

A.L. Towe
M.D. Mann

Physiology and Biophysics, University of
Washington School of Medicine, Seattle,
Washington, and Physiology and
Biophysics, University of Nebraska
Medical Center, Omaha, Nebraska, USA

Brain Size/Body Length Relations Among Myomorph Rodents

Key Words

Brain/body relations
Body length/weight relations
Myomorph rodents
Allometry

Abstract

The relation between cranial volume and body length was examined in 45 species of myomorph rodents to determine how accurately the former can be estimated from the latter. On average within species, cranial capacity was directly proportional to body length (proportional to the cube root of body weight). On average across species, cranial capacity was directly proportional to the square of body length (proportional to the two-thirds power of body weight). Geometric similarity held within species, but the differences in habitus among species within the same genus generated genus slopes that differed from those defined by strict geometric similarity. It was found that cranial capacity could be estimated as accurately from body length as from body weight, and that body length was better if any differences in habitus were involved (because body length is relatively insensitive to habitus). Therefore, body length (or some strong correlate thereof) may serve well as the primary variable in brain paleoallometry.

Introduction

Body mass plays a central role in allometric study, primarily because it includes the combined mass of all body organs and secondarily because it figures prominently in many physiological processes (e.g., temperature regulation and metabolism). Its use in brain allometry strongly affects how we think about brain evolution and has led to the idea that surface-to-volume ratio [Jerison, 1973] or basal metabolic rate [Armstrong, 1983; Martin, 1981] may be fundamental scaling constraints. Yet, among the various body organs, the brain has least reason to vary strongly with body mass. The fossil record suggests that Mesozoic mammals were small [Lillegraven et al., 1979] and shows clearly that the size range of mammals increased through time to include larger forms. The size range of brains increased also but at a slower rate [Jerison, 1973]. The function $E = kP^b$

(where E is brain size, P is body weight, k is the allometric constant, and b is the allometric slope) describes the brain/body mass distribution for extant mammals quite well when b is near seven-tenths. On the other hand, the exponent for the relation *within* species, at least among myomorph rodents, varies from 1/6 to 3/5, with a mean of 1/3 [Mann et al., 1988], suggesting that if the adults of a species are geometrically similar, brain size varies directly with body length.¹ If generally true, then skeletal length may serve as an important measure in studies of brain evolution.

Radinsky [1967] suggested that the area of the foramen magnum might serve as a relevant variable; however, that area varies both with body size and with absolute brain size, compromising its usefulness. Jerison [1971] and Radinsky [1978] used skeletal body length (BL) of fossil specimens for estimating body weight, and they used the weight and length ranges recorded for carnivores and ungulates

Michael D. Mann
Department of Physiology and Biophysics
University of Nebraska Medical Center
Omaha, NE 68198-4575/USA

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0006-8977/92/0391-0017
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in the 1964 edition of 'Mammals of the World', by E.P. Walker, to obtain the relations $P=0.021BL^{3.03}$ (J) and $P=0.024BL^{3.01}$ (R). However, Radinsky [1967] found the relation to hold *only* when carnivores and ungulates were combined; when considered separately, they yielded exponents of $b=2.73 \pm 0.29^2$ and 3.45 ± 0.22^2 , respectively. The bulkiness of the large ungulates and litheness of small ungulates, that is, habitus, explains the large exponent, but the small exponent for carnivores is less easily understood. Pagel and Harvey [1988] would ascribe the low slope to the use of brain weights from one group of animals and of body weights from another. When Davis [1962] took both measures from the same animals, he found an exponent of 3.34, consistent with the greater bulkiness of the big cats. In both cases, however, the rule of geometric similarity is violated.

Perhaps body length might serve as the primary variable, rather than serving merely as a means for estimating body mass. In the present study, we examine the extent of geometric similarity among myomorph rodents at the species and genus levels and examine the usefulness of body length for the study of brain allometry and, ultimately, brain evolution. Rodents make up the vast majority of extant mammals and have an extensive fossil record, occasionally including both skulls and vertebrae. When these data are combined with the evidence available from associated teeth, clues to the relation between life style and brain size may be obtained.

Materials and Methods

All measurements were made on specimens in the Museum of Vertebrate Zoology at the University of California, Berkeley. The relation of body weight to cranial volume in 62 species of myomorph rodents has been described previously [Mann et al., 1988], the present study was based on a subset of those data, plus one additional species (*Rattus assimilis*). The rule for inclusion in this study was that each species sample contain at least 12 adult specimens; juveniles were excluded. This yielded a sample of 1,457 specimens (45 species from 10 cricetid genera, two murid genera, and one heteromyid genus).

Body length was calculated from the data on each museum specimen tag by subtracting tail length from total length (thus allowing any specimen with a broken tail to be included). Length measurement techniques vary among collectors, introducing a bit more noise into the data than in weight measurements. Cranial volume was measured by the shot-displacement method described previously by Mann et al. [1988], who argued that cranial volume may be taken as equivalent to brain weight, with little loss of accuracy. At most, the two values differ

by a small, constant percentage over the limited range of brain size in this study. All the tables and equations adhere to the cgs system.

Means (\bar{X}), standard deviations (SD) and errors (SE), coefficients of correlation (r) and variation (CV) and least squares regressions (slope = a) were routinely calculated. In addition, reduced major axes (slope = b) of Kermack and Haldane [1950] and the ratio of the coefficients of variation (slope = B) were calculated for each species and genus. The percent error $(100[(X_e - X_o)/X_o])$, where X_e and X_o are the expected and observed values) in estimating each variable from the overall relations was also calculated.

Results

Attention was restricted to adult specimens of all species³ in which at least 12 specimens were available for study, in order to obtain stable samples. However, the data set was not uniform; the *within species* correlations between body weight and body length for the 45 species fell into two groups, one of which (41 sp.) ranged $0.59 < r < 0.99$, $\bar{r} = 0.83 \pm 0.10$ (SD), and the other of which (4 sp.) ranged $0.19 < r < 0.44$, $\bar{r} = 0.36 \pm 0.10$ (SD). The mean standard error (SE) and mean coefficient of error (CE = $100 \text{ SE}/\bar{r}$) for the correlations were, respectively, 0.06 and 8.8% in the first group and 0.21 and 75% in the second group. The four species of the second group deviated so far from the main sample that they were excluded from the formal analysis (including them would increase the scatter and range but would not change the conclusions). Their data points were included as open squares in the relevant illustrations.

Relation of Body Length to Body Weight

For strong geometric similarity to exist among myomorph rodents, body weight must be directly proportional to the cube of body length. How well this condition was met in the present sample is shown in figure 1, where the points defined by mean body weight and mean body length for each species distribute closely along the regression slope $a=0.322$ ($B=0.331$; $b=0.330$). The correlation value of 0.988 accounts for 97.6% of the total variance, suggesting that the relation $P = kBL^3$ may hold across the myomorph rodents. However, the best-fit relation $P = 0.0242BL^{3.034}$ yielded body weights differing from the observed weights by a mean *absolute* percentage error of 11.6 across the 41 species. When partitioned by genus (table 1), much of that error was seen to be due to differences in habitus; body weights were systematically overestimated for all five species of *Microtus*, 4 of 5 species of *Peromyscus* and 9 of 11 species of *Rattus* and underestimated for 10 of 11 species of *Neotoma*. Thus, the overall relation for the myomorph rodents yields significant errors in some genera. The magnitude of errors is shown graphically in figure 2 for *Rattus*

¹ If $E \propto P^{1/3}$ and $P \propto BL^3$, then $E \propto BL$, where BL is body length.

² 95% confidence limits.

³ The term species will be used either for species or for subspecies.

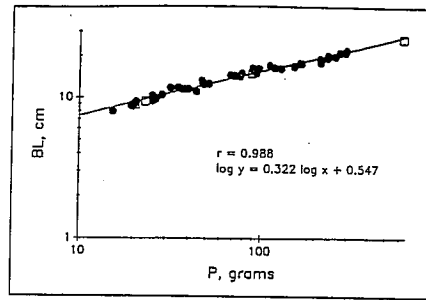


Fig. 1. Relation between mean body length and mean body weight among the 41 (dots) plus four (squares) species of myomorph rodents, showing the overall geometric similarity among these rodents.

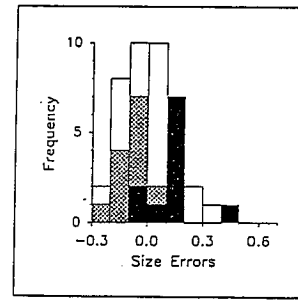


Fig. 2. Distribution of size errors for 41 species, with body weight estimated from body length ($P=0.0242BL^{3.034}$). Ordinate, number of species; abscissa, (expected-observed)/observed body weight. Black area, *Rattus*; hatched area, *Neotoma*; clear area, others.

and *Neotoma*, as well as the other 19 species, using $P=0.0242BL^{3.034}$ for the calculations. Thirty-five of the 41 estimates were within 20% of the observed weights, but only 20 of the 41 were within 10%. Thus, wood rats are bulkier (have heavier habitus) than Old World rats.

The slopes for body length on body weight *within* species (Appendix) ranged from 0.227 to 0.528, with a mean of 0.349 ± 0.009 (SE), quite close to the value of 1/3 required for the idea of geometric similarity to be tenable. These slopes formed a 'normal-appearing' distribution around the mean, as though sampling errors accounted for much of the data. Although the mean slope remained near 1/3 as the number of species was increased, the standard error progressively decreased. Thus, the slope of 0.339 from the single species, *M. calif. calif.* ($n=213$), changed to a mean slope of 0.325 ± 0.057 for the 11 species with 34 or more specimens, and then to a mean slope of 0.334 ± 0.009 for the 20 species with 27 or more specimens. It appears from this 'trend analysis' that the sample slopes reflect variations around a 'real' slope of 1/3 and that geometric similarity holds *within* species.

Table 2 records the estimates of body weight/body length relations at the genus level, using the mean weight and length values for each species in four genera. The slopes for these four genera were less than 3 (mean reciprocal slope: $\bar{b}_{BL/P}=0.375 \pm 0.010$ [SE]), and all correlations equaled or exceeded 0.95 (except the full *Rattus* sample, where inclusion of *R. norv.* decreased it to $r=0.66$). The odd-even tests showed that estimated slopes may vary widely; a large sample of species must be obtained within each genus in order to estimate slopes and intercepts more

accurately. Even so, it is evident that genus slopes are generally steeper than the species slopes within the genus, implying that geometric similarity does not necessarily hold across a genus, smaller species are lighter in habitus than larger species within many genera of rodents.

Relation of Cranial Volume to Body Size

The correlations between cranial volume and body weight varied widely among species (Appendix) but were generally higher [$\bar{r}_{E,P}=0.636 \pm 0.032$ (SE)] than those

Table 1. Percent errors ($100[X_e - X_o]/X_o$) \pm SE in estimating body weight from body length ($P = 0.0242BL^{3.034}$) and in estimating brain weight from body length ($E = 0.0054BL^{2.069}$) and from body weight ($E = 0.0709P^{0.673}$). N is number of species

Genus	N	E(BL)	E(BL)	E(P)
<i>Rattus*</i>	10	15.4 \pm 3.8	-8.1 \pm 2.5	-15.7 \pm 2.6
<i>Peromyscus</i>	5	11.6 \pm 6.0	-8.7 \pm 5.1	-14.3 \pm 4.8
<i>Clethrionomys</i>	1	9.0	24.5	17.8
<i>Microtus</i>	5	6.5 \pm 4.9	35.8 \pm 8.0	30.2 \pm 4.7
<i>Phenacomys</i>	1	3.5	40.2	38.1
<i>Signadon</i>	1	-2.5	22.8	24.6
<i>Onychomys</i>	2	-10.4	-14.3	8.9
<i>Neotoma</i>	11	-10.5 \pm 2.0	-3.4 \pm 3.1	2.7 \pm 2.5
<i>Perognathus</i>	2	-15.4	12.7	-1.1
<i>Mus</i>	1	-16.9	5.1	20.9
<i>Phyllotis</i>	1	-20.5	-16.1	-1.6
Overall	41	1.2 \pm 2.3	1.9 \pm 3.1	1.9 \pm 3.0

* *R. norvegicus* deleted from sample.

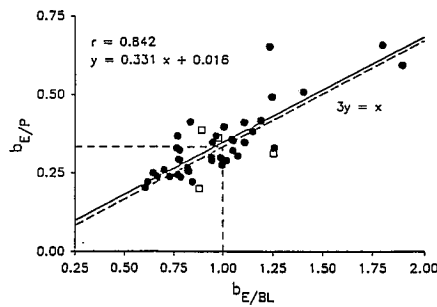


Fig. 3. Relation between E/P and E/BL slopes for 41 (dots) plus four (squares) species of myomorph rodents. Solid line, linear regression ($y = 0.331x + 0.016$); dashed line, slope defined by geometric similarity ($b_{E/P} = 1/3$).

Table 2. Best-fit power functions for body weight (P) on body length (BL) in four genera of myomorph rodents, based on mean values for each species. Species of *Rattus* and *Neotoma* partitioned into odd and even for last four analyses

Genus	N	Power function	Correlation
<i>Microtus</i>	5	$P = 0.058BL^{2.65}$	0.97
<i>Neotoma</i>	11	$P = 0.070BL^{2.71}$	0.97
<i>Peromyscus</i>	5	$P = 0.079BL^{2.50}$	0.95
<i>Rattus</i>	11	$P = 0.001BL^{4.28}$	0.65
<i>Rattus</i> *	10	$P = 0.038BL^{2.83}$	0.96
<i>Rattus</i> *-odd	5	$P = 0.011BL^{3.29}$	0.99
<i>Rattus</i> *-even	5	$P = 0.280BL^{2.09}$	0.96
<i>Neotoma</i> -odd	6	$P = 0.028BL^{3.01}$	0.99
<i>Neotoma</i> -even	5	$P = 0.268BL^{2.27}$	0.96

* *R. norvegicus* removed from sample.

Table 3. Average species slopes and their standard errors ($b \pm SE$) for body weight versus body length (P/BL), brain size versus body length (E/BL) and brain size versus body weight (E/P) for four different genera of myomorph rodents. N is number of species

Genus	N	P/BL	E/BL	E/P
<i>Microtus</i>	5	2.956 ± 0.112	0.937 ± 0.116	0.324 ± 0.052
<i>Neotoma</i>	11	2.832 ± 0.111	0.926 ± 0.044	0.330 ± 0.016
<i>Peromyscus</i>	5	2.889 ± 0.317	1.517 ± 0.138	0.546 ± 0.061
<i>Rattus</i>	11	3.069 ± 0.156	0.828 ± 0.039	0.274 ± 0.016
Overall	32	2.942 ± 0.082	0.986 ± 0.053	0.343 ± 0.021

between cranial volume and body length [$\bar{r}_{E:BL} = 0.581 \pm 0.037$ (SE)]. Paired comparisons showed the former to be higher than the latter in 33 of 41 species (80%). However, in the 11 samples having 34 or more specimens, only 6 (55%) of the former were higher [$\bar{r}_{E:P} = 0.671 \pm 0.050$ (SE) and $\bar{r}_{E:BL} = 0.684 \pm 0.054$ (SE)]. 'Trends analysis' did not reveal any convergence of the correlations toward a specific value with increasing sample size, though the correlations remained in the neighborhood of 2/3, both for body weight and for body length.

The mean slopes of cranial volume on body weight and body length shown in the Appendix were $\bar{b}_{E/P} = 0.337 \pm 0.016$ (SE), $r = 0.636$, and $\bar{b}_{E/BL} = 0.968 \pm 0.042$ (SE), $r = 0.581$. As shown in figure 3, the pairs of slopes scattered loosely around the linear regression of slope $a = 0.331$, the correlation of $r = 0.842$ accounting for only 71% of the variance. Though the line does not differ from $3b_{E/P} = b_{E/BL}$, variation around the line was quite large. Rather than clustering around (1, 1/3), the samples scattered widely around the line defining geometric similarity. This same result is evident in table 3, where the mean species slopes for *Microtus* and *Neotoma* are near 1/3 and 1, but those for *Peromyscus* are well above, and those for *Rattus* below, these values. Even so, all slopes for body length on body weight were close to 1/3, as required for geometric similarity to hold within species (which is a necessary, but not sufficient, condition).

The correlations of mean cranial volume with mean body length (0.957) and with mean body weight (0.956) were the same in log-log space, but they differed a bit in linear space (0.961 and 0.932, respectively). Because weight errors are distributed in three dimensions, whereas length errors are confined to one dimension, the correlation of cranial volume with the cube root of body weight in linear coordinates ought to be higher: it was 0.968, compared to the 0.961 value for cranial volume:body length. Thus, it is possible to translate from the cube of body length to body weight with little loss of accuracy among the myomorph rodents.

Body length is relatively insensitive to habitus, and hence should yield a valid and reliable estimate of cranial volume (unless the latter also varies with habitus). Figure 4A and B reveals how much the estimated brain weights differed from the observed brain weights when $E = 0.0054BL^{2.069}$ and $E = 0.0709P^{0.673}$ were used for the calculations. The error distributions for *Rattus* and *Neotoma* almost superimposed when body length was used, but they diverged when body weight was used, reflecting the heavier habitus of wood rats. It is evident from table 1 that brain sizes for *Microtus* (and also *Phenacomys*, *Sigmodon* and

Clethrionomys, with one species each) were greatly overestimated by both power functions. On the other hand, body length predicted mean brain size for *Rattus* and *Peromyscus* with greater accuracy than did body weight.

Overall Comparisons

Figure 5 shows the distribution of mean cranial volumes as a function of mean body length for the 41 (plus 4) species of this study expressed as a minimum convex polygons (fig. 5A) and as genus polygons (fig. 5B). These are comparable to figures 1 and 2 of Mann et al. [1988], though they do not include as many species, and some means are based on smaller samples. The best-fit regression line of $E=0.0054BL^{2.069}$ for these rodents suggests that mean brain size varies as the square of mean body length and, therefore, as the $2/3$ power of body weight (the exponent value implied by the relations $P \propto BL^{3.034}$ and $E \propto BL^{2.069}$ is 0.682). Each genus occupies the same relative position on the cranial volume/body length graph in figure 5B that it does on the cranial volume/body weight graph in figure 2 of Mann et al. [1988], and the same relative slope relations are present, both at the species and genus levels. Given geometric similarity in interbreeding populations, it may be concluded that *within* species, $E \propto P^{1/3}$ and $E \propto BL$, whereas *across* all species, $E \propto P^{2/3}$ and $E \propto BL^2$.

Discussion

Clearly, body length can be used interchangeably with body weight in allometric studies. The relation $P=0.0242BL^{3.034}$, nearly identical to that found by Jerison [1971] and Radinsky [1978] for carnivores and ungulates, provides a fairly accurate translation from body length to body weight in myomorph rodents. The approximate form $P=BL^3/41$ serves well. However, its accuracy depends on sample size and on range; both habitus and genus slope compromise the translation. In order to study fossil material, it may be necessary to assume that both the habitus and genus slopes associated with extant rodent lines are the same as in past forms (unless a good estimate of habitus can be made from the fossil material). If body length serves as the primary variable in brain allometry, then habitus need be of little concern; only the genus slope is relevant.

Whether or not there exists a single brain weight/body weight slope among demes is clearly an issue that remains to be resolved. Pagel and Harvey [1988] argue that a slope of $3/4$ applies at all taxonomic levels, the lower slopes seen in lower taxons largely being due to the error structure between the two variables. However, the 'trend analyses'

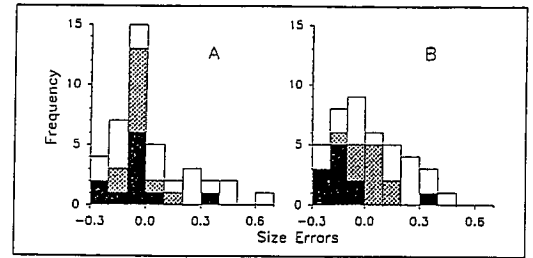


Fig. 4. Distribution of size errors for 41 species, with cranial capacity estimated from (A) body length ($E=0.0054BL^{2.069}$) and (B) body weight ($E=0.0709P^{0.673}$). Details as in figure 2.

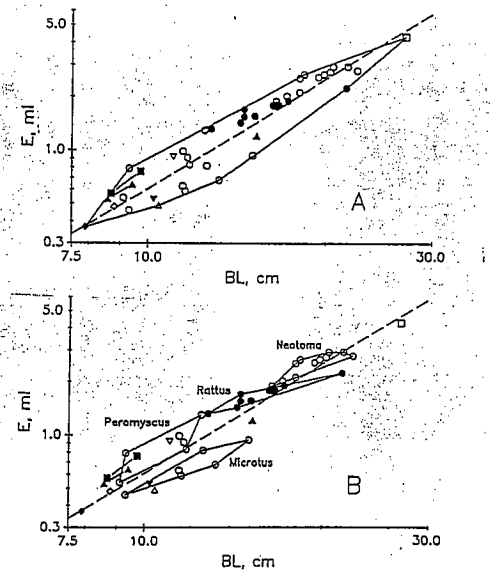


Fig. 5. Minimum convex polygons for overall sample (A) and by genus (B). Each genus marked by different symbol.

in the present study point to the existence of different slopes at different taxonomic levels. Most species slopes are between $1/5$ and $2/5$, but the data of Mann et al. [1988] suggest that a slope near $1/3$ may exist within all interbreeding populations, the deviations from that value being due to sampling variations. Their data for 62 species of myomorph rodents scatter in the neighborhood of $1/3$ and converge

toward that value as sample size is increased: the weighted mean slope was 0.341. The data of Latimer [1942] on 162 male and 159 female domestic dogs yielded brain weight/body weight slopes of 0.318 and 0.317, respectively. Lande [1979] put the species slope at 0.36, the slope also calculated for random genetic drift in *Mus domesticus*. The results of the present study are consistent with the statement that $E \propto P^{1/3}$ and $E \propto BL$, within species.

It has long been argued that animals must become progressively more stocky with increasing body size in order to support their greater mass, and the slope $b_{P/BL} = 3.45$ found for ungulates [Radinsky, 1978] is consistent with that argument. Although geometric similarity may not hold within all species (for example, the data of Herre and Thiede [1965] yield $b_{P/BL} = 2.04$ for guanacos and $b_{P/BL} = 3.40$ for vicuñas), it held for the rodents in the present study. However, it did not hold across species. The slopes for the four genera containing at least 5 species were quite varied, though their mean slope was $\bar{b}_{P/BL} = 3.03 \pm 0.37$ (SE). By removing *R. norv.* from the sample, the slope for *Rattus* became 2.83 (table 2), and the mean slope for the four genera became 2.67 ± 0.06 (SE), quite close to the slope found by Radinsky [1978] for carnivores ($b_{P/BL} = 2.73$), and consistent with the idea that larger species of *Rattus* have relatively longer bodies than smaller species. Mass does not appear to impose any strong structural limitations on such small animals.

It may be argued that body length is an ideal variable for allometric analysis, not only because it simplifies paleoallometry, but also because the skeleton is less susceptible than body weight to the vagaries of diet and health of the animal [Rosenzweig, 1968]. The present study shows that body weight and length are effectively interchangeable within

species. It also shows that the probable error associated with a particular specimen, whether fossil or recent, depends on the taxonomic level of the reference sample. The relationships for myomorph rodents differ between genus and species: overall, $b_{E/BL} = 2.07$, whereas the species slopes ranged from 0.60 to 1.89 [$\bar{b}_{E/BL} = 0.97 \pm 0.04$ (SE), and the mean genus slope was $\bar{b}_{E/BL} = 1.57 \pm 0.18$ (SE)]. These slopes have the same relative relation as the overall slope (0.693), mean genus slope (0.456) and mean species slope (0.338) reported by Mann et al. [1988], that is, in the ratio of 6:4:3.

Murids diverged from cricetids in mid-Miocene times, so the finding by Mann et al. [1988] that Old World rats of the same body size as wood rats have much smaller brains was unexpected. But that result disappeared when body length served as the allometric reference. In fact, as the data in figure 5 suggest, *Microtus* may be the 'odd' group. Exclusion of *Microtus* would decrease the overall slope and decrease the dispersion around that slope. Confining attention to *Rattus*, *Neotoma* and *Peromyscus* (deleting *R. norvegicus*) yields the overall power function $E = 0.0096BL^{1.885}$, with $r = 0.99$ (accounting for 98% of the variance). Calculations based on that relation yield mean errors of -0.013 ± 0.022 , -0.004 ± 0.029 and 0.042 ± 0.063 (SE) for the three genera, respectively. Equally-close approximations to observed cranial capacities are obtained for all other genera (e.g., mean errors of 0.026 for *Onychomys* and 0.035 for *Perognathus*). In this view, the voles (*Microtus*) have relatively small brains and must be treated separately. It is apparent that body length or some strong correlate thereof (e.g., vertebral lengths) may serve as the primary variable in allometric study, especially with fossil material.

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Appendix

Subspecies	P	BL	E	CV _P †	CV _{BL} †	CV _E †	b _{BL/P} †	r _{BL/P} †	b _{E/BL} †	r _{E/BL} †	b _{E/P} †	r _{E/P} †	n
<i>Arborimus longicaudus</i> **	20.4	8.8	0.48	26.0	6.6	8.2	0.249	0.462	1.254	0.645	0.512	0.593	14
<i>Clethrionomys gapperi arizonensis</i>	25.5	10.2	0.53	21.3	11.9	3.8	0.556	0.929	0.617	0.454	0.220	0.542	17
<i>Microtus c. californicus</i>	47.1	13.1	0.68	19.7	8.9	7.4	0.339	0.706	1.126	0.370	0.382	0.462	213
<i>M. longicaudus alticola</i>	37.7	11.4	0.63	27.1	8.8	6.9	0.318	0.939	0.768	0.507	0.244	0.540	30
<i>M. montanus yosemite</i>	39.5	11.5	0.59	25.9	8.3	5.1	0.334	0.936	0.604	0.433	0.202	0.539	15
<i>M. o. oregoni</i>	20.6	9.3	0.46	20.4	7.9	10.9	0.394	0.806	1.246	0.048	0.491	0.064	32
<i>M. t. townsendii</i>	51.5	12.5	0.82	32.6	10.4	11.0	0.317	0.815	0.943	0.660	0.299	0.779	18
<i>M. xanthognathus*</i>	89.1	14.9	0.94	26.7	8.9	5.3	0.227	0.385	0.880	0.116	0.200	0.547	22
<i>Ondatra zibethica bernardi*</i>	629.3	26.9	4.31	12.9	4.5	4.4	0.369	-0.208	0.980	0.079	0.362	0.605	15
<i>Phenacomys i. intermedius</i>	28.5	10.4	0.49	27.0	9.8	12.2	0.349	0.891	1.192	0.263	0.416	0.488	17
<i>Neotoma a. albigula</i>	164.5	17.9	2.54	19.1	6.7	7.1	0.341	0.905	1.044	0.770	0.356	0.792	34
<i>N. cinerea acraia</i>	213.8	19.3	2.57	22.2	8.6	8.9	0.394	0.847	1.005	0.827	0.396	0.852	16
<i>N. c. occidentalis</i>	296.1	21.6	2.95	34.9	10.9	10.8	0.301	0.963	0.990	0.834	0.298	0.849	16
<i>N. fuscipes bullator</i>	300.9	22.4	2.80	23.0	7.4	8.2	0.312	0.921	1.110	0.788	0.347	0.865	17
<i>N. f. fuscipes</i>	236.4	20.4	2.94	29.7	11.1	7.9	0.386	0.721	0.667	0.613	0.257	0.861	19
<i>N. f. luciana</i>	234.9	19.7	2.67	23.0	8.4	8.2	0.365	0.815	0.949	0.529	0.347	0.728	43
<i>N. l. lepida</i>	128.3	16.3	1.89	36.2	11.8	11.1	0.306	0.824	0.945	0.758	0.290	0.778	34
<i>N. micropus canescens</i>	215.5	18.2	2.67	31.9	12.0	9.4	0.372	0.944	0.779	0.651	0.290	0.794	14
<i>N. m. micropus</i>	260.1	20.2	2.75	14.8	5.2	5.8	0.370	0.765	1.108	0.536	0.410	0.692	22
<i>N. s. stephansi</i>	152.7	17.0	2.02	21.5	10.0	8.4	0.477	0.910	0.768	0.635	0.567	0.638	19
<i>N. (Teanopus) phenax</i>	168.2	17.9	2.12	18.4	6.1	5.7	0.326	0.778	0.819	0.605	0.267	0.463	23
<i>Onychomys leucogaster brevicaudus</i>	26.4	9.7	0.76	20.1	5.9	6.6	0.311	0.638	1.032	0.463	0.321	0.404	86
<i>O. torridus pulcher</i>	19.4	8.7	0.51	20.1	6.7	5.3	0.328	0.642	0.728	0.929	0.238	0.509	60
<i>Peromyscus californicus insignis</i>	31.6	11.6	0.91	9.8	5.3	6.6	0.528	0.779	1.234	0.137	0.651	0.200	16
<i>P. g. guatemalensis</i>	48.2	12.4	1.30	29.0	7.5	9.2	0.261	0.805	1.257	0.659	0.329	0.473	22
<i>P. lepturus</i>	34.9	11.7	0.83	22.1	8.0	13.3	0.365	0.689	1.798	0.226	0.655	0.274	12
<i>P. maniculatus sonoriensis</i>	20.3	9.1	0.54	13.8	4.2	7.4	0.312	0.652	1.894	0.435	0.590	0.545	30
<i>P. m. mexicanus</i>	36.8	11.4	0.99	14.7	5.2	7.1	0.361	0.695	1.404	0.157	0.506	0.592	20
<i>P. t. truei*</i>	23.2	9.3	0.79	15.5	6.8	6.3	0.434	0.351	0.892	0.046	0.387	0.096	30
<i>Phyllotis darwini chilensis</i>	43.9	11.0	0.92	25.9	9.9	9.8	0.380	0.790	0.966	0.754	0.367	0.839	27
<i>Sigmodon hispidus berlandieri</i>	93.7	15.1	1.21	30.0	9.1	9.1	0.414	0.866	0.778	0.840	0.322	0.828	28
<i>Mus domesticus</i>	15.4	7.9	0.37	28.6	9.0	10.8	0.335	0.766	1.052	0.697	0.353	0.647	55
<i>Rattus a. assimilis</i>	111.4	17.1	1.90	31.6	10.4	8.9	0.314	0.899	0.820	0.651	0.257	0.737	84
<i>R. colletti</i>	76.3	14.2	1.43	66.7	16.9	14.0	0.261	0.933	0.845	0.878	0.221	0.923	30
<i>R. conatus</i>	67.7	14.4	1.55	46.9	14.7	11.9	0.309	0.980	0.827	0.864	0.255	0.861	60
<i>R. fuscipes</i>	89.5	16.3	1.81	16.8	5.0	5.0	0.285	0.800	1.017	0.247	0.289	0.317	29
<i>R. leucopus</i>	96.7	16.2	1.78	34.6	12.7	10.7	0.323	0.955	0.821	0.868	0.265	0.893	38
<i>R. lutreolus</i>	95.9	16.1	1.79	35.4	10.5	8.4	0.302	0.912	0.783	0.625	0.236	0.568	37
<i>R. niobe stephansi</i>	47.4	12.7	1.32	23.0	7.5	8.3	0.282	0.586	1.076	0.373	0.304	0.651	15
<i>R. norvegicus</i>	275.7	21.5	2.24	45.8	18.3	11.6	0.387	0.940	0.644	0.784	0.249	0.856	18
<i>R. r. rattus</i>	118.6	16.5	1.79	22.2	9.4	7.8	0.494	0.864	0.835	0.686	0.412	0.818	20
<i>R. ruber</i>	70.9	14.4	1.70	36.7	15.2	11.8	0.380	0.871	0.772	0.674	0.293	0.810	29
<i>R. tunneyi</i>	78.0	15.0	1.56	45.8	15.5	10.9	0.356	0.988	0.665	0.750	0.237	0.764	28
<i>Perognathus c. californicus</i>	25.4	9.4	0.64	17.7	5.1	4.9	0.276	0.771	0.996	0.471	0.275	0.588	13
<i>P. fallax pallidus</i>	19.8	8.6	0.53	16.1	7.1	5.3	0.432	0.717	0.763	0.086	0.329	0.240	20
Mean				26.9	9.3	8.6	0.349	0.833	0.968	0.581	0.337	0.636	
Standard deviation				10.9	3.4	2.5	0.059	0.104	0.279	0.245	0.110	0.215	

‡ Classified as *Phenacomys longicaudus* in Mann et al. [1988].

* Species not included in formal analyses.

† Subscript indicates variable or variables for that parameter.