Brain Behav. Evol. *31*: 111–124 (1988)

0006–8977/88/0312–0111 $ 2.75/0

Brain/Body Relations among Myomorph Rodents

M.D. Mann[a], *S.E. Glickman*[b], *A.L. Towe*[c]

[a] Department of Physiology and Biophysics, University of Nebraska Medical Center, Omaha, Nebr., USA;
[b] Professor of Psychology, University of California, Berkeley, Calif., USA;
[c] Professor of Physiology and Biophysics, University of Washington School of Medicine, Seattle, Wash., USA

Key Words. Brain/body relations · Cranial volume · Cricetids · Murids · Allometry

Abstract. The observed increase in brain size (E) with body size (P) 'from mouse to elephant' may be described by a power relation $E = kP^b$, where b is near ⅔ or ¾. That this reflects a single, strong interaction between brain and body evolution is challenged by two observations: (1) different species with the same body size may have markedly different brain sizes, and (2) the value of b at the species level is usually nearer ⅓ than ⅔. Furthermore, the idea that a bigger brain means greater versatility on the part of its owner makes a strong statement about such animals. We examined these notions by measuring cranial volumes of 1,480 skulls from 62 subspecies of cricetid and murid rodents. Values of k and b were obtained by computing a reduced major axis on E and P across all specimens ($b = 0.693$), and when specimens were partitioned by genus ($\bar{b} = 0.456$) and subspecies level ($\bar{b} = 0.338$). Thus, the overall slope of 7/10 is not a simple extension of the developmental rules at the subspecies level (b near ⅓) nor even at the genus level (b near 4/9). Rather, it may reflect the most likely path for an interbreeding population subjected to varying selective pressures on one or more correlated traits. Furthermore, among the rodents studied, folivorous subspecies averaged about ⅔ as much brain as granivorous, insectivorous or generalist subspecies of the same body weight. Also, Old World rats, which may be more versatile than wood rats, gained their competitive advantage despite having relatively smaller brains.

Introduction

Small animals have small brains and large animals have large brains, but it is not clear why this is so. The overall brain/body relation is usually described by a power function in which brain mass (E) is directly proportional (through scaling constant k) to body mass (P) raised to some power (b). Briefly stated, $E = kP^b$. This relationship appears to be descriptive, to a first approximation, across the various families of mammals, and, with different scaling constants, across birds, reptiles and fishes [Jerison, 1973]. The existence of a relatively orderly overall trend of increasing brain size 'from mouse to elephant' reinforces the idea that one basic interaction underlies the brain/body relation.

Various studies place the value of b at ⅔ [Rensch, 1960; Jerison, 1973; Gould, 1975] or at ¾ [Martin, 1981; Armstrong, 1983]. Arguments to 'explain' these values in terms of the surface-to-volume relation for $b = ⅔$ [Jerison, 1973] or of a tenuous metabolic connection for $b = ¾$ [Martin, 1981] are not compelling and fail to explain how the different species that have the same body mass can have significantly different brain masses. The existence of such 'vertical allometries' [Calder, 1984] is an important challenge to the idea that there exists one basic interaction between brain and body size, expressed through the slope of the overall allometric relation.

Brain/body relations at the genus level have been described by power functions with significantly smaller values for b, usually near ⅓ [Gould, 1966,

1971; Lande, 1979]. If one basic interaction underlies mammalian brain/body relations, then either vertical allometry is noise, or the relations in lower taxonomic categories – called 'second-order strategies' [Western, 1979], to distinguish them from the fundamental interaction – reflect local allometries with *negative* exponents [Huxley and Teissier, 1936; we have adopted this terminology so as not to confound the term 'negative allometry' as used by Gould, 1966]. Neither alternative seems likely. The present study was undertaken to obtain detailed information about local brain/body relations, from subspecies through families, and to determine whether the overall mammalian relation might be understood in terms of those local relations. As Calder [pers. commun.] puts it: 'Physical laws are taxonomically blind, so size effects must extend within species and beyond.'

The myomorph rodents [Wood, 1955] are favorable objects for study in that they are small and form a closely related assemblage, many members of which retain a generalized rodent structure. They appeared in early Oligocene, when the major patterns of jaw musculature that are used to distinguish modern rodents were evolving [Wood, 1955, 1965]. The paramyid rodents were well established by late Paleocene, but the major radiation apparently had to await the extinction of the rodent-like multituberculate and tillodont mammals [Kurten, 1971]. Among the myomorph rodents, the cricetids, heteromyids and zapodids evolved rapidly during the Oligocene, the cricetid line radiating broadly into myriad different life styles. The murids appear to have arisen from cricetid stock in the tropical forests of southeast Asia in the late Miocene [Petter, 1966; Lavocat, 1967], and soon became the dominant form, gradually spreading from that region. Now, the cricetids and murids form a largely complementary world distribution [Kingdon, 1974] and account for nearly two thirds of living forms of rodents. The murids are said to be more active, more versatile and speedier than comparable cricetids, giving them a competitive advantage and suggesting that they may have quickly evolved larger brains – that some selective pressure lifted them above the main rodent scaling function. If so, then after being displaced above that scaling function, further diversification, taking advantage of the 'new neural equipment', should have carried them along a path determined by the basic interaction that is proposed to affect all animals.

Methods

Cricetids of the subfamilies Cricetinae and Microtinae were compared with murids of the genus *Rattus*; a few other genera were also examined. Measurements were made on 1,480 specimens, including 41 juveniles, from 62 subspecies in 12 genera of 3 families (Appendix I). They spanned body weights from 15 to 650 g, and included granivores, herbivores, omnivores and insectivores. All measurements were carried out on specimens in the collection at the University of California Museum of Vertebrate Zoology at Berkeley, made available through the kind auspices of Professor William Lidicker (all original measurements for this study are on file at the MVZ, UC, Berkeley). The specimens had been gathered and prepared by various collectors over the past half century. Each specimen had been weighted, measured, and sexed at the time of collection, each had been carefully classified at the museum, and each had an intact skull available for volumetric measurement. The date and locale of collection had also been recorded, and in many cases the number and length of embryos, or their absence, had been noted.

Cranial volume, which will be loosely termed brain size or brain weight in this paper, was measured using 8- and 9-gauge shot. The skull was held nose down while shot was poured through the foramen magnum. The skull was repeatedly tapped to ensure compaction of the shot, until the cranium was filled. The shot was then poured into an EXAX No. 20025 10-ml graduated cylinder, scaled in 0.1-ml units, or when the cranial volume was about 1.0 ml or less, into a shot-counter tray that aligned the shot and that was calibrated in 0.01-ml units for 9-gauge shot. Shot size was selected such that it would not enter any of the foramina of the skull. For about the first 200 measurements, two observers independently estimated the level of the shot in the graduated cylinder to the nearest 0.01 ml, and the average was recorded. About half the time, the estimates agreed exactly, and they rarely differed by more the 0.02 ml (in which cases the skull was remeasured). Repeated independent measurements, accomplished by refilling the cranium, yielded the same results. A year later, one of us (ALT) remeasured a series of specimens selected by another of us (MDM) and encoded by museum specimen number. The results differed from the earlier measurements by less than 0.01 ml in average absolute magnitude. Because of this repeatability, it was decided that the measurements made by a single observer were sufficiently accurate. Similar checks with the shot counter yielded even greater repeatability, and paired measurements with the graduated cylinder and the shot counter in the neighborhood of 1.0 ml showed the two methods to yield a continuous volume scale. An additional check, made with very small skulls using 20-gauge shot in a modified tuberculin syringe, yielded numbers that differed from the above measures by less than 0.01 ml in average absolute magnitude.

Cranial volume was estimated from dried skulls, and was taken as equivalent to 'brain size', which is directly proportional to brain weight. Because the density of the brain is close to one and the brain completely fills the cranium [during most of the year, Yaskin, 1984; Dark et al., 1987], the cranial volume values in this study may be taken as equivalent to brain weight. At worst, they differ by a small percentage that is constant over the range of brain sizes under study, so that the trends that emerged from the analysis were not affected by this factor.

The presence or absence of embryos was noted by the collectors for many specimens; when present, their number and length were

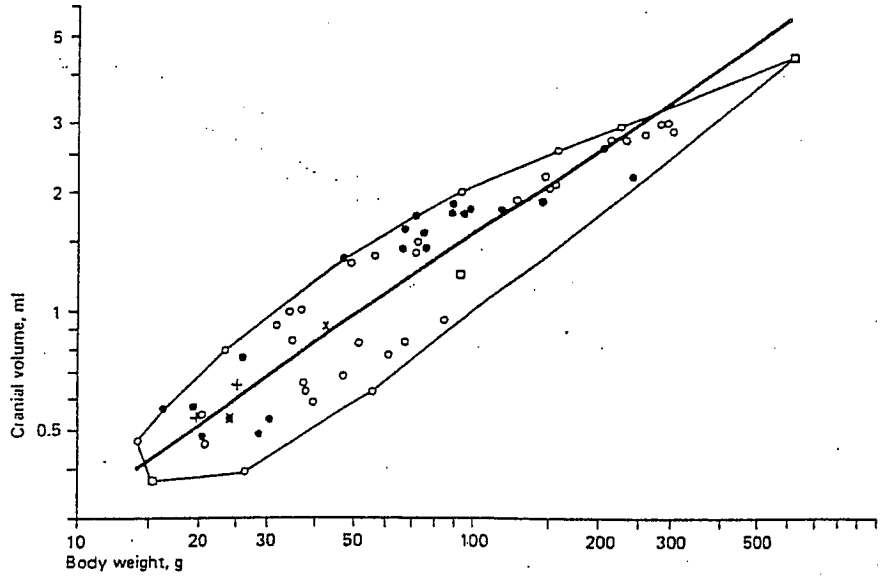

Fig. 1. Log-log plot of mean body weight versus mean cranial volume for each subspecies studied. The reduced major axis of the distribution (b = 0.693) is plotted as a heavy line. A minimum convex polygon is fitted to the entire set of data.

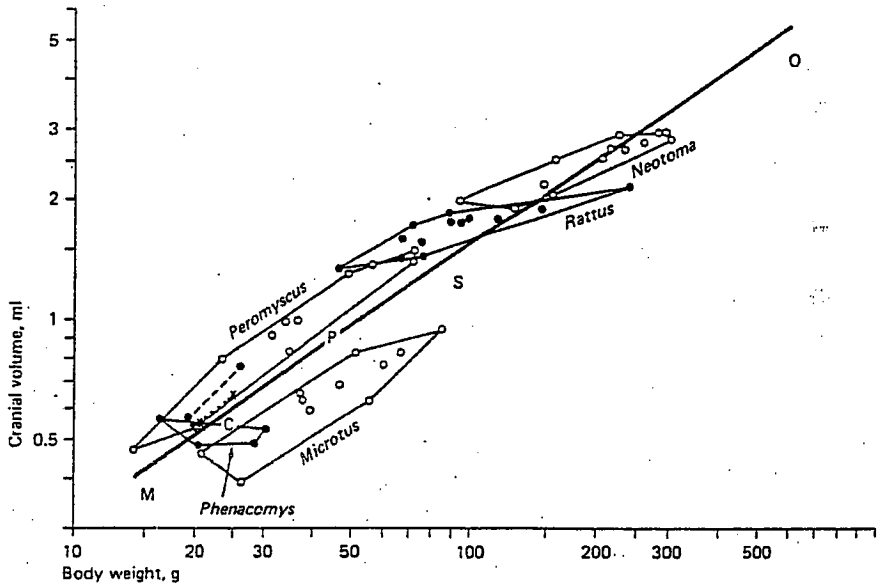

Fig. 2. Log-log plot of mean body weight versus mean cranial volume for each subspecies studied. The reduced major axis is plotted as in figure 1. Minimum convex polygons enclose genera with 4 or more subspecies represented. ●---● = Values for *Onychomys;* +···+ = Values for *Perognathus*. The single letters, O, S, M, C, and P, represent values for the single species in the genera *Ondatra, Sigmodon, Mus, Clethrionomys*, and *Phyllotis*, respectively.

often recorded. In some instances, the size of the testes had been recorded. Both female and male body weights were thus affected, but to a negligible extent. Excluding zeros, the average number of embryos was 4.9 (standard deviation, SD = 2.6; maximum = 13). Thus, the distribution was highly skewed (but specimens with only one embryo were rare), and correction for embryo weight had a negligible effect on brain/body weight ratios (a small change in the big number of each E,P pair). Therefore, the recorded weights were used, uncorrected for embryo or testis weight.

Two general forms of analysis were used: the method of minimum convex polygons [Jerison, 1973] and the reduced major axis [Kermack and Haldane, 1950; Clarke, 1980; Harvey and Mace, 1982]. Because both brain size and body size were subject to errors of measurement, and their correlation exceeded 0.95 in only one case, the standard regression analysis could be somewhat, and in some cases seriously, misleading. Clarke [1980] presented a method for comparing reduced major axes, using a test statistic derived from the logarithm of the reduced major axis (log b, from Appendices I and II), the number of skulls measured and the correlation coefficient for P and E. This statistic can be compared with the Student t distribution. In this study, variability of either body weight or cranial volume is often expressed as the coefficient of variation, calculated as:

Coefficients of variation (CV) = 100% × SD/mean.

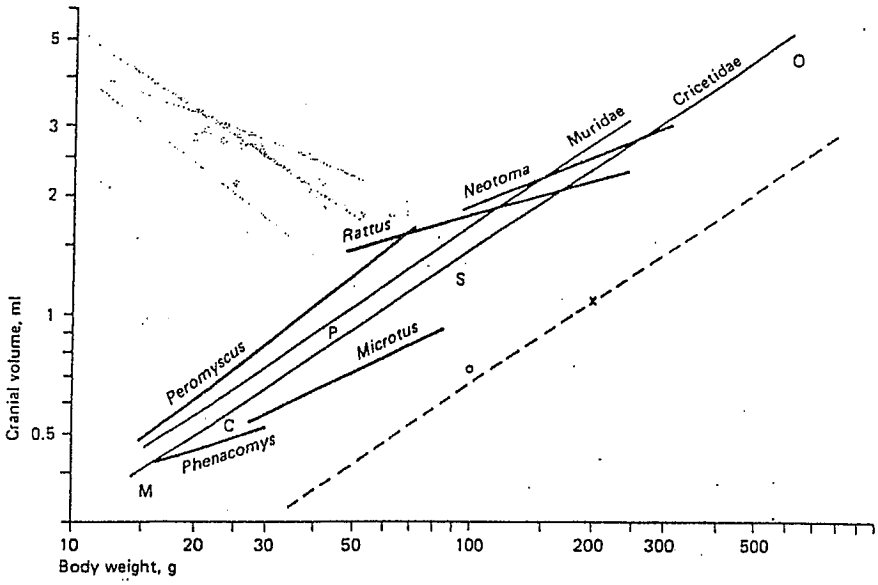

Fig. 3. Log-log plot of mean body weight versus mean cranial volume for various genera in the families Muridae and Cricetidae. The reduced major axes for the two families are plotted as thin lines, the lengths of the two lines spanning the range of body weight values. The reduced major axes for genera with more than 4 subspecies are drawn. Values for *Ondatra*, *Mus*, *Sigmodon*, *Phyllotis* and *Clethrionomys* are indicated as in figure 2. The dashed line is plotted with a ⅔ slope through the value for *P. montanus* (×); the value for *T. mordax* (O) lies nearby.

Results

Mean values of body weight and cranial volume for each of the 62 subspecies are shown in figure 1, using the standard log-log plot to reduce the apparent variance and reveal any overall trend. Even so, the mean values scatter rather widely. The outer data points are connected to form a minimum convex polygon, after the manner of Jerison [1973]; the overall trend is clearly evident. The reduced major axis for this data set, shown as a heavy line in figure 1, has a slope of 0.693, between the controversial ⅔ and ¾ slopes. Thus, over less than 2 log units of body weight, the 'standard' mammalian allometric relation is evident. This result seems to reinforce the idea that there is but one basic interaction underlying the standard relation, but the vertical variation, amounting to 0.4 log unit, should not be overlooked.

Genus slopes. The same data are plotted in figure 2, but the minimum convex polygons now enclose each of the 5 genera for which 4 or more subspecies were measured. A different picture emerges in that more 'area' is enclosed above than below the reduced major axis, and there are 5 species or subspecies above for every 4 below that axis. It is evident that the brain of a vole *(Microtus)* is half as large as that of a deer mouse *(Peromyscus)* of comparable body size, and it is the presence of the voles that raises the axis to a slope of 0.693. On the other hand, voles seem 'bulkier' than deer mice. Were this taken into account, the difference might diminish, and the overall slope would decrease. The issue of habitus was not addressed in this study.

A more important issue arises in figure 2: the minimum convex polygons do not lie exactly parallel to the overall 0.693 slope. The reduced major axes associated with the 5 genera shown in figure 3 ranged from 0.287 *(Rattus)* to 0.792 *(Peromyscus)*, with a weighted average of 0.456. This was significantly lower than the 0.693 slope obtained by treating the 1,133 specimens as a single group rather than as five different groups. Each of the genus slopes shown in figure 3 and in Appendix I is well placed, but only *Peromyscus* comes close to the overall slope for mammals in general. The body weight ranges in 4 of the genera spanned a 5- to 20-fold interval, and removal of extremes had little effect on the computed slopes. The average genus slope, after removal of juveniles (Appendix II), was 0.462, only slightly higher than with juveniles. It appears that each genus may have its own unique brain/body scaling relation.

Species slopes. The slope of the scaling relation decreased even more when computed for individual subspecies. Some of the brain/body (E:P) plots formed strongly elliptical distributions, whereas others were more compact and rounded. In order to fix a slope for the latter more accurately, a large sample was required; in the case of *Microtus californicus*

Table I. Estimated Student t values for comparisons of reduced major axes (genera with 2 or more species)

	Phenacomys	*Onychomys*	*Peromyscus*	*Neotoma*	*Rattus*	*Perognathus*
Microtus	2.2391[a] (32)	4.3007[c] (159)	9.7409[c] (157)	1.9600[a] (314)	10.5412[c] (336)	0.8239[d] (32)
Phenacomys		3.8629[c] (35)	5.5990[c] (33)	1.6721[d] (32)	0.6455[d] (32)	2.3140[a] (35)
Onychomys			3.5843[c] (146)	5.6257[c] (157)	11.4132[c] (152)	1.2984[d] (37)
Peromyscus				11.2492[c] (154)	18.2887[c] (147)	3.3446[b] (34)
Neotoma					8.3822[c] (293)	1.5166[d] (32)
Rattus						4.3863[c] (31)

Degrees of freedom presented in parentheses. [a] $p < 0.05$; [b] $p < 0.01$; [c] $p < 0.001$; [d] not significant.

californicus, 214 specimens were measured. The computed slope of 0.389 was higher than for most subspecies, and much higher than for conspecifics *Microtus californicus sanctidiegi* (0.236) and *Microtus californicus scirpensis* (0.216). However, the latter two samples were small, and removal of the two juveniles of *M. c. scirpensis* increased the slope to 0.436 and decreased the E:P correlation from 0.94 (Appendix I) to 0.65 (Appendix II), reflecting the decreased range. The average slope for 10 subspecies of *Microtus* was 0.316, significantly lower than the overall slope of 0.459 associated with that genus (*Microtus ochrogaster minor* was omitted because of the small sample size). The E:P relationship for the two species of grasshopper mice *(Onychomys)* yielded slopes of 0.356 (n = 90) and 0.234 (n = 62). Again, these values were lower than the overall genus slope of 0.581 (or the steeper genus slope of 0.602 obtained after removal of 3 juveniles). Using the 45 subspecies in which 10 or more specimens were measured yielded a mean slope of 0.338 (SD = 0.106). Expanding to the 53 subspecies having four or more specimens available for study yielded a mean slope of 0.340 (SD = 0.114). Evidently, the average E:P scaling relation at the subspecies level approximates a ⅓ power function, but there is considerable variation among the different subspecies. After removing juveniles, the range of subspecies slopes, from 0.146 for *Neotoma mexicana* to 0.655 for *Peromyscus lepturus*, was as broad as that for the genus slopes, though the specific values were lower.

Family slopes. As the sample was extended to larger assemblages, the slopes converged toward the overall value of 0.693. The slopes for murids (0.697) and cricetids (0.675) are shown in figure 3. Clearly, the overall mammalian relation has been attained at the family level, and it appears that murids have somewhat larger brains than cricetids. However, the separate genus slopes in figure 3 tell a different story: wood rats have larger brains than Old World rats of the same body size. If the concept of 'encephalization' [Jerison, 1973] is raised, *Rattus niobe stevensii*, the smallest of the Old World rats in this study, comes out on top, closely followed by several of the larger deer mice. But these statements are based on the slopes for the family to which each genus belongs. A possibly more 'basic' reference is shown as the dashed line of slope ⅔ in figure 3. It passes through the point marked × for the Paleocene multituberculate, *Ptilodus montanus*, and near the point marked o for the Mesozoic triconodont, *Triconodon mordax*, both estimated by Jerison [1973] from data provided by Simpson. From this vantage point, the rodents have 2–3 times more brain than these earlier mammalian forms, and the differences in encephalizatoin between the deer mice, Old World rats and wood rats pale into insignificance. The primary question concerns how the rodent brains became so large.

Differences in slope. The reduced major axes for genera range widely, from 0.220 *(Clethrionomys)* to 0.793 *(Peromyscus)*. Table I presents the estimated Student t values and the associated degrees of freedom for comparisons of genera with 2 or more species represented. The slope for *Peromyscus* is significantly different from that of every other genus in the table. In a rank order listing of genera, the reduced major axis for each genus is significantly different from that for all other genera that are more than one rank away, with the exception that *Perognathus* and *Neotoma* are not significantly different. On the other hand, genera that are contiguous in ranking are not significantly

Table II. Reduced major axes for genera

Genus	n[a]	n_m	n_f	b_m	b_f	b
Clethrionomys	17	5	12	0.200	0.197	0.220
Microtus[b]	354	190	164	0.461	0.452	0.458
Ondatra	15	8	7	0.511	0.226	0.362
Phenacomys	32	17	15	0.298	0.403	0.322
Neotoma	272	124	148	0.439	0.470	0.448
Onychomys	149	85	64	0.695	0.532	0.608
Peromyscus	136	85	51	0.786	0.806	0.793
Phyllotis	27	16	11	0.286	0.479	0.367
Sigmodon	28	18	10	0.354	0.290	0.322
Mus	55	32	23	0.392	0.263	0.353
Rattus	310	149	161	0.272	0.318	0.291
Perognathus	33	23	10	0.525	0.579	0.508
All	1,428	754	674	0.667	0.721	0.692

[a] n = Number of specimens excluding juveniles; subscripted values are for males and females alone, unsubscripted for both together.
[b] Two animals in Appendices I and II were not sexed.

Table III. Variance in brain and body at species and genus level

Genus	CV_e[a]	CV_p[a]	$\bar{b}^b_{species}$	b^b_{genus}
Clethrionomys	5.7	24.8	–	–
Microtus	7.8	26.0	0.32	0.46
Ondatra	4.4	12.3	–	–
Phenacomys	10.2	26.5	0.36	0.32
Neotoma	8.8	27.5	0.31	0.42
Onychomys	6.6	21.0	0.30	0.61
Peromyscus	8.5	16.8	0.49	0.79
Phyllotis	11.0	28.0	–	–
Sigmodon	9.1	30.3	–	–
Mus	10.8	28.6	–	–
Rattus	11.2	36.7	0.32	0.29
Perognathus	5.2	17.3	0.31	0.51
All[d]	8.9	27.0		

[a] CV for cranial volume (e) and body weight (p), expressed as percents.
[b] Average reduced major axis for species within a genus.
[c] Reduced major axis for genus.
[d] Means weighted by number of species per genus.

different, except for *Peromyscus* and *Onychomys*, and *Neotoma* and *Microtus*.

Sex. The foregoing analyses were made for all specimens, regardless of sex and age. When partitioned by sex, females were found to weigh less and have smaller brains, but their E:P ratios were greater than in males. The increase was precisely along the overall trend of the genus to which the specimen belonged, rather than along their associated subspecies slope. Whether taken by subspecies or by genus (table II), the reduced major axes for the brain/body relations in males and females were essentially the same. Only the muskrat *(Ondatra)* deviated significantly, with the brain/body relation for males having a slope of 0.511 and for females of 0.226. The museum collection of *Ondatra* contained only 15 usable specimens (8 male; 7 female), leaving the statistical significance of the difference open. Although the precise values of the parameters change slightly for most groups when parcelled by sex, they do not alter the arguments.

Age. Of the 1,480 specimens, 41 were identified as juveniles, and there may have been a few more in the collection. Exclusion of the known juveniles from the analyses increased the average P by 0–26% and E by 0–7%, and the SD decreased in every case (Appendix II). This in no way affected the nature of the arguments presented here. The juveniles appeared mainly to extend the brain/body trend for their subspecies into smaller weights and volumes. However, the reduced major axes for subspecies changed slightly when juveniles were excluded, decreasing in 6 and increasing in 12 subspecies. Unfortunately, the number of juveniles in the museum collection is not sufficiently large to allow estimation of the slopes for juveniles alone.

Variability. The average variation around mean cranial volume was much smaller than that around mean body weight in all subspecies studied. In the largest sample, taken on *M. c. californicus*, the CV were CV_e = 7.4% and CV_p= 19.7%, the latter being much smaller than the overall mean of 27.0%. The values in table III show that there was marked variation among the different genera. There was also marked variation among the subspecies within each genus. For exam-

ple, in *Peromyscus* CV_p ranged from 9.8 to 29.0%, with a mean of 16.8%, whereas in *Rattus* CV_p ranged from 16.8 to 66.7%, with a mean of 36.7%. This variation did not relate to sample size; restricting the analysis to the 31 subspecies in which 20 or more specimens were measured had little effect on either the mean values or the variations within each genus. For example, in *Peromyscus* CV_p ranged from 13.8 to 29.0%, with a mean of 18.3%, whereas in *Rattus* the range remained unchanged, but the mean rose to 41.4%. Mean values for CV_e and CV_p in *Microtus* and *Neotoma* changed very little. The weighted means for all 31 subspecies rose slightly, to $CV_e = 9.5\%$ and $CV_p = 29.7\%$, revealing that the variation in the larger samples was somewhat greater than in the smaller samples – the reverse of what was expected. However, specimens of the same subspecies taken at different locales sometimes showed systematic differences in body size that could account for the greater variation in a few of the larger samples. For example, the 61 specimens of *Rattus conatus* came from six different locales in Queensland, Australia. The subgroups from three of these locales yielded the values shown in table IV. Clearly, much of the variation in the overall sample resulted from combining subpopulations of the same species. Although the samples from Mulgrave River and nearby Gordonvale do not differ statistically, they appear to be different, and the sample from Massy Creek seems to represent a very different population, perhaps of a smaller subspecies. A similar situation was seen in *Neotoma fuscipes bullatior*, shown in table IV; here, there were significant differences among samples of the same subspecies taken at different locales. On the other hand, the specimens of *Rattus colletti*, which showed the greatest variation in body weights ($CV_p = 66.7\%$), were all obtained from the same locale. The range in body weight, from 24.4 to 215.2 g, may have been spuriously large. Two females weighing 37.3 and 49.5 g had seven and six embryos, respectively, but some of the smaller specimens showed only mild tooth wear, suggesting that they might have been juveniles. After excluding these specimens, all less than 37 g body weight, and the three heaviest specimens, the range decreased markedly (122.0–37.1 = 84.9; n = 20), yielding a mean body weight of 74.6 g (down from 76.3 g) and a CV_p of 37.4% (down from 66.7%). Whether the three largest specimens can be regarded as unrepresentative is, of course, unknown.

Table III also shows the average of the slopes for the species in each genus, along with the associated genus slopes calculated by combining all individuals in each genus. For both *Phenacomys* and *Rattus*, the genus slopes were smaller than the average species slopes, whereas in every other instance they were larger. The reduced major axes for *Microtus*, *Neotoma* and *Rattus* varied widely, spanning ranges that were larger than the mean values for each genus. Only *Peromyscus*, with an equally large range (0.362), had a mean value (0.487) larger than the range of species slopes. Clearly, the general trend across a genus is not reflected in the trends within the interbreeding populations that make up a genus. On the other hand, the trends within each subspecies were fairly strong, as reflected in the E:P correlations recorded in Appendices I and II. One correlation was strongly negative, and two were near zero, but most were strongly positive. After removal of juvenile specimens, the mean correlation was 0.593, the median was 0.644, and 26% of the values were greater than 0.800. The range of reduced major axes associated with high correlations (0.221 for $r \geq 0.8$, *Rattus tiomanicus*, with only 4 specimens, was not included), was half that associated with low correlations (0.453 for $r < 0.5$), and the mean slopes were 0.327 ± 0.069 and 0.399 ± 0.140, respectively. Thus, it appears that the E:P relation within local interbreeding populations may best be approximated by using samples with relatively high correlations.

Table IV. *R. conatus* and *N.f. bullatior*

Locale	n	$\bar{P} \pm SD$[a]	CV_p[b]	$\bar{E} \pm SD$[c]	CV_e[d]
R. conatus					
Massy Creek	16	46.9 ± 12.4	26.4	1.44 ± 0.12	8.6
Mulgrave River	15	70.6 ± 24.7	34.9	1.61 ± 0.13	7.9
Gordonvale	18	93.8 ± 30.4	32.5	1.69 ± 0.13	7.7
N.f. bullatior					
Shandon	5	243.2 ± 68.5	28.2	2.59 ± 0.23	9.0
Cammatti Creek	4	281.6 ± 29.2	10.4	2.74 ± 0.20	7.4
San Miguel	8	346.5 ± 54.2	15.6	2.97 ± 0.10	3.4

n = Sample size.
[a] Mean ± SD of body weight in grams.
[b] CV of body weight, expressed as percent.
[c] Mean ± SD of cranial volume in ml.
[d] CV of cranial volume, expressed as percent.

Discussion

Multiple allometries. Neighborhood allometry differs from regional allometry, which in turn differs from global allometry [Gould, 1966; Jerison, 1973]. Although much attention has been given to the global mouse to elephant relationship, little light has been shed on what happens within interbreeding population to yield that relationship. Among the myomorph rodents, the intraspecific brain/body relations, reflected in the reduced major axis, exhibit powers (b values) ranging from 0.15 to 0.65, with an average of 0.34. Yet, it is from the chaos of a myriad such short-range orders that the overall, long-range order (mouse to elephant) derives. And each intermediate-range order (tribe, genus, family) itself derives from some subset of that subspecies chaos, and in turn contributes to the long-range order. In this circumstance, it is difficult to envision one basic interaction to account for the overall value of b. Were such the case, then the net of all the 'second-order strategies' [Western, 1979] would make brains relatively smaller with increasing body size, within subspecies, species, genera, and tribes; i.e. they would be allometries with negative exponents. It seems more likely that any basic constraint would provide the neighborhood allometries, out from which the regional and global allometries might evolve.

Martin [1981], apparently impressed by the similarity of the exponents in brain/body and metabolic rate/body size allometries, concluded that adult brain size 'may be constrained both by the resources channelled to the embryo from the mother and by mode of reproduction (vivipary versus ovipary)'. He offered no mechanisms by which this constraint might operate, nor why an embryo within an egg (which is warmed by its parents) faces a fundamentally different problem than an embryo within its mother, nor why twins do not differ from their single-borne congeners. Harvey and Bennett [1983] recognized that if the constraint were to operate across mammals, it could not account for the lower exponents found for closely related species; some special effect would be required. They suggested that body size may respond 'more readily to selection in evolutionary time than does brain size', adding that 'an evolutionary lag may exist until brain size adjusts to the optimal scaling value'. If so, then few closely related assemblages of species have enjoyed enough 'evolutionary time' to adjust to the 'optimal scaling value'. The genus *Rattus*, with a current exponent near 0.29, dates from late Miocene [Petter, 1966; Lavocat, 1967], whereas the genus *Peromyscus*, with a current exponent near 0.79, traces only to Pliocene times [Hibbard, 1968]. Clearly something more than evolutionary time is involved. In their study of geomyoid rodents, Hafner and Hafner [1984] were unable to find 'a link between brain size and metabolic rate', and Huesner [1982] showed that the ¾ exponent in the metabolism/body size relationship is an artifact caused by variation in the scaling coefficient across animals of different sizes.

Regional and neighborhood allometries. Most Mesozoic mammals, including the forerunners of placental mammals, were small [Lillegraven et al., 1979]. The large mammals attained their brain and body sizes along some path, and the large dispersion in the global picture bespeaks many independent paths, not subject to the same constraints in the same degree. Certainly, the rodents examined in the present study display quite different brain/body trends, with the deer mice having twice as much brain as voles of comparable body size, and with generic brain/body slopes ranging from 0.29 for Old World rats to 0.79 for deer mice. Genera with shallow slopes, such as *Rattus* and *Phenacomys*, evidently have been under strong pressure to increase body size, whereas those with steeper slopes, such as *Peromyscus*, have been under strong pressure to increase brain size independently of body size. Those genera with intermediate slopes may have experienced pressures for both larger brains and larger bodies. Mace and Eisenberg [1982] found a genus slope of 0.71 for 13 species of *Peromyscus*, close to our slope of 0.79 for 7 subspecies. Using the data of Roderick et al. [1976] on mice selected for high and low brain weights after 16 generations, Lande [1979] calculated a slope of 0.77, consistent with the suggestion that the genus slope of *Peromyscus* reflects strong selection for increased brain size.

Like the genus slopes, the subspecies slopes are markedly variable. Restricting attention to samples of 30 or more specimens, the range in slopes was from 0.22 to 0.59, with an average of 0.34. Table III records, for 7 genera, the average slopes for the subspecies comprising each genus, along with the overall genus slopes; in 5 genera, the average subspecies slope is shallower than the genus slopes. The deer mice *(Peromyscus)* present a particularly interesting case in that their average subspecies slope was steep (0.48) and the range of slopes was large (0.29–0.66). Perusal of Appendix I reveals that the 7 subspecies with 6 or more

measured individuals form two groups, one with 5 light subspecies and the other with 2 heavy subspecies *(Peromyscus guatamalensis guatamalensis* and *Peromyscus thomasi).* The average slopes of 0.56 and 0.31 for these two groups suggest divergence toward separate genera, the light group having experienced pressures for increased brain size and the heavy group for increased body size. Clearly, the deer mice comprise a heterogeneous assemblage that merits further study.

All of these interpretations depend upon the descriptiveness of the samples. The family slopes for the murids and the cricetids are the same as the overall mammalian slope, yet in a sense this is an accident of the particular samples. Had *Mus* not been studied (the values given by Calder [1984] for *Mus*, table 12-3, differ significantly from those of our sample, but taking those values would not significantly alter the slopes discussed here), the murid family slope would have been that of the genus *Rattus* (0.287 rather than 0.697). If only *Microtus* and *Neotoma* had been studied, a cricetid family slope of 0.802 would have been obtained on this 14-fold weight interval. On the other hand, if only *Peromyscus* and *Neotoma* had been studied, a cricetid family slope of 0.570 would have been obtained over the same weight interval. In lumping the 4 genera of the microtine tribe and the 5 genera of the hesperomyine tribe, slopes of 0.612 and 0.591 were obtained, respectively. The 'real' cricetid family slope of 0.675, obtained by lumping all 9 genera, reflects the large number of small microtines relative to the broader body weight range of the hesperomyines. These sampling problems force one to question the meaning of apparent 'trends' in brain/body relations beyond the limited E:P neighborhood of very closely related genetic lines.

Variability. Another major concern is the homogeneity of the samples. Table III records the CVs of cranial volume and body weight for the different genera; those for cranial volume (CV_e) ranged from 4.4 to 11.2%, and those for body weight ranged from 12.3 to 36.7%. The magnitudes of the CVs did not vary with the magnitude of either E or P, but the steeper the genus slope, the smaller the CV. The CV_e values were more varied than those reported by Yablokov [1974] for brain weight in small mammals (6–7%) and by Brown et al. [1926] and Latimer and Sawin [1955] for rabbits (5–8.4%). However, agreement with other studies was good. For example, King [1955] obtained CV_e = 6.3% for *Peromyscus maniculatus*, and we found CV_e = 7.4% for *Peromyscus maniculatus sonoriensis*, using 30 adult specimens (CV_p = 13.8%). On the other hand, Count's [1947] data for brain weight in orangutans yield CV_e = 13.9%, exceeding our highest value for rodents.

Yablokov [1974] put body weight variation at 12–15% for rodents and insectivores, in sharp contrast to our values of 16.8–36.7%. Count's [1947] data yield a CV_p of 38.9%, more in line with our values. However, some of the variability we found in body weight may relate to differences between local populations of the same subspecies or to lumping different subspecies. By partitioning the samples according to the locale of collection, variability could be reduced and 'subpopulations' identified. Table IV shows an instance where at least two subspecies may have been combined, and where partitioning by locale reduced the variability. Table IV also shows an instance in which three subpopulations of the same subspecies showed substantial differences in mean body size, and in which even brain size may have differed significantly (Shandon vs. San Miguel samples). Errors of measurement may play a significant role in samples in which the ranges in P and E are restricted. Hence, the accuracy of placement of both slope and intercept values in the relation $E = kP^b$ is decreased. Nonetheless, the picture obtained in the present study, after carefully 'cleaning up' the observations, suggests that, (a) the average species slope is about ⅓, (b) there are real and significant differences in slopes among species, and (c) these differences relate to the genus to which the species belong.

Minimum brain size. Using log-log coordinates to display allometric relationships has the advantage of expanding the small end of the scale and reducing the apparent scatter, but it also carries the disadvantage that a description of convenience may be taken to reflect a fundamental process [Calder, 1984]. Order can be imposed and scatter reduced in other ways. When not immersed in a power function model, the issue of 'the right amount of brain' takes on a different character. Suppose that the amount of body tissue under control by a unit of neural tissue is a significant metric and that P:E approximates that amount of tissue. The smallest rodent measured in this study, the house mouse, gets along well with just 0.37 g of brain in a 15.4 g body (P:E = 42). At 48.2 g body weight, the deer mouse, *P. g. guatamalensis*, has a P:E ratio of 37, near that of the house mouse, whereas a vole of the same body weight, *M.c. californicus*, has the much larger P:E ratio of 70. The vole might therefore be re-

Table V. Dietary correlates of brain size

Subspecies	$\overline{P}$[a]	$\overline{E}$[a]	$\overline{E}:\overline{P}$	EQ[b]	Dietary preference
Peromyscus truei truei	23.2	0.79	0.034	1.44	seeds, nuts, fruits
Onychomys leucogaster brevicaudus	26.4[c]	0.76	0.029	1.27	insects
Perognathus c. californicus	25.4	0.64	0.025	1.10	seeds
Clethrionomys gapperi arizonensis	25.3[c]	0.53	0.021	0.91	green vegetation
Phenacomys i. intermedius	28.5	0.49	0.017	0.78	green vegetation
Microtus ochrogaster minor	26.1	0.39	0.015	0.66	green vegetation, especially grass

[a] Mean body weight (P) or cranial volume (E).
[b] Encephalization quotient computed as $E_{observed}/E_{expected} = E_{obs}/0.066P^{0.673}$.
[c] Data from Appendix II.

garded as more 'efficient' in terms of neural investment, were it of the same habitus as the house or deer mouse, but it is not. The smallest known mammals, the little shrew and the bumblebee bat, weigh about 2 g as adults. Assuming that 2 g represent a lower limit on homeotherm size and that a P:E ratio of about 20 represents a biological minimum, the minimum brain would be 0.1 g. Such a brain would have of the order of 10^8 neurons to regulate about 1.75 g of body (blood and bones subtracted), including its interaction with the environment.

Order out of chaos. In view of the wide range of slopes encountered in this study at different taxonomic levels of analysis, the idea that one basic interaction generates the overall mammalian brain/body relation loses much of its attraction. If the slopes at the subspecies level reflect the phenotypic expression of a basic developmental relationship unique to each interbreeding population (as shown in Appendices I and II, brain:body size correlations were high in most subspecies), then neither the genus nor the family slopes can be understood as simple extrapolations of that basic relationship; something else is involved. Because the subspecies brain/body relation is strong, any selection favoring larger brains in a population would indirectly also favor larger bodies, and the magnitude of that indirect selection would depend upon the steepness of the subspecies slope. It is quite possible that the overall relation for mammals, with a power in the neighborhood of 7/10, reflects the most probable pathway taken through a series of 'random' selective steps. The strength of the brain/body relation and the slope associated with any subspecies would thus define the range of possible evolutionary pathways open to that subspecies. This problem has been addressed by Lande [1979] in terms of multivariate statistics; the conclusions drawn are similar to those that emerge from a simple 'geometric' model which we will develop in a subsequent paper.

Ecological correlates of brain size. Rodents are ideal for study of the relations between brain size, body size, body shape, and life-style. Mace et al. [1981] examined these variables in a variety of rodents and concluded that diet is the best predictor of relative brain size. Rodents that ate fruits, seeds and insects had 'relatively larger' brains than those that ate foliage. Assembling groups of rodents into narrow weight ranges (see Appendices) sorts them by brain size (vertical allometry), and reveals, in keeping with the general conclusions of Clutton-Brock and Harvey [1980] and Mace et al. [1981], that folivorous rodents have significantly smaller brains than granivorous, insectivorous and generalist rodents. The pattern revealed in table V was found at all five body weights examined, centered on 20.0, 25.8, 36.8, 47.6 and 95.2 g (weight bins from 1.2 to 5.5 g). The average brain size of the folivores was 2/3 that of the other rodents, at each body weight examined. In order to understand why this difference exists, it is necessary to specify the particular behavioral details associated with (required by) these dietary preferences. In line with modern approaches to the study of foraging, such details might involve the searching and handling phases of eating, which include detection/discrimination, manipulation, and perhaps storage and retrieval of food. At a more general level, ecological variables need to be translated into behavioral tasks, to further our understanding of why brains get bigger.

Appendix I

Taxonomic group	n	$\bar{P}$	SD	$\bar{E}$	SD	b	k	r
Cricetidae[1]	1,050	92.3	107.7	1.26	0.90	0.673	0.066	0.92
Microtinae[1]	426	64.7	110.4	0.79	0.69	0.609	0.068	0.93
Clethrionomys								
C. gapperi arizonensis	19	24.2	6.0	0.53	0.03	0.232	0.252	0.73
Microtus[1]	360	46.8	18.2	0.68	0.12	0.459	0.119	0.78
M. californicus	226	48.0	11.3	0.69	0.06	0.380	0.159	0.53
M. c. californicus	214	47.1	9.3	0.68	0.05	0.389	0.153	0.43
M. c. sanctidiegi	5	60.5	17.3	0.77	0.05	0.236	0.293	0.71
M. c. scirpensis	7	67.0	31.4	0.82	0.11	0.216	0.339	0.94
M. longicaudus alticola	30	37.7	10.2	0.63	0.04	0.244	0.263	0.55
M. montanus yosemite	15	39.5	10.0	0.59	0.03	0.202	0.280	-0.54
M. ochrogaster	9	45.9	17.6	0.54	0.12	0.571	0.061	0.95
M. o. minor	3	26.1	4.0	0.39	0.01	-	-	-
M. o. ochrogaster	6	55.8	11.7	0.61	0.06	0.429	0.109	0.78
M. oregoni oregoni	32	20.6	4.2	0.46	0.05	0.518	0.097	-0.07
M. p. pennsylvanicus	9	37.2	6.8	0.65	0.05	0.458	0.124	0.44
M. t. townsendii	18	51.5	16.8	0.82	0.09	0.299	0.256	0.78
M. xanthognathus	24	85.1	26.2	0.93	0.05	0.167	0.448	0.41
Ondatra								
O. zibethica bernardi	15	629.3	77.2	4.31	0.19	0.362	0.419	0.61
Phenacomys[1]	32	24.7	7.8	0.48	0.05	0.322	0.174	0.49
P. albipes	1	16.4	-	0.56	-	-	-	-
P. intermedius celsus	1	30.2	-	0.53	-	-	-	-
P. i. intermedius	17	28.5	7.7	0.49	0.06	0.416	0.122	0.49
P. longicaudus	15	20.4	5.3	0.48	0.04	0.311	0.188	0.59
Hesperomyinae[1]	624	111.2	101.7	1.57	0.89	0.590	0.109	0.97
Neotoma[1]	280	205.6	78.8	2.49	0.42	0.419	0.272	0.84
N. albigula albigula	36	159.5	37.3	2.52	0.21	0.313	0.519	0.86
N. cinerea	33	250.1	92.4	2.74	0.35	0.349	0.405	0.89
N. c. acraia	17	206.8	54.2	2.54	0.25	0.341	0.415	0.88
N. c. occidentalis	16	296.1	103.4	2.95	0.32	0.298	0.549	0.85
N. fuscipes	90	251.3	67.9	2.78	0.26	0.313	0.496	0.73
N. f. annectans	10	284.5	46.9	2.95	0.16	0.357	0.394	0.66
N. f. bullatior	17	300.9	69.2	2.80	0.23	0.352	0.379	0.86
N. f. fuscipes	20	227.9	78.2	2.89	0.29	0.259	0.718	0.92
N. f. luciana	43	234.9	54.1	2.67	0.22	0.347	0.404	0.73
N. goldmani	2	94.2	4.7	1.99	0.04	-	-	-
N. l. lepida	34	128.3	46.4	1.89	0.21	0.289	0.045	0.78
N. mexicana	7	148.6	60.7	2.17	0.12	0.138	1.097	0.65
N. micropus	36	242.7	56.1	2.72	0.20	0.296	0.538	0.76
N. m. canescens	14	215.5	68.8	2.67	0.25	0.290	0.567	0.79
N. m. micropus	22	260.1	38.6	2.75	0.16	0.410	0.281	0.69
N. s. stephensi	19	152.7	32.9	2.02	0.17	0.367	0.320	0.64
Teanopus phenax	25	156.8	49.1	2.05	0.28	0.300	0.458	0.93
Onychomys[1]	152	23.3	6.0	0.68	0.10	0.581	0.110	0.71
O. leucogaster brevicaudus	90	26.0	5.7	0.76	0.06	0.356	0.239	0.65
O. torridus pulcher	62	19.4	3.9	0.57	0.03	0.234	0.288	0.51
Peromyscus[1]	136	32.8	14.5	0.89	0.27	0.793	0.057	0.84
P. californica insignis	16	31.6	3.1	0.91	0.06	0.650	0.097	0.20
P. floridana	2	34.0	5.7	0.98	0.03	-	-	-
P. grandis	2	72.5	13.4	1.48	0.04	-	-	-
P. g. guatamalensis	22	48.2	14.0	1.30	0.12	0.329	0.367	0.47
P. lepturus	12	34.9	7.7	0.83	0.11	0.655	0.082	0.27
P. maniculatus sonoriensis	30	20.3	2.8	0.54	0.04	0.590	0.092	0.55

Appendix I (continued)

Taxonomic group	n	$\bar{P}$	SD	$\bar{E}$	SD	b	k	r
P. mexicanus mexicanus	20	36.8	5.4	0.99	0.07	0.506	0.161	0.53
P. polionotus leucocephalus	1	14.0	–	0.47	–	–	–	–
P. thomasi	9	66.5	11.1	1.38	0.06	0.250	0.483	0.41
P. t. thomasi	6	71.4	8.4	1.39	0.05	0.293	0.398	0.03
P. t. cryophilus	3	56.7	9.9	1.35	0.08	–	–	–
P. truei truei	30	23.2	3.6	0.79	0.05	0.387	0.236	0.10
Phyllotis								
P. darwini chilensis	28	42.9	12.0	0.91	0.10	0.365	0.233	0.89
Sigmodon								
S. hispidus berlandieri	28	93.7	28.4	1.21	0.11	0.322	0.283	0.83
Muridae[1]	380	80.5	64.8	1.48	0.52	0.697	0.076	0.87
Mus								
M. domesticus	55	15.4	4.4	0.37	0.04	0.353	1.051	0.65
Rattus[1]	325	91.5	63.8	1.67	0.27	0.287	0.070	0.87
R. colletti	30	76.3	50.9	1.43	0.20	0.221	0.568	0.92
R. conatus	61	66.8	32.3	1.54	0.20	0.260	0.527	0.88
R. fuscipes	29	89.5	15.0	1.81	0.09	0.289	0.495	0.32
R. leucopus	38	96.7	33.5	1.78	0.19	0.265	0.537	0.89
R. lutreolus	41	89.4	37.7	1.74	0.21	0.264	0.542	0.81
R. niobe stevensii	15	47.4	10.9	1.32	0.11	0.304	0.411	0.65
R. norvegicus	21	243.5	138.4	2.13	0.39	0.267	0.510	0.95
R. rattus diardii	1	147.0	–	1.86	–	–	–	–
R. r. rattus	21	116.3	27.7	1.78	0.15	0.373	0.303	0.83
R. ruber	29	70.9	26.0	1.70	0.20	0.293	0.484	0.81
R. surifer	6	95.5	24.0	1.72	0.20	0.442	0.226	0.82
R. tiomanicus	4	67.2	12.7	1.58	0.19	0.621	0.116	0.82
R. tunneyi	30	76.0	36.1	1.55	0.17	0.227	0.591	0.81
Heteromyidae								
Perognathus[1]	34	21.8	4.7	0.57	0.06	0.509	0.119	0.69
P. c. californicus	13	25.4	4.5	0.64	0.03	0.275	0.262	0.59
P. fallax pallidus	21	19.6	3.3	0.53	0.03	0.346	0.189	0.36

n = Sample size; $\bar{P}$ = mean body weight; $\bar{E}$ = mean cranial volume; b = reduced major axis; k = intercept at 1 g body weight; r = Pearson's correlation coefficient for log P and log E.

[1] Family and genus values computed only for species with n > 3.

Appendix II. Changes from Appendix I after removing juveniles

Taxonomic group	n	$\bar{P}$	SD	$\bar{E}$	SD	b	k	r
Cricetidae[1]	1,032	93.2	108.4	1.26	0.91	0.674	0.066	0.92
Microtinae[1]	420	65.2	111.1	0.79	0.69	0.612	0.067	0.93
Clethrionomys								
C. gapperi arizonensis	17	25.3	5.4	0.53	0.02	0.220	0.261	0.54
Microtus[1]	356	47.0	18.2	0.68	0.12	0.458	0.119	0.80
M. californicus	224	48.2	11.1	0.69	0.06	0.395	0.150	0.55
M. c. scirpensis	5	84.1	14.2	0.88	0.06	0.436	0.128	0.65
M. xanthognathus	22	89.1	23.8	0.94	0.05	0.200	0.384	0.55

Appendix II (continued)

Taxonomic group	n	$\bar{P}$	SD	$\bar{E}$	SD	b	k	r
Hesperomyinae	612	112.4	102.8	1.58	0.90	0.591	0.094	0.97
Neotoma[1]	272	209.6	76.2	2.51	0.41	0.448	0.232	0.83
N. albigula albigula	34	164.5	31.4	2.54	0.18	0.356	0.415	0.80
N. cinerea	32	254.9	89.5	2.76	0.34	0.362	0.376	0.87
N. c. acraia	16	213.8	47.5	2.57	0.23	0.396	0.309	0.85
N. fuscipes	89	253.4	65.4	2.78	0.25	0.335	0.439	0.69
N. f. fuscipes	19	236.4	70.1	2.94	0.23	0.257	0.726	0.86
N. mexicana	5	169.5	60.1	2.21	0.12	0.146	1.050	0.52
Teanopus phenax	23	168.2	30.9	2.12	0.12	0.267	0.542	0.46
Onychomys[1]	149	23.5	5.9	0.69	0.10	0.608	0.101	0.71
O. leucogaster brevicaudus	88	26.4	5.3	0.76	0.05	0.358	0.336	0.51
O. torridus pulcher	61	19.4	3.9	0.57	0.03	0.238	0.284	0.51
Phyllotis								
P. darwini chilensis	27	43.9	11.1	0.92	0.09	0.367	0.232	0.84
Muridae[1]	365	89.1	65.5	1.48	0.53	0.707	0.071	0.88
Rattus[1]	310	93.9	64.2	1.68	0.27	0.291	0.464	0.86
R. conatus	60	67.7	31.8	1.55	0.20	0.263	0.521	0.90
R. leucopus	33	105.2	26.7	1.83	0.14	0.283	0.493	0.76
R. lutreolus	38	94.2	34.9	1.78	0.17	0.244	0.594	0.66
R. norvegicus	18	275.7	126.3	2.24	0.26	0.249	0.564	0.86
R. r. rattus	20	118.6	26.3	1.79	0.14	0.412	0.251	0.82
R. tunneyi	28	78.0	35.7	1.56	0.16	0.237	0.560	0.76
Heteromyidae								
Perognathus[1]	33	22.0	4.6	0.57	0.06	0.508	0.119	0.66
P. fallax pallidus	20	19.8	3.2	0.53	0.03	0.330	0.198	0.24

n = Sample size; $\bar{P}$ = mean body weight; $\bar{E}$ = mean cranial volume; b = reduced major axis; k = intercept at 1 g body weight; r = Pearson's correlation coefficient for log P and log E.

[1] Family and genus values computed only for species with $n > 3$.

References

Armstrong, E.: Metabolism and relative brain size. Science *220:* 1302–1304 (1983).

Brown, W.H.; Pearce, L.; Van Allen, C.M.: Organ weights of normal rabbits. J. exp. Med. *43:* 733–741 (1926).

Calder, W.A. III: Size, function and life history (Harvard, Cambridge 1984).

Clarke, M.R.B.: The reduced major axis of a bivariate sample. Biometrika *67:* 442–446 (1980).

Clutton-Brock, T.H.; Harvey, P.H.: Primates, brains and ecology. J. Zool. *190:* 309–324 (1980).

Count, E.W.: Brain and body weight in man: their antecedents in growth and evolution. A study in dynamic somatometry. Ann. N.Y. Acad. Sci. *67:* 993–1122 (1947).

Dark, J.; Dark, K.A.; Zucker, I.: Long day lengths increase brain weight and DNA content in the meadow vole, *Microtus pennsylvanicus*. Brain Res. (in press, 1987).

Gould, S.J.: Allometry and size in ontogeny and phylogeny. Biol. Rev. *41:* 587–640 (1966).

Gould, S.J.: Geometric similarity in allometric growth: a contribution to the problem of scaling. Am. Nat. *105:* 113–136 (1971).

Gould, S.J.: Allometry in primates, with emphasis on scaling and the evolution of the brain; in Szalay, Approaches to primate paleobiology. Contributions in primatology, vol. 5, pp. 244–292 (Karger, Basel 1975).

Hafner, M.S.; Hafner, J.C.: Brain size, adaptation and heterochrony in geomyoid rodents. Evolution *38:* 1088–1098 (1984).

Harvey, P.H.; Bennett, P.M.: Brain size, energetics, ecology and life history patterns. Nature *306:* 314–315 (1983).

Harvey, P.H.; Mace, G.M.: Comparisons between taxa and adaptive trends: problems of methodology; in King's College Sociobiology Group, Current problems in sociobiology. (Cambridge University, Cambridge 1982).

Heusner, A.A.: Energy metabolism and body size. I. Is the 0.75

mass exponent of Kleiber's equation a statistical artifact? Resp. Physiol. *48:* 1–12 (1982).

Hibbard, C.W.: Paleontology; in King, Biology of *Peromyscus*, special publ. No. 2 (Am. Soc. Mammalogists, Shippensburg, PA (1968).

Huxley, J.S.; Teissier, G.: Terminology of relative growth. Nature *137:* 780–781 (1936).

Jerison, H.J.: Evolution of the brain and intelligence (Academic Press, New York 1973).

Kermack, K.A.; Haldane, J.B.S.: Organic correlation and allometry. Biometrika *37:* 30–41 (1950).

King, J.A.: Body, brain and lens weight of Peromyscus. Zool. Jb. Abt. II *32:* 177–188 (1955).

Kingdon, J.: East African mammals: An atlas of evolution in Africa, vol. 2-B: Hares and rodents (Academic Press, New York 1974).

Kurten, B.: The age of mammals (Columbia, New York 1971).

Lande, R.: Quantitative genetic analysis of multivariate evolution, applied to brain:body allometry. Evolution *33:* 402–416 (1979).

Latimer, H.B.; Sawin, P.B.: Morphological studies of rabbits. XII. Organ size in relation to body weights in adult of small-sized Race X. Anat. Rec. *143:* 81–97 (1955).

Lavocat, R.: A propos de la dentition des rongeurs et du problème de l'origine de Murides. Mammalia *31:* 205–216 (1967).

Lillegraven, J.A.; Kielan-Jaworowski, Z.; Clemens, W.A.: Mesozoic mammals. The first two-thirds of mammalian history (University of California, Berkeley 1979).

Mace, G.M.; Eisenberg, J.F.: Competition, niche specialization and the evolution of brain size in the genus *Peromyscus*. Biol. J. Linnean Soc. *17:* 243–257 (1982).

Mace, G.M.; Harvey, P.H.; Clutton-Brock, T.H.: Brain size and ecology in small mammals. J. Zool. *193:* 333–354 (1981).

Martin, R.D.: Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature *293:* 57–60 (1981).

Petter, F.: L'origine de Murides. Plan cricétin et plan murin. Mammalia *30:* 205–225 (1966).

Rensch, B.: Evolution above the species level (Columbia University Press, New York 1960).

Roderick, T.H.; Wimer, R.E.; Wimer, C.C.: Genetic manipulation of neuroanatomical traits; in Petrovich, McGaugh, Knowing, thinking and believing, pp. 143–178 (Plenum Press, New York 1976).

Western, D.: Size, life history, and ecology in mammals. Afr. J. Ecol. *17:* 185–204 (1979).

Wood, A.E.: A revised classification of the rodents. J. Mammal. *36:* 165–187 (1955).

Wood, A.E.: Grades and clades among rodents. Evolution *19:* 115–130 (1965).

Yablokov, A.V.: Variability of mammals (Amerind, New Delhi 1974).

Yaskin, V.A.: Seasonal changes in brain morphology in small mammals; in Merritt, Winter ecology of small mammals, special publ. No. 10, pp. 183–191 (Carnegie Mus. Nat. Hist., Pittsburgh 1984).

Dr. Michael D. Mann
Department of Physiology and Biophysics
University of Nebraska Medical Center
Omaha, NE 68105 (USA)