density	References
Ammospermophilus harrisi	127	93, 115	32	115
Apodemus agrarius	20	674	1240	16, 113, 333, 719
Apodemus flavicollis	36	398, 552	949	16, 22, 60, 61, 113, 280, 474, 715
Apodemus sylvaticus	33	398	2550	79, 217, 270, 280, 457, 496, 654, 715
Arvicanthus abyssinicus	70	475	12400	475
Arvicanthus niloticus	103	151, 309, 519, 607	862	150, 546, 657
Arvicola terrestris	143	674	30900	8, 9, 467
Auliscomys micropus	71	515	257	515
Baiomys taylori	7	93, 291	1550	522, 632
Callomyscus bailwardi	22.5	683	400	232
Callosciurus caniceps	257	580, 731	21	287
Callosciurus nigrovittatus	170	408, 580, 731	6.5	287
Callosciurus notatus	210	408, 580, 731	111	287
Calomys callosus	40	497	400	497
Calomys expulsus	40	497	1350	497
Calomys musculinus	40	497	286	497
Cavia aperea	487	398	2040	570
Citellus fulvus	1020	496, 732	278	354
Citellus pygmaeus	222	1	1250	1, 221
Clethrionomys gapperi	27	93	1160	83, 470, 584
Clethrionomys glareolus	23	398, 412, 582, 674	1890	3, 16, 22, 23, 60, 61, 113, 280, 281, 325, 435, 444, 474, 520, 551, 611, 654, 715
Clethrionomys occidentalis	31	732	556	241
Clethrionomys rutilus	28	93, 582	4600	702
Coendu prehensalis	4000	110	40.3	110, 183
Cricetulus migratorius	30.5	490	250	232
Cryptomys hottentotus	68.7	247, 607, 617	741	247
Ctenomys opimus	241	516	247	497, 516
Ctenomys peruanus	400	497	4200	497, 516
Cynomys ludovicianus	1130	93	2470	369
Dasymys incomptus	88	18, 151, 283, 398, 553, 607, 617	1940	48, 148, 150, 461, 606
Dasyprocta leporina	2700	182	90	183
Dasyprocta punctata	2000	185	100	212, 619
Delanymys brooksi	5	151	985	149, 150
Dendromus mesomelas	13.5	149, 151, 553	1980	148, 150, 461
Dendromus mysticalis	8.2	149, 151	1170	150, 461
Desmodillus auricularis	55	617	1429	119
Dicrostonyx groenlandicus	56	87, 237	585	205, 237, 375
Dipodomys agilis	60	93, 260	504	120, 418, 449
Dipodomys deserti	108	76, 93	469	41, 42
Dipodomys elator	145	732	1450	567
Dipodomys heermanni	72	93	950	129
Dipodomys merriami	38.5	93, 115, 260, 346, 347, 620	1209	41, 42, 56, 114, 115, 120, 599, 620, 701
Dipodomys microps	65	76, 93, 346, 347	1310	41, 42

Appendix (*cont.*)

Species	Mass (g)	References	Density	References
Rodentia (*cont.*)				
Dipodomys ordii	53	76, 93	449	56, 229, 522, 599, 701
Dipodomys spectabilis	145	93	205	598, 701
Echimys chrysurus	475	269	7	269
Echimys semivillosus	400	497	40	183
Eothenomys smithi	35	134, 732	1610	653
Erethizon dorsatum	8620	93	3.9	547
Eutamias minimus	39	76, 93, 677	1700	677
Eutamias townsendi	97	93	531	241
Gerbillurus paeba	26	617	1950	119
Glaucomys volans	69	93, 429	293	429
Heteromys anomalus	69	427	1090	183, 497, 572
Heteromys desmarestianus	65	215	695	212, 215
Hybomys trivirgatus	63	282	91	282
Hydrochaerus hydrochaerus	32 800	398, 683	104	183, 184, 733
Irenomys tarsalis	44.5	515	325	515
Lagurus curtatus	30	93	666	379
Lemmus trimucronatus	81	87, 93	2900	87, 375
Lemniscomys griselda	54	607, 617	387	648
Lemniscomys striatus	65	151, 282, 398, 553	777	48, 112, 149, 150, 398, 461
Liomys pictus	44	182	1380	127
Liomys salvini	39	215	620	215
Makalata armatus	400	110	175	110
Malacomys edwardsi	64	126, 283	256	283, 284
Marmota flaviventris	3400	93	296	21, 645
Marmota marmota	3950	398, 674	616	721
Melomys cervinipes	65	33, 97, 574	667	33, 34, 711
Meriones persicus	116	398	150	232
Microcavia australis	250	570	2390	570
Microtus agrestis	36	582, 674	2200	280, 281, 477
Microtus arvalis	27	398, 399, 674	3770	22, 161, 520
Microtus californicus	71	93	19 900	38, 376, 406
Microtus longicaudatus	47	93	7500	130
Microtus mexicanus	35	93	3000	130
Microtus montanus	43	93, 677	6750	210, 677
Microtus ochrogaster	35	93	12 000	377, 436, 437, 448
Microtus oeconomus	49	93, 582	4500	244, 272, 702
Microtus pennsylvanicus	49	93	4040	55, 83, 249, 257, 377, 584
Mus bufo	8.6	151, 553	380	148, 150
Mus minutoides	6.4	18, 151, 290, 553, 607, 617	868	48, 112, 148, 150, 461
Mus musculoides	8.5	282	699	282
Mus triton	11.8	20, 151, 553, 607	919	112, 148, 150, 461
Mylomys dybowskii	108	151, 553	189	48, 112
Myomys daltoni	34	283	3170	283
Neacomys guianae	17.8	269	31	269
Neofiber alleni	254	54, 683	9880	54
Neotoma floridana	250	291	140	31
Neotoma fuscipes	248	77, 93	93	418
Neotoma lepida	130	77, 78, 93, 600	1610	58, 78, 418
Neotoma micropus	260	93	1600	556, 701
Ochrotomys nuttalli	21	93	351	410, 616
Octodon degus	218	233, 394	14 000	394
Oenomys hypoxanthus	86	19, 151, 553	4220	148, 150, 461

Species	Mass (g)	References	Density	References
Oryzomys bauri	65	121	2300	121
Oryzomys bicolor	49	269	50.2	183, 269, 497
Oryzomys capito	42	201, 212	532	183, 201, 212, 213, 269
Oryzomys concolor	35	110	129	110, 183, 269
Oryzomys eliurus	40	497	1050	497
Oryzomys longicaudatus	30	233	620	233
Oryzomys macconnelli	76.5	269	58.8	269
Oryzomys nigripes	24.1	679	2455	497, 679
Oryzomys oniscus	40	497	200	497
Oryzomys palustris	59	93	1900	614
Oryzomys simplex	40	497	1700	497
Oryzomys subflavus	50	269	100	269
Otomys angoniensis	136	20, 607, 617	2970	657
Otomys irroratus	121	146, 151	2700	148, 150, 461
Pelomys fallax	112	553, 606, 607, 617	1110	148, 150
Perognathus flavus	7.4	93, 115	294	115, 522, 701
Perognathus intermedius	17	93	480	701
Perognathus longimembris	7.5	76, 93, 346, 347	214	114, 449
Perognathus parvus	20	76, 93	2970	379
Perognathus penicillatus	15	76, 93, 115	701	701
Peromyscus boylii	28	93	585	80, 127
Peromyscus californicus	42	93, 291	4790	447, 449
Peromyscus eremicus	23	93, 291	293	115, 418, 449, 701
Peromyscus gossypinus	35	53, 93, 291	4650	53, 614, 616
Peromyscus leucopus	21	93, 291	1890	286, 419, 478, 615, 633, 701
Peromyscus maniculatus	20	76, 93, 291, 677	1060	38, 118, 203, 229, 241, 379, 418, 449, 470, 522, 527, 558, 581, 615, 640, 677, 701
Peromyscus polionotus	15	291	1040	143, 499
Peromyscus truei	24	76, 93	4450	447
Phyllotis darwini	52	233	4090	233
Phyllotis osilae	39	157, 516	434	157, 516
Phyllotis pictus	44	157	263	157
Praomys erythroleucus	53	309, 310, 398	876	309
Praomys natalensis	50	151, 283, 479, 553, 606, 607, 617, 648	777	112, 148, 150, 283, 606, 648, 657
Praomys tullbergi	38	186, 282, 398	1900	283, 284
Proechimys guyannensis	316	201	1060	201
Proechimys semispinosus	800	185, 253	583	212, 213
Psammomys obesus	70	260	79	140
Rattus cremoriventer	72	408, 580	27	287
Rattus exulans	62	408, 709	4480	173, 287, 652, 703, 709
Rattus fuscipes	125	33, 71, 574	1770	33, 34, 711
Rattus muelleri	321	407, 408, 580, 717	38	287
Rattus rattus	122	151, 260, 408, 491, 553, 607	3650	652
Rattus tiomanicus	112	408	227	287
Rattus villosissimus	251	45	3350	101
Rattus whiteheadi	54	408, 580	50	287

Appendix (*cont.*)

Species	Mass (g)	References	Density	References
Rodentia (*cont.*)				
Reithrodon auritus	85	497	69	497
Reithrodontomys fulvescens	21	93	598	337, 506, 522
Reithrodontomys megalotis	16	76, 93, 115	1530	38, 118, 418, 449, 522, 701
Rhabdomys pumilio	44	20, 617, 648,	224	119
Rhipidomys mastacalis	115	497, 734	144	183
Saccostomus campestris	45	18, 151, 607, 617	870	648
Sciurus carolinensis	530	93	701	32, 65, 220, 466, 471, 673
Sciurus granatensis	275	497	45	183
Sciurus griseus	680	93	431	316
Sciurus langsdorffi	275	497	300	497
Sigmodon fulviventer	120	25, 93, 329	1460	522
Sigmodon hispidus	129	93, 291, 338, 498	2220	118, 211, 337, 498, 522, 595, 614, 632, 701
Sigmomys alstoni	50	497	50	183
Spermophilus armatus	350	93	5130	612
Spermophilus franklini	500	93	500	476
Spermophilus richardsonii	351	93, 720	3280	720
Spermophilus spilosoma	107	93, 115	105	115, 701
Spermophilus tridecemlineatus	200	93	318	200, 229
Spermophilus undulatus	800	93	330	99
Stochomys longicaudatus	71	282, 398, 553	94	283
Sundasciurus tenuis	100	580, 731	23	287
Synaptomys cooperi	27	239	1850	239
Tachyoryctes splendens	200	359, 553, 554	3822	148, 150, 554
Tamias striatus	97	93, 260	2060	646, 716
Tamiasciurus hudsonicus	207	93, 155	148	345, 392, 724
Tatera kempii	101	283	725	48, 283
Taterillus gracilis	51	283, 309, 310	528	283
Taterillus pygargus	62	310	550	544, 545
Thamnomys dolichurus	42	151, 359, 553	343	148, 150, 461
Thomomys bottae	154	51, 93	2200	308, 512
Thomomys talpoides	93	93, 677	2480	278, 559, 677
Uranomys ruddi	34	282	214	48, 283
Zapus hudsonicus	18	93	6430	584
Zapus princeps	29	93	330	81
Zygodontomys brevicauda	56	734	279	183, 497
Carnivora:				
Ailuropoda melanoleuca	118 000	683	0.121	605
Edentata:				
Bradypus infuscatus	2700	182	407	182, 183
Choloepus hoffmanni	3500	182	190	182
Marsupialia:				
Caluromys philander	300	110	150	110
Lasiorhinus latifrons	25 000	695	20.8	695
Macropus parryi	12 000	182	47	182
Macropus robustus	31 900	655	15	174, 175
Megaleia rufa	41 400	152	0.7	104, 487, 488
Phascolarctos cinereus	11 000	182	100	182
Potorous apicalis	1360	182, 268	19.6	363
Pseudocheirus peregrinus	872	182, 655	125	182, 661
Schoinobates volans	1250	671	83	671
Setonix brachyurus	3000	167, 182	511	182, 363
Trichosurus caninus	2800	35	150	182

Species	Mass (g)	References	Density	References
Trichosurus vulpecula	2080	167, 655	75	136, 168, 169, 621
Vombatus ursinus	22 500	182, 683	11	421
Wallabia agilis	10 000	182	20	182
MAMMALS—Secondary consumers ('Insect-eaters')				
Insectivora:				
Blarina brevicauda	17.8	39, 93	621	616
Crocidura bicolor	3.8	20, 607	153	148
Crocidura hildegardeae	10.6	39	392	148
Crocidura occidentalis	33.4	20, 39, 607	81.7	148
Elephantulus edwardii	55	276	1400	563
Erinaceus europeaus	805	39, 735	600	621
Sorex araneus	9.3	39, 582	1046	280, 281, 621, 736, 737, 738, 739
Sorex arcticus	8	93	564	83, 736
Sorex cinereus	4.2	93	1207	83, 741
Sorex longirostris	4.5	93	69	616
Sorex minutus	5.3	39	621	280, 281, 738, 739
Sorex vagrans	7	93	717	674
Sylvisorex lunaris	18.5	39	949	148
Sylvisorex megalura	5.3	39	1103	148
Talpa europea	76	39	1045	621, 740
Tupaia glis	134	39, 580	74	287
Primates:				
Arctocebus calabarensis	210	109	7	109
Loris tardigradus	220	39, 109	59	524
Rodentia:				
Akodon azarae	25	291	8670	497
Akodon longipilis	51.4	233	3815	233
Akodon urichi	45	497	200	183
Bolomys amoenus	25.4	157, 158, 516	2020	157, 516
Lophuromys flavopunctatus	50	125, 151	1610	149, 150, 277, 461
Lophuromys sikapusi	64	151, 282, 290, 398	319	48, 112, 283
Notiomys valdivianus	27.1	515	45	515
Notiomys macronyx	70.9	515	297	515
Onychomys torridus	23.8	115	294	56, 115, 522, 701
Oxymycterus rutilans	85	497	620	497
Rhinosciurus laticaudatus	253	731	10.8	287
Zelotomys hildegardeae	51	18, 151	69	112, 607
Carnivora:				
Conepatus semistriatus	1800	183	10.75	183
Meles meles	10 900	479	2.82	380, 479
Mephitis mephitis	2404	678	8.5	202, 678
Melursus ursinus	105 000	642	0.29	135, 390, 642
Mungos mungo	1430	571, 579	18.1	571
Nasua narica	9070	93	1.6	387
Otocyon megalotis	3750	276	1.88	687
Proteles cristatus	8000	276, 579	0.75	687
Spilogale putorius	595	93	5	202
Vulpes pallida	3250	276	6.9	545
Pholidota:				
Manis tricuspis	2800	182	50	182

Appendix (*cont.*)

Species	Mass (g)	References	Density	References
Edentata:				
Dasypus novemcinctatus	3500	182	13.3	182
Myrmecophaga tridactyla	20 000	182	0.18	183
Tamandua tetradactyla	4000	182	6	183
Marsupialia:				
Antechinus stuartii	35	33, 71, 182	1689	33, 34, 182
Isoodon obesulus	560	182	19.8	182
Marmosa cinerea	80	110, 183	51	110, 183
Marmosa murina	45	110	63	110
Marmosa robinsoni	40	182	180	183, 214
Sminthopsis crassicaudata	15	742	50	742
MAMMALS—Secondary consumers ('Vertebrate-flesh-eaters')				
Marsupialia:				
Philander opossum	338	110, 128, 269, 314	105	110, 214
Sarcophilus harrisii	5700	182	11.6	182
Carnivora:				
Acinonyx jubatus	50 000	276	0.0601	160, 176, 202, 259, 588
Alopex lagopus	5500	46, 93,	0.175	676
Bassariscus astutus	1020	93	2.2	666
Canis adustus	5440	160	0.23	160
Canis aureus	12 500	276	0.258	293, 545
Canis latrans	14 000	46, 93, 252	0.296	98, 122, 202, 482, 664
Canis lupus	45 600	46, 93, 260	0.02	202, 230, 234, 335, 509, 710
Canis simensis	10 000	276	2	469
Crocuta crocuta	65 000	160, 276	0.506	160, 588, 687, 698
Cryptoprocta ferox	9500	11	1	11
Cuon alpinus	16 000	46, 305	0.625	330
Dusicyon thous	6500	70	4	183
Eira barbara	5000	539	2	183
Felis concolor	59 500	93, 267, 665	0.02	267, 306, 371
Felis onca	85 500	93, 260	0.01	372
Felis pardalis	13 600	93, 182	0.25	183
Felis sylvestris	4380	267, 276, 579	0.414	545, 592, 687
Felis yagouaroundi	7480	93	0.73	183
Fossa fossana	1800	11	3.85	11
Galictis vittata	4800	183	2.4	183
Galidia elegans	820	11	6	11
Genetta genetta	1780	276	2.13	545, 687
Herpestes sanguineus	525	276, 573, 579, 617	1.5	573
Ichneumia albicauda	3700	276, 579	1.93	687
Lutra perspillata	5000	294	5	294
Lycaon pictus	20 700	46, 276, 568	0.022	588
Lynx canadensis	10 200	93	0.13	510
Lynx lynx	28 600	267	0.043	202, 267, 320
Martes americana	883	93	1.2	623
Martes pennanti	3250	547, 548	0.235	547, 548
Mungotictis decemlineata	670	11, 12	8.2	11, 12
Mustela erminea	78.9	608	10.53	608
Mustela nivalis	80	197, 356	36	197, 257, 356, 413
Panthera leo	150 000	160, 267, 588	0.13	69, 160, 172, 189, 202, 223, 588, 626

Species	Mass (g)	References	Density	References
Panthera pardus	41 400	160, 177, 568, 743	0.21	160, 177, 293, 465
Panthera tigris	130 000	267, 294, 305	0.056	63, 294, 465
Panthera uncia	71 700	267	0.012	321
Taxidea taxus	8620	93	2.2	450, 480
Ursus maritimus	386 000	93	0.0162	388
Vulpes vulpes	5440	93, 411	1.6	411
MAMMALS—Diets unclassifiable				
Carnivora:				
Canis mesomelas	8160	276, 579	2.26	153, 588, 687
Potos flavus	2490	110, 182	14.4	110, 183
Procyon lotor	10 700	93	3.4	202, 231
Procyon cancrivorus	7050	183	7.1	183
Ursus americanus	153 000	93	0.818	44, 135, 196, 334, 344, 395, 409, 420, 718
Ursus arctos	233 000	93, 362	0.129	44, 362, 438, 514
Marsupialia:				
Didelphis marsupialis	1070	110, 182, 269, 744	69	110, 182, 183, 744
AMPHIBIA				
Desmognathus fuscus	1.56	94	34 800	94
Eurycea bislineata	0.12	94	657 000	94
Gyrinophilus porphyriticus	4.4	94	27 500	94
Plethodon cinereus	0.63	94	289 000	94
REPTILIA				
Agama agama	16	696	4820	696
Agama rupelli	35.2	696	400	696
Ameiva quadrilineata	58.4	745	3100	30
Anolis angusticeps	2.76	745	98 300	596
Anolis bonairensis	3.15	49	131 800	49
Anolis carolinensis	9.44	629	56 400	596
Anolis distichus	1.93	596	95 700	596
Anolis sagrei	6.53	629	391 000	596
Bassiliscus vittatus	182	745	750	30
Cnemidophorus murinus	27.7	49	55 600	49
Eremias spekei	2.3	696	21 000	696
Eumeces fasciatus	6.05	662	18 500	662
Gonatodes antillensis	0.843	49	420 000	49
Hemidactylus brookii	4.1	696	3000	696
Holodactylus sp.	5.7	696	1200	696
Latastia longicauda	13.3	696	467	696
Lygodactylus picturatus	3.22	696	3580	696
Mabuya brevicollis	34.0	696	700	696
Mabuya buettneri	129	745	1528	29
Mabuya maculilabris	58.4	745	891	29
Mabuya quinquetaeniata	26.6	696	200	696
Pachydactylus tuberculosus	9.75	696	2133	696
Panaspis nimbaensis	17.9	745	272	29
Riopa sundevalli	10.8	696	1200	696
Sceloporus olivaceus	25	732	3090	662
Uromastix acanthinurus	2170	262	181	262
Uta stansburiana	1.96	662	13 600	662
Varanus exanthematicus	1500	696	26.7	696
Varanus komodoensis	12 000	629	2	30
Varanus niloticus	750	696	50	696

Appendix (*cont.*)

Species	Mass (g)	References	Density	References
PISCES				
Abramis brama	238	43, 302	21 400	43, 302
Acerina cernua	9.1	302	234 000	302
Acerina schratser	11	302	450	302
Alburnus alburnus	1.95	302, 441	6.39×10^{6}	302, 441
Aspius aspius	17	302	14 400	302
Barbus barbus	1100	302	200	302
Blicca bjoerkna	7.75	302	120 000	302
Chaenobryttus coronarius	51.4	248	10 200	248
Chondrostoma nasus	24	302	21 600	302
Cottus gobio	5	137, 432	1.13×10^{7}	137, 432
Cyprinus carpio	175	302	10 000	302
Esox lucius	549	302	1639	302
Gasterosteus aculeatus	0.5	432	2.50×10^{6}	432
Gobio albipinnatus	11	302	200	302
Gobio gobio	2.48	302, 441	18 100	302, 441
Hippoglossoides platessoides	200	426	33 400	426
Ictalurus natalis	151	248	3020	248
Ictalurus nebulosus	300	248	1630	248
Lepomis gibbosus	29.6	248	1140	248
Lepomis macrochirus	30	248	355 000	248
Lepomis microlophus	48.7	248	20 500	248
Leuciscus cephalus	54.5	302	18 200	302
Leuciscus idus	74.7	302	41 100	302
Leuciscus leuciscus	2.17	302, 441	133 000	302, 441
Micropterus dolomieui	130	508	12 500	508
Nemacheilus barbatula	11	432	400 000	432
Notemigonus crysoleucas	0.7	105	9200	105
Perca flavescens	1.57	105	524 000	105
Perca fluviatalis	34.6	302	62 000	302
Phoxinus phoxinus	2.5	432	1.80×10^{6}	432
Pimephales promelas	0.289	105	523 000	105
Pomoxis negromaculatus	105	248	16 900	248
Rutilus rutilus	9.46	43, 302, 441	586 000	43, 302, 441
Salmo gairdnerii	239	302	58 500	302
Salmo salar	41	432	400 000	432
Salmo trutta	19	138, 302, 432, 746	193 000	138, 302, 432, 746
Salvelinus fontinalis	7.22	105, 585	13 600	105, 585
Scardinius erythropthalamus	51.6	302	3830	302
Semotilus atromaculatus	0.766	105	23 900	105
Semotilus margarita	0.922	105	143 000	105
Stizostedion lucioperca	379	302	279	302
Stizostedion vitreum	335	684	1880	684
Tinca tinca	525	302	300	302
Vimba vimba	76.6	302	2800	302
TERRESTRIAL ARTHROPODS				
Anomma nigricans	0.00917	405	3.49×10^{7}	405
Armadillidium vulgare	0.024	583	4.30×10^{8}	583
Bootettix punctatus	0.086	460	42 560	460
Camponotus acvapimensis	0.0051	405	2.20×10^{8}	405
Carabodes minusculus	0.0000284	59	9.70×10^{9}	59
Chamobates schützi	0.0000083	59	4.20×10^{9}	59
Leptopterna dolabrata	0.0183	428	2.29×10^{6}	428
Ligidium hypnorum	0.0069	627	1.30×10^{8}	627
Ligidium japonicum	0.0087	583	5.50×10^{7}	583
Nanhermannia nana	0.0000172	59	1.59×10^{9}	59
Narceus americanus	2.5	564	290 000	564
Neophilaenus lineatus	0.00254	297	2.94×10^{7}	297

Species	Mass (g)	References	Density	References
Olodiscus minima	0.0000156	59	2.10×10^9	59
Orchelimum fidicinium	0.156	613	2.21×10^7	613
Philoscia muscorum	0.00241	641, 644	2.12×10^8	641, 644
Platynothrus peltifer	0.000056	59	1.30×10^9	59
Pogonomyrmex badius	0.0066	72, 258	1.16×10^7	72, 258
Porcellio scaber	0.009	583	7.00×10^7	583
Tetramorium caespitum	0.000603	73	4.87×10^9	73
Trichoniscus pusillus	0.000664	530, 644	8.11×10^8	530, 644
Tracheoniscus rathkei	0.021	564	1.61×10^7	564
Trimerotopsis saxatalis	0.144	163	201 250	163
OTHER TERRESTRIAL INVERTEBRATES				
Acanthinula aculeata	0.00943	439	7.15×10^7	439
Agriolimax laevis	0.0737	328	380 000	328
Agriolimax reticulatus	2.07	328	1.29×10^6	328
Allolobophora caliginosa	0.218	531	5.39×10^7	531
Allolobophora chlorotica	0.153	531	2.97×10^6	531
Allolobophora longa	1.18	531	3.58×10^6	531
Allolobophora muldali	0.0155	531	1.24×10^7	531
Allolobophora rosea	0.116	531	3.44×10^7	531
Arianta arbustorum	0.554	439	4.40×10^6	439
Arion ater	1.25	328	1.21×10^6	328
Arion fasciatus	0.158	328	6.13×10^6	328
Arion hortensis	0.155	328	5.88×10^6	328
Arion intermedius	0.0638	328	1.90×10^7	328
Arion subfuscus	0.272	328	790 000	328
Carychium tridentatum	0.0002	439	1.20×10^8	439
Cepaea nemoralis	0.15	704	4.03×10^6	704
Clausilia bidentata	0.00947	439	450 000	439
Cochlicopa lubrica	0.00383	439	900 000	439
Columella edentula	0.000837	439	3.37×10^6	439
Dendrobaena mammalis	0.0282	531	2.54×10^7	531
Dendrobaena rubida	0.0529	531	2.31×10^6	531
Discus rotundatus	0.00519	439	1.35×10^7	439
Ena obscura	0.0184	439	3.82×10^6	439
Euconulus fulvus	0.00166	439	1.57×10^6	439
Hygromia hispida	0.00112	439	670 000	439
Hygromia striolata	0.0281	439	8.54×10^6	439
Lehmannia marginata	0.544	328	250 000	328
Lumbricus castaneus	0.0585	531	1.36×10^7	531
Lumbricus terrestris	1.86	531	9.09×10^6	531
Marpessa laminata	0.0045	439	1.80×10^6	439
Millsonia anomala	0.944	391	1.80×10^7	391
Octolasion cyaneum	0.606	531	7.51×10^6	531
Punctum pygmaeum	0.000186	439	6.72×10^7	439
Pupilla muscorum	0.000314	439	670 000	439
Retinella nitidula	0.00488	439	7.86×10^6	439
Retinella pura	0.00123	439	2.47×10^7	439
Retinella radiatula	0.00240	439	450 000	439
Vallonia pulchella	0.00112	439	670 000	439
Vitrea contracta	0.000717	439	3.91×10^7	439
Vitrea pellucida	0.00275	439	1.57×10^6	439
AQUATIC INVERTEBRATES				
Alona quadrangularis	4.78×10^{-6}	264	9.27×10^9	264
Ampelisca brevicornis	0.0126	364	9.15×10^7	364
Anatopynia goetghebueri	0.0000476	264	8.93×10^9	264
Anodonta anatina	5.53	481	1.17×10^7	481
Anodonta minima	5.39	481	388 000	481

Appendix (*cont.*)

Species	Mass (g)	References	Density	References
AQUATIC INVERTEBRATES (*cont.*)				
Anodonta piscinalis	6.47	668	1.49×10^{6}	668
Asellus aquaticus	0.000939	331, 430	2.19×10^{7}	331, 430
Arthripsodes ancylus	0.0005	561	6.00×10^{6}	561
Baetis rhodani	0.00216	722	2.90×10^{8}	722
Baetis vagans	0.000486	688	2.68×10^{9}	688
Bithynia tentaculata	0.0255	331, 443	1.84×10^{7}	331, 443
Calospecta dives	0.00198	564	2.66×10^{10}	564
Chaoborus flavicans	0.00446	331	1.75×10^{9}	331
Chironomus anthracinus	0.00722	331	8.95×10^{9}	331
Chironomus longistylus	0.000166	264	2.44×10^{8}	264
Chironomus plumosus	0.00455	430, 542	1.07×10^{8}	430, 542
Cladotanytarsus mancus	0.000128	542	9.40×10^{8}	542
Corixa germari	0.0222	137	1.91×10^{9}	137
Crangonyx richmondensis	0.000715	442	2.83×10^{8}	442
Cryptochironomus supplicans	0.000301	430	4.28×10^{8}	430
Cypria opthalmica	5.56×10^{-6}	264	1.71×10^{10}	264
Daphnia cucullata	6.52×10^{-6}	322	1.19×10^{10}	322
Daphnia hyalina	6.52×10^{-6}	322	2.27×10^{10}	322
Ephemerella subvarica	0.0021	690	3.06×10^{9}	690
Erpobdella octoculata	0.00423	188, 430	1.17×10^{8}	188, 430
Eurycercus lamellatus	0.0000119	24, 331	1.05×10^{8}	24, 331
Ferrissia rivularis	0.00229	92	7.03×10^{8}	92
Gammarus tigrinus	0.00424	43	3.40×10^{9}	43
Glyptotendipes glaucus	0.000112	264	1.87×10^{9}	264
Glyptotendipes paripes	0.0021	430, 542	2.17×10^{9}	430, 542
Gyraulus deflectus	0.00114	251	5.37×10^{9}	251
Gyraulus parvus	0.000864	178	6.00×10^{7}	178
Hedriodiscus truquii	0.075	634	1.40×10^{7}	634
Helobdella stagnalis	0.00186	331, 393, 430	2.33×10^{8}	331, 393, 430
Heterotrissocladius oliveri	0.00027	694	1.64×10^{9}	694
Hexagenia limbata	0.011	307	4.74×10^{7}	307
Hyalella azteca	0.00418	15, 133, 442, 564	1.91×10^{9}	15, 133, 442, 564
Hydra oligactis	0.0000629	430	4.13×10^{8}	430
Hydrozetes lacustris	4.46×10^{-6}	264	4.10×10^{10}	264
Ilyocryptus sordidus	8.87×10^{-6}	264	3.22×10^{9}	264
Ilyodrilus hammoniensis	0.00978	331	5.50×10^{9}	331
Isoplastis monilis	0.0000281	264	3.33×10^{8}	264
Lacuna vincta	0.003	91	1.00×10^{7}	91
Limnephilus lunatus	0.00119	264	4.40×10^{7}	264
Limnocalanus macrurus	0.0000118	565	2.55×10^{10}	565
Limnochironomus pulsus	0.000556	430, 542	9.55×10^{8}	430, 542
Littorina saxatalis	0.00158	91	2.36×10^{8}	91
Lumbriculus variegatus	0.00181	430	6.58×10^{8}	430
Lymnaea palustris	0.0366	178, 315	8.00×10^{8}	178, 315
Melampus lineatus	0.006	91	1.29×10^{8}	91
Microtendipes chloris	0.000128	339	4.95×10^{9}	339
Microtendipes sp.	0.00171	542	8.95×10^{8}	542
Modiolus demissus	0.49	381	7.80×10^{6}	381
Monodacna pontica	1.49	668	786 000	668
Mytilus edulus	0.02	91	4.71×10^{8}	91
Nassarius obsoletus	0.025	91	3.50×10^{7}	91
Neanthes virens	2.75	342	5.19×10^{6}	342
Oligophleboides sigma	0.00154	517	4.50×10^{9}	517
Orconectes virilis	9	462	1.02×10^{6}	462
Otomesostoma auditivum	0.000133	430	2.40×10^{8}	430
Pacifastacus lenuisculus	20	2	925 000	2
Parachironomus tener	0.000156	542	7.78×10^{8}	542
Pentaneura monilis	0.0000184	430	1.63×10^{8}	430

Species	Mass (g)	References	Density	References
Physa gyrina	0.0054	251	7.78×10^{8}	251
Physa integra	0.0057	178	3.11×10^{8}	178
Pisaster ochraceus	629	507	200 000	507
Pisidium casertanum	0.000633	264, 331	5.20×10^{9}	264, 331
Pisidium compressum	0.00102	251	4.00×10^{9}	251
Potamophylax cingulatus	0.0486	504	3.38×10^{7}	504
Potamothrix hammoniensis	0.00348	332	2.90×10^{10}	332
Pristina idrensis	0.000059	264	5.05×10^{10}	264
Procladius choreus	0.000439	430, 542	1.83×10^{9}	430, 542
Procladius pectinatus	0.00233	331	3.00×10^{8}	331
Procladius sagittalis	0.0000776	264	8.89×10^{8}	264
Pseudodiamensa arctica	0.0027	694	1.22×10^{8}	694
Psilotanypus rufovittatus	0.000556	542	6.70×10^{9}	542
Rhitrogena semicolorata	0.00819	722	2.32×10^{8}	722
Scobicularia plana	0.000083	312, 313, 564,	1.14×10^{8}	312, 313, 564
Sialis lutaria	0.0056	250, 264	1.53×10^{8}	250, 264
Skistodiaptomus oregonensis	0.000015	566	1.57×10^{11}	566
Strongylocentrotus droebachensis	2.64	456	3.68×10^{7}	456
Tanytarsus eminulus	0.000015	264	4.60×10^{9}	264
Tanytarsus holochlorus	0.000334	542	4.31×10^{9}	542
Tanytarsus inopterus	0.000284	542	3.59×10^{9}	542
Tanytarsus jucundus	0.00205	15	7.19×10^{9}	15
Tanytarsus lugens	0.000426	542	4.51×10^{9}	542
Tegula funebralis	0.702	564	6.00×10^{8}	564
Thermocyclops hyalinus	2.22×10^{-6}	90	7.54×10^{11}	90
Triplya sp.	3.13×10^{-6}	264	1.56×10^{6}	264
Unio pictorum	5.84	481, 668	5.26×10^{6}	481, 668
Unio tumidus	6.97	481, 668	2.50×10^{6}	481, 668
Valvata humeralis	0.00192	251	2.09×10^{9}	251
Vejdovskyella comata	8.23×10^{-6}	264	4.19×10^{10}	264

Mass is in grams, density in number of individuals per square kilometre. Reference numbers refer to the Appendix bibliography.

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