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THE TAXON-LEVEL PROBLEM IN THE EVOLUTION OF MAMMALIAN BRAIN SIZE: FACTS AND ARTIFACTS

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Brain size scales against body size with a slope of around 0.75 across mammalian orders, when both variables are plotted on logarithmic axes (Bauchot 1978; Martin 1981; Hofman 1982; Harvey and Bennett 1983; Martin and Harvey 1985). However, it has long been known that the slope of the allometric line of best fit relating brain size to body size in mammals differs depending on the taxonomic level within which slopes are estimated (Snell 1891; Dubois 1897; see also reviews in Gould 1966, 1971, 1975; Martin and Harvey 1985). A comprehensive review of the across-species allometry of brain size in over 800 mammals showed consistent increases in slope with taxonomic level (Martin and Harvey 1985). Across 15 order points within the class, brain size scaled against body size with a slope of 0.72; 95% confidence intervals included 0.75 but excluded 0.67. However, among families or superfamilies within orders, the allometric slopes averaged 0.66. Average slopes declined to 0.58 among genera points within families and to 0.48 among species within genera. Other authors using smaller data sets have reported similar but somewhat shallower slopes. For closely related genera or among species within a genus, slopes between 0.2 and 0.5 have been reported (Bauchot and Stephan 1964; Jerison 1973; see also Gould 1975; Lande 1979). This pattern of slopes increasing at higher taxonomic levels gives rise to the set of parallel lines shown in figure 1. Shallower slopes represent the typical (idealized) allometry seen among species within a genus. However, the slope increases steeply when the means of each genus are connected.

How might this pattern of interspecific slopes increasing with taxonomic level arise? Lande (1979) proposed that the changing slopes could be explained by patterns of selective forces operating differentially on brain and body size over evolutionary time. Lande stated that "selective forces which acted to differentiate very closely related forms operated predominantly on overall body size and that changes in brain weights were largely a correlated response" (p. 411). The correlated response in brain size, according to Lande, would show the shallow slope characteristic of closely related species within a genus. However, Lande argued that over evolutionary time, "natural selection is able to adjust brain size to accumulated changes in body size" since "diversification in brain and body

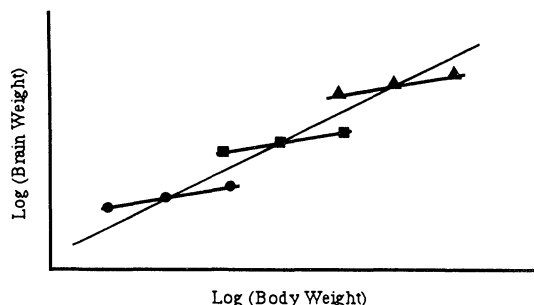


FIG. 1.—Idealized representation of the change in allometric slope with taxonomic level. The three shallow slopes represent the relationship that might be found for species within each of three different genera. The steeper line represents the slope connecting the means of the respective genera.

weights at higher taxonomic levels involved a greater net directional selection on brain sizes than on body sizes'' (p. 412). This would increase the slope among species more distantly related over that among, for example, species within a genus.

Gould (1975) proposed an ontogenetic mechanism to explain how the slope connecting closely related species could be shallower than that connecting species more distantly related. Like Lande, Gould (1975, fig. 12) speculated that the shallow slopes connecting the brain and body sizes of closely related species reflect selection for increased body size, with a correlated response in brain size. However, steeper slopes would arise between these closely related species and their descendant species, according to Gould (1975), if selection acted to prolong the period of early ontogenetic brain and body growth. During early development, the brain scales against the body with a slope often approaching 1.0 (Sacher 1982; Hofman 1983; Martin 1983; Passingham 1985). Thus, descendant species that evolved by selection acting to prolong this period would differ from their ancestors by having bigger bodies. But they would also have brains much bigger than would be expected from extending the shallow line that describes the divergence resulting from selection for body size alone. This would yield a pattern of shallow slopes among the closely related ancestral species but steeper slopes between them and the descendant species. Riska and Atchley (1985) advance an explanation similar to Gould's.

In this paper, we present an alternative explanation for the regular increase in slopes with taxonomic level. We argue below, and provide supporting results from a simulation study, that some or all of the general pattern of interspecific slopes increasing with taxonomic level could arise as a statistical artifact owing to the distribution of sampling error in interspecific allometric data and to the methods employed to estimate allometric lines of best fit. The artifact that we have identified should be ruled out before ascribing changes in slope in a particular data set to evolutionary processes.

We first review the statistical methods commonly employed in allometric studies and the assumptions they make. We then describe patterns of error variability

in brain size and body size, showing that they do not conform to the assumptions of any of these techniques. Finally, we demonstrate, with a simulation study designed to mimic mammalian brain- and body-size data, that a regular increase in slope with increasing taxonomic level emerges as a consequence of error-variability patterns alone, regardless of which technique is used to analyze the data.

THEORY AND METHODS

Techniques of Allometric Analysis

Since the relationship of brain size and body size seems to conform to a power function of the form $Y = aX^b$ (Huxley 1932; Gould 1966), the variables are usually logarithmically transformed to yield the linear allometric relationship $\log Y = \log a + b \log X$. Three statistical techniques are commonly employed to estimate the slope and intercept of the allometric line of best fit: least-squares regression (model-1 regression), major-axis analysis (model-2 regression), and reduced-major-axis analysis (for discussions of each method and formulas, see Kuhry and Marcus 1977; Sokal and Rohlf 1981; Seim and Saether 1983; Hofman 1986). Each method is derived from the same general structural-relations model (Sprenst 1969; Rayner 1985) by making different assumptions about the nature of error variability in X and Y .

Estimates of b from least-squares regression are obtained by assuming that Y but not X may contain error. For most allometric applications, the assumption of no error in X is incorrect, leading to least-squares regression consistently underestimating the true value of b . The major-axis slope relating X and Y is an estimate of the major axis of the bivariate ellipse of paired X and Y values. To estimate the slope, major-axis regression assumes that the error variance of the two variates is equal. Departures from this pattern can lead to a consistent over- or underestimation of the true slope by the major axis. Because it allows error in both variates, the major-axis regression has been suggested as an alternative to the least-squares regression (Sokal and Rohlf 1981; Harvey and Mace 1982; Hofman 1986) and is widely used (Jerison 1973; Martin 1981, 1983; Hofman 1983; Harvey and Clutton-Brock 1985; Gittleman 1986). Reduced-major-axis analysis estimates the slope by assuming that the ratio of the two error variances equals the ratio of the two actual variances in the raw data. The slope of the reduced major axis is simply the ratio of the standard deviation of Y to the standard deviation of X . As with the major-axis slope, departures from the assumed error pattern can cause reduced-major-axis slopes consistently to overestimate or to underestimate the true slope.

The accuracy of the estimate yielded by each of these methods is thus a function of the extent to which its assumptions hold in the actual data. In practice, all three estimators yield similar results when the correlation between X and Y is high, because high correlations imply small amounts of error, and as a result, differences among the techniques become less pronounced. But for lower values of the correlation, the estimates from the three methods can diverge substantially (Harvey and Mace 1982; Hofman 1986). We now turn to an analysis of error patterns in real data in an attempt to judge their expected effects on the estimates yielded by each method.

Sources of Error in Comparative Brain- and Body-Size Data

To analyze the relationship of brain and body weight within a genus, a line of best fit is calculated for the species means within that genus. For analyses within higher taxonomic levels, lines of best fit are calculated across the means of the taxonomic groups that comprise the higher taxa; for example, genera means are used to calculate best-fit lines within families. The estimates of species-typical and higher-level means vary about their true values because of measurement error and sampling error.

Measurement error caused by unreliable scales or measures is probably small in studies of brain and body size. Measurement error can easily be estimated by repeated measurement of the same specimen. We regard this source as negligible in this study. Sampling error, however, is probably not negligible. For estimating species-typical means, sampling error may arise from two sources: the variance of the trait in the population from which the observations are drawn, and the variance of the population means of the trait within the species. Since body and brain sizes vary widely among adults within species, samples may or may not yield accurate estimates of the population mean. Populations can also differ from each other. Since species-typical values in allometric studies are often obtained from reports about only a few individuals from a population, these two sources of sampling error may not be averaged out.

As means of higher taxonomic groups are calculated, sampling error arises specific to each level. For example, a genus mean may contain sampling error caused by variation in the species values, plus additional sampling error because not all of the species within that genus may have been sampled.

The above considerations led us to investigate the sampling errors for brain- and body-size values used in comparative analyses. We calculated the within-population variances of brain and body size in 23 data sets that included raw data on brain and body size for individuals within a species (all mammals). The 23 species include five orders and range in size from mice (*Acomys*, *Apodemus*, *Mus*) to a llama (*Lama guanicoe*). We reasoned that calculating within-population variances for each species would give us a lower-bound estimate of sampling variability in comparative studies. It is a lower bound because it lacks the sampling variability introduced by differences among populations within a species and has none of the sampling variability introduced at higher taxonomic levels.

The data for each species were logarithmically transformed before analysis, removing any tendency for the means and variances of the populations to co-vary. Most of the data sets contained males and females, but we found no evidence that their variability was greater than that of data sets with exclusively one sex. Care was taken to delete juveniles or underweight animals (some data came from medical research projects) to avoid inflating the variability in body size. The results are reported in table 1. The average standard deviation of body size was 0.092 versus 0.034 for brain size. Deleting six studies with standard deviations for body size clearly outside the distribution ($SD > 0.13$) decreases the average standard deviation to 0.072 for body size and 0.032 for brain size.

The ratio of the average standard deviation of brain size to the average standard deviation of body size for the 23 data sets in table 1 is 0.37, which increases to 0.44 when the six studies with large standard deviations for body size are removed.

TABLE 1

STANDARD DEVIATIONS OF LOGARITHMICALLY TRANSFORMED BODY AND BRAIN WEIGHTS
IN INTRASPECIFIC DATA SETS

SPECIES*	SEX†	STANDARD DEVIATION		N
		log(BW)	log(BRW)	
<i>Erinaceus europaeus</i> ^a	m,f	0.068	0.035	20
<i>Crocidura orientalis</i> ^a	m	0.075	0.020	18
<i>Tenrec ecaudatus</i> ^a	m	0.063	0.057	9
<i>Suncus murinus</i> ^a	m,f	0.103	0.035	12
<i>Nesogale talazaci</i> ^a	?	0.149	0.048	14
<i>Setifer setosus</i> ^a	m,f	0.133	0.049	16
<i>Microcebus murinus</i> ^a	m,f	0.080	0.037	11
<i>Callithrix jacchus</i> ^b	m,f	0.078	0.042	23
<i>Alouatta villosa</i> ^b	m,f	0.046	0.052	10
<i>Macaca mulatta</i> ^b	m,f	0.092	0.062	11
<i>Cebus capucinus</i> ^b	m,f	0.075	0.034	10
<i>Lama guanicoe</i> ^c	m,f	0.062	0.023	13
<i>Apodemus sylvaticus</i> ^d	m	0.054	0.026	72
<i>Apodemus sylvaticus</i> ^d	f	0.076	0.023	54
<i>Acomys cahirinus dimidiatus</i> ^e	m	0.068	0.018	16
<i>Acomys cahirinus dimidiatus</i> ^e	f	0.091	0.022	12
<i>Acomys cahirinus minous</i> ^f	m	0.142	0.029	30
<i>Acomys cahirinus minous</i> ^f	f	0.179	0.024	6
<i>Papio papio</i> ^g	m	0.152	0.023	16
<i>Papio papio</i> ^g	f	0.157	0.031	14
<i>Felis domesticus</i> ^h	?	0.068	0.036	17
<i>Mus musculus</i> ⁱ	m	0.043	0.028	24
<i>Mus musculus</i> ^j	?	0.063	0.016	42
AVERAGE		0.092	0.034	

NOTE.—All data are for adults. BW, body weight; BRW, brain weight; N, sample size.

* SOURCES.—*a*, Bauchot and Stephan 1966; *b*, Bauchot and Stephan 1969; *c*, Herre and Thiede 1975; *d*, Klemmt 1960; *e*, Kretschmann 1966; *f*, Kretschmann 1968; *g*, Riese and Riese 1952; *h*, Röhrs 1959; *i*, Schönheit 1970; *j*, Wingert 1969.

† Males or females only or mixed groups. In some cases, sex was not specified.

Lande (1979) also estimated the ratio of brain-size to body-size variability in mammals, and derived a range of 0.40 to 0.50. Our estimates suggest that logarithmically transformed body-size values can be expected to be around 2.30 to 2.70 times as variable as logarithmically transformed brain-size values. If this figure is representative and if the higher-order components of sampling variability have a similar pattern, error from sampling variability in mean body size should also tend to be about 2.30 to 2.70 times that of brain size in comparative data sets.

Effects of Error Patterns on Estimated Slopes

The data in table 1 show that the assumptions of the least-squares and major-axis methods are not met in brain-size–body-size data: there is substantial error variability in body size, and the error variances of brain and body size are not equal. Whether the assumptions of the reduced-major-axis regression are met depends on whether the ratio of the interspecific variances of brain and body size is equivalent to the ratio of sampling-error variances.

The ratio of sampling-error variance of brain size to sampling-error variance of

TABLE 2
DESCRIPTIVE STATISTICS AND ALLOMETRIC RELATIONSHIPS IN THE SIMULATED DATA
AND IN EIGHT COMPARISON DATA SETS

ORDER*	SAMPLE SIZE	LOG-TRANSFORMED VALUES†		r_{xy}	SLOPE	METHOD
		BW (SD)	BRW (SD)			
“Interorder” ^a	1000	0.537 (0.644)	1.470 (0.495)	0.993	0.742 0.744 0.745	regression major axis reduced major axis
Insectivores ^b	69	0.473 (0.705)	0.708 (0.490)	0.948	0.658 0.681 0.695	regression major axis reduced major axis
Rodents ^b	221	-0.950 (0.607)	0.403 (0.316)	0.938	0.489 0.501 0.521	regression major axis reduced major axis
Primates ^c	124	0.538 (0.651)	1.668 (0.514)	0.946	0.777 0.779 0.790	regression major axis reduced major axis
Carnivores ^d	113	0.648 (0.728)	1.490 (0.495)	0.958	0.652 0.669 0.680	regression major axis reduced major axis
Chiroptera ^e	225	—	—	0.950	0.802 0.844	regression reduced major axis
Interorder ^f	684	—	—	0.974	0.714 0.733	regression reduced major axis
Interorder ^g	249	—	—	0.960	0.703 0.732	regression reduced major axis
Interorder ^h	309	—	—	0.979	0.760	major axis

NOTE.—The tabled values are based on logarithmically transformed data. When authors did not report descriptive statistics, the reduced-major-axis slope was found as the regression slope divided by the correlation coefficient. BW, body weight (kg); BRW, brain weight (g); SD, standard deviation; r_{xy} , correlation coefficient.

* SOURCES.—*a*, Simulated data; *b*, literature; *c*, Harvey and Clutton-Brock 1985; *d*, Gittleman 1986; *e*, Eisenberg and Wilson 1978; *f*, Bauchot 1978; *g*, Hofman 1982; *h*, Martin 1981.

body size is about $(0.4)^2 = 0.16$, using the within-species estimates from table 1. We examined large data sets from mammals (table 2) to assess actual brain- and body-size variances. In data from 124 primate species (Harvey and Clutton-Brock 1985), the ratio of brain- to body-size variance was 0.63. The same ratio was 0.46 for 113 carnivores (Gittleman 1986). Data on 221 rodents and 69 insectivores from assorted literature sources yielded ratios of 0.27 and 0.48, respectively. Hofman (1982) reported a ratio of brain-size to body-size variance of 0.53 (obtained as the square of the reduced-major-axis slope) for 249 species from 13 mammalian orders. These estimates suggest that the ratio of 0.16 for the error variances is less than the ratio of actual variances, and thus the assumptions of the reduced-major-axis regression also are not met.

The estimates of sampling error allow us to draw the following conclusions. Least-squares regressions consistently underestimate the true slope because of sampling error in body size. Major-axis analysis is influenced most by the variable with the largest variance. The relatively larger amount of sampling variability in

body size than in brain size tends to flatten the bivariate ellipse, thereby reducing the slope. Finally, greater amounts of sampling error in body size than in brain size relative to their respective actual variances tend to increase the denominator of the ratio of the two standard deviations (the formula for the reduced major axis) more than the numerator, thereby decreasing the slope.

This analysis provides the necessary conditions for explaining the taxon-level problem as an artifact: all three techniques commonly employed in allometric analysis can be expected to underestimate the true value of the slope because of error patterns in comparative data. What we have not shown is whether the amount by which they underestimate is largest at the lowest levels and progressively decreases at the higher taxonomic levels. Such a situation is plausible because, at the lowest taxonomic levels—for example, among species within a genus—the proportion of error to true variance is relatively higher than it is among, say, families within an order. At this higher level, actual variance has increased, and sampling-error variance should stay roughly constant; sampling error from lower levels is partially averaged out, but higher-order sampling-error variance components are added. Partial evidence for actual variance increasing faster than sampling-error variance is seen in the increasing correlations at higher taxonomic levels (Martin and Harvey 1985). We now turn to a computer simulation to test this argument.

Simulation of Taxon-Level Problem

We simulated values of brain and body size for 1000 “species.” By assigning these values to an arbitrary taxonomy, we were able to examine whether slopes changed with taxonomic level; slopes for species within genera were compared with slopes calculated for groups within successively higher taxa.

Our simulation model includes only two components of variance in the simulated-species values. One is the variance from the correlated differences in brain and body weight across species. Our model assumes that the variation in true brain and body sizes can be described by a single allometric line with a given slope. We make no assumptions about causality in using this line. That is, the slope of the line is assumed to describe only the empirical relationship between brain and body sizes, not to describe how changes in body size bring about changes in brain size or vice versa. The second variance component is sampling error. We used our estimates of sampling error from table 1 to apply a random amount of error to the true value of each species.

We have not modeled any independent sources of variation in brain or body size (i.e., sources of variance that are independent of the covariation between brain and body size) because so little is known about them. But their effects are predictable. Independent body-size variation, for example, would lower the true slope within a taxon, perhaps even an entire order, but it will not alter the pattern of effects caused by sampling error. The taxon-level effect is seen within orders that have shallower slopes, such as the insectivores and rodents (Martin and Harvey 1985). Our intent is to use the relative amounts of error in brain and body size that we have identified in comparative data to determine whether the general pattern of increasing slopes with taxonomic level could arise.

The simulated values were created as follows. First, we used a uniform random-

number generator to create a vector of 1000 values for body size. (We do not mean to imply that body sizes are uniformly distributed across mammals. However, this makes no difference to the statistics, which are sensitive only to the distribution of errors.) Brain size was calculated as body size raised to the 0.75 power. Taking logarithms of both variables yielded a perfect linear relationship between them with a slope of 0.75. This slope was chosen because it is widely accepted as the value relating brain size to body size in mammals; however, any value could have been chosen. The logarithmically transformed body sizes across the 1000 values were scaled to a mean of 0.54 (kg) with a standard deviation of 0.68. Logarithmically transformed brain-size values were scaled to a mean of 1.47 (g) with a standard deviation of 0.51. These values roughly conform to the patterns and average values within orders for brain size measured in grams and body size measured in kilograms in the eight comparison data sets shown in table 2. The ratio of the two standard deviations is 0.75, within rounding error, which is what it must be to yield a slope of 0.75 when the correlation is perfect.

The second component of variance was the sampling error. We generated two independent, normally distributed error vectors of 1000 observations each. If brain and body sizes were measured on the same individuals, the sampling errors would tend to be correlated. However, it is often true that brain and body weights in comparative data sets are derived from separate sources. The errors were scaled to have means of zero and standard deviations of 0.025 and 0.062, respectively, for the simulated brain and body size. The ratio of the two error values is 0.40, roughly corresponding to the average of the two ratios derived from the intraspecific data sets: one from the entire set, the other deleting the six studies with large standard deviations. The value of 0.062 for body-size error variance is about 1% of the total variance, which roughly conforms to the relationship of body-size error (estimated in table 1) to the total variability in body size in the comparison data sets. Brain-size error was determined from the value for body size to make their ratio 0.40. In using these error values we are assuming that species means for brain and body size in comparative data sets are based on one observation. Many comparative observations are probably based on two to five individuals, which would reduce sampling error by the square root of the sample size. This would reduce the range but not change the pattern of the effects we report below. However, our estimates of error do not include the additional sampling error above the population level.

The brain- and body-size error values were added to the logarithmically transformed “true” values. Adding the random error after taking logarithms of the true values makes the error variance constant throughout the range of true scores.

Analysis of Simulated Phylogeny

The 1000 paired values of brain and body size were assigned to a taxonomy consisting of 100 genera in 20 families and 5 orders. The taxonomy was constructed according to the procedure described below. In all cases, there were 10 species per genus, 5 genera per family, and 4 families per order. We chose these combinations so that all same-level comparisons (e.g., between genera) would be based on the same number of data points.

Before analysis, the data set of 1000 species was ordered by “body weight.”

Because species values in actual data sets tend to overlap from one genus to the next (i.e., not all species in one genus have smaller body weights than all species in the next genus), we did not simply assign to the genera 10 species in order of body weight. Rather, we made the species of successive genera overlap by randomly moving each brain-body pair up or down along the 0.75 brain-body slope. Amounts to be moved were obtained from a normal distribution with a mean of zero and a standard deviation of 0.14. This amount was chosen so that the average within-genus standard deviation in body weight would be about one-fourth of the overall standard deviation of body weight in the entire sample. We arrived at this amount by calculating within-genus standard deviations of body size for over 70 different mammalian genera from data reported in the literature. The average of these standard deviations was approximately one-fourth of the standard deviations for body size in the mammalian data sets reported in table 2.

Moving the species values this way has only a negligible (random) effect on the overall means and standard deviations, and it has no effect on the true slopes within genera, families, or orders. It does increase the estimated slopes within genera by increasing the within-genera variances in body and brain size compared to what they would have been if the overlap had not been added. Other ways of making genera overlap could have been employed. Our method and the amount of overlap seemed reasonable from inspection of the data sets we reported on in table 2. After moving the species by these random amounts, they were returned to their original order (now not ordered by "body weight") and successive groups of 10 were chosen to form genera. From among the genera, successive groups of 5 were chosen to form families. Four successive families made up an order.

Least-squares, major-axis, and reduced-major-axis slopes were then calculated on the species values within each genus, the average of generic points within each family, and average family values within each order. The interorder line was calculated across the five order means.

RESULTS

Across all 1000 species, the squared correlation between the logarithmically transformed brain-size and body-size values was 0.987, indicating that body size accounted for 98.7% of the variance of brain size. The slope of the least-squares regression was 0.742; of the major axis, 0.744; and of the reduced major axis, 0.745. Table 2 reports these values along with results from eight comparison data sets. Although our data set is quite similar to the real data, it has a slightly closer fit to the allometric line. This closer fit may occur because, as we pointed out earlier, real data contain additional sources of independent variation in brain and body size, which we have not modeled. However, in the two data sets most directly comparable to ours (Bauchot 1978; Martin 1981), body size accounts for an average of 95.3% of the variance of brain size, or a mere 3.4% less than in our simulated data. This suggests that we have not overestimated the amount of error in allometric data.

The results of the analyses at successive taxonomic levels are reported in table 3. Despite correlations averaging 0.83 within genera, least-squares slopes at this

TABLE 3

CHANGE OF SLOPE WITH TAXONOMIC LEVEL FOR REGRESSION, MAJOR-AXIS, AND REDUCED-MAJOR-AXIS ESTIMATES OF THE ALLOMETRIC SLOPE

TAXONOMIC LEVEL	NO. OF SUBTAXA	COMMON			
		Correlation	Regression	Major Axis	Reduced Major Axis
Order 1					
Order	4	0.998	0.720	0.721	0.721
Family	5	0.938	0.813	0.864	0.869
Genus	10	0.841	0.579	0.611	0.688
Order 2					
Order	4	0.998	0.723	0.734	0.735
Family	5	0.886	0.596	0.619	0.653
Genus	10	0.909	0.611	0.646	0.671
Order 3					
Order	4	0.999	0.722	0.723	0.723
Family	5	0.913	0.702	0.780	0.784
Genus	10	0.843	0.588	0.640	0.685
Order 4					
Order	4	0.997	0.788	0.790	0.790
Family	5	0.977	0.692	0.703	0.709
Genus	10	0.732	0.492	0.576	0.660
Order 5					
Order	4	0.999	0.739	0.740	0.740
Family	5	0.885	0.561	0.592	0.631
Genus	10	0.825	0.573	0.646	0.692
Interorder	5	0.999	0.749	0.749	0.749

NOTE.—Number of subtaxa indicates that within each simulated order there were four families based on five genera each. Each genus was based on 10 pairs of species values. Thus, the tabled values for genus are averages of 20 interspecific correlations or slopes. The tabled family values are averages of four intergeneric correlations or slopes of five genera each. The order values are based on the four families per order. The average correlation and slope within each taxonomic level is reported for each method as the common slope.

taxonomic level averaged only 0.57. The slopes increase with taxonomic level in each of the simulated orders, and the increase is generally monotonic over the three taxonomic levels. Least-squares slopes averaged 0.67 at the family level with an average correlation of 0.92, and 0.74 based on an average correlation of 0.99 within orders. Each of the methods underestimates the true slope of 0.75. The effect is most pronounced for least squares and least pronounced for reduced major axis. Figure 2 plots the change in slope with taxonomic level, averaged across the five orders.

The reciprocal of the X -on- Y regression slope defines the upper bound of the Y -on- X regression slope (reported in table 3), assuming a perfect correlation between X and Y . In 47% of the genera, 51% of the families, and four of the orders, the upper-bound value was less than 0.75. This shows how one might be misled into concluding that 0.75 is outside the upper bound of possible slopes for a particular data set.

Confidence intervals are a more conservative approach to defining the limits of a regression slope because they take into account the sample size. Confidence

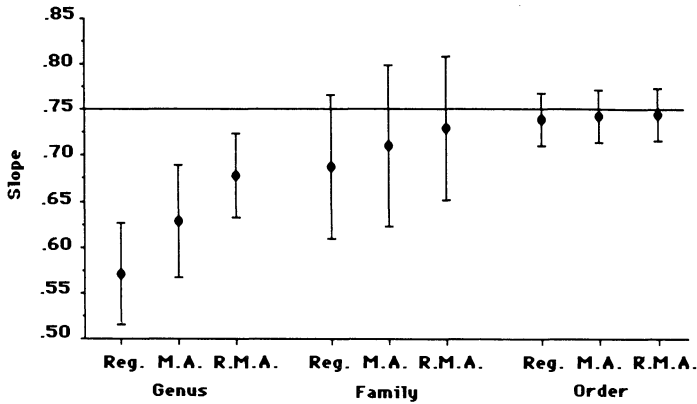


FIG. 2.—Plot of regression (Reg.), major-axis (M.A.), and reduced-major-axis (R.M.A.) estimates of the slope at three taxonomic levels. The plotted values are the averages across orders of the results reported in table 3. The genus values are the average of 100 within-genus slopes, family values are averages of 20 within-family slopes, order values are averages of 5 within-order slopes. Error bars, \pm SE.

intervals are wide because of our small sample sizes. Nevertheless, the 95% confidence intervals for the generic regression slopes do not include 0.75 in about one-third of the genera. The major-axis slopes are more variable. In about one-fifth of the cases, one would conclude that 0.75 was outside the upper 95% confidence bound. The family-level confidence intervals are wide because the family slopes are based on only five genera each. Only one 95% confidence interval excludes 0.75. The family-level confidence intervals would be reduced by approximately two-thirds by doubling the sample size to 10. Similarly, none of the order confidence intervals excludes 0.75.

DISCUSSION

Our simulations show that a regular increase in slope with taxonomic level, similar to that seen in studies of mammalian brain–body-size allometry, can arise as a consequence of error variation alone in comparative data. These results held for each of the three techniques used to estimate allometric lines of best fit. Several authors (Martin 1981; Harvey and Mace 1982; Hofman 1982; Martin and Harvey 1985) have recognized that least-squares regression, which assumes that error is present in only one variable, is inappropriate for most allometric applications. Major-axis analysis and, to a lesser extent, reduced-major-axis analysis have been recommended in its place, since these methods adjust estimates for error in both variates. But because of the distribution of errors in brain–body-size data, the assumptions are not well met for any of the methods.

The pattern of changes in slope with taxonomic level in our simulations is very similar to that reported for real data from a comprehensive study of the allometry of brain size in mammals (Martin and Harvey 1985). But, despite the ability of our simple error model to explain the general pattern of increasing slopes, the results

of our study do not demonstrate that in *all* instances in actual data sets the true slope relating brain size to body size is really 0.75 (or any single value) and that the measured value, should it be less, is just an artifact. We chose the value of 0.75 to simulate because it is generally regarded as the value relating brain size to body size across mammals. Regardless of the true slope, a pattern of increasing slopes, found when lines are fitted across successively higher taxonomic groups, can be produced by the distribution of error variation that we identified in comparative data.

Our results should not be taken to indicate that observed changes in slope with taxonomic level can always be accounted for by sampling error. But, before a regular change in slope with taxonomic level is granted evolutionary significance, it is necessary to test whether it could have arisen from the amounts and distribution of errors we have identified. Slopes fitted among species within genera averaged about 0.17 units less than slopes fitted across families within orders, in our simulations, and similar increases have been found in slopes fitted to real data (Martin and Harvey 1985). Other data sets exhibit more or less change than we have found, depending on the number of species studied and the number of individuals used in deriving estimates of species means. Preliminary work applying our error estimates to real data shows that correcting for error can bring about substantial increases in slope in many instances, whereas in other cases, lower slopes appear correct. Confidence intervals established around slopes at successive taxonomic levels can be used to determine how much change to expect by chance. Despite regular increases in slope with taxonomic level (as found in Martin and Harvey 1985), most confidence intervals include those of the slope estimated at the next level. Alternatively, general linear models that incorporate estimates of error in finding slopes are available (Sprent 1969; Kuhry and Marcus 1977; Rayner 1985).

We did not model influences on brain and body size that are independent of the brain-body-size relationship, since little is known of the magnitude of their influence. But their effects on allometric slopes are predictable. Any factor that, for example, increases variation in body weight among a group of species independent of brain weight decreases the allometric slope. When body weight is controlled for, frugivorous primate species have relatively larger brains than their folivorous relatives (Clutton-Brock and Harvey 1980). Since folivorous species tend to have bigger bodies, the slope relating brain to body size in samples containing species from these two diet groups is relatively shallow. A similar example has been reported in bats (Eisenberg and Wilson 1978). Frugivorous bats have relatively large brains, whereas insectivorous bats have relatively small brain size. However, frugivorous bats have a somewhat larger average body size than insectivorous bats, leading to a steep slope between families from these two diet types. The important point for our simulations is that inclusion of simulated independent influences on brain or body size would not have effected the *pattern* of our results, but rather the true slopes and thus the amount of change in slope resulting from error.

Failure to recognize the ways in which error influences allometric slopes in comparative data can lead to unsound conclusions. Sometimes, shallow slopes are

found with very high correlations, suggesting that steeper slopes can be ruled out. However, unless shallow slopes are expected on theoretical grounds, the sample size is large, or the slope is replicated independently, the result should be treated cautiously, lest one risk unwittingly capitalizing on chance. In our simulated data, there were instances of correlations above 0.90 among species within genera, with slopes of less than 0.50; and for roughly half of the genera and family slopes, one would have been misled into concluding that 0.75 lay outside of the theoretical upper bound of the regression line. A consequence of changing slopes is that intercepts also change. Thus, the pattern of shallow slopes within genera in figure 1 gives rise simultaneously to "grade shifts" or differences in mean elevation among groups. Do our results suggest that all grade shifts are mere artifacts? Certainly not, though they do caution that many apparent grade shifts may be nothing more than the passive consequence of a slope made shallow by error.

One of the major uses of allometry is to employ the allometric line of best fit as a "criterion of subtraction" (Gould 1975). The deviations of brain size from its allometric line with body size can be treated as a new variable from which body size has been removed. Whether a particular value lies above or below the line, or the extent to which it lies above or below the line, depends on the slope of the line. Our results suggest that deviations calculated from slopes determined at lower taxonomic levels are often biased. But deviations from the allometric line fitted across higher taxonomic levels should be less so. Slopes at higher taxonomic levels are also less likely to be influenced by a few diverse taxa having many species. If, however, there is a good theoretical reason to test deviations from a line thought to represent more-recent evolutionary adaptation, or it is thought that differences among higher taxa may be producing an effect independent of brain and body size, then a line fitted at the appropriate taxonomic level should be employed.

Since each of the line-fitting methods we studied showed the taxon-level effect, we cannot offer a simple solution to the problem of estimating the allometric line. Although the reduced-major-axis estimate consistently had the highest slopes, it has two serious drawbacks for routine use, both related to its failure to use any of the covariance information in the data. When the correlation is small, this can lead to erroneous conclusions about the functional relationship between two variables. Gould (1975) gave an example from Bauchot (1972), in which a series of reduced-major-axis lines was calculated and interpreted for data with a sample correlation of zero. The reduced major axis is also sensitive to sources of systematic variance in the data other than those attributable to the two variables. Any systematic factor that increases variance of brain size independent of body size (such as diet or habitat) would directly inflate the reduced-major-axis estimate. All the methods give a similar result when the correlation is high because a high correlation implies little error or other sources of variance in the data. The general linear models mentioned above may hold hope for better estimation (Sprent 1969; Kuhry and Marcus 1977; Rayner 1985), but they require explicit estimates of the amounts and nature of the error in the data.

Finally, at least two other allometric relationships demonstrate changes in slope with taxonomic level (Bennett and Harvey 1985, 1987); brain size and metabolic

rate in birds show taxon-level effects against body size. Research similar to that described here could determine the extent to which these changes may be statistical artifacts.

SUMMARY

The allometric exponent relating brain to body size across diverse selections of mammals is about 0.75, when calculated as the slope of the line of best fit from logarithmically transformed data. However, the slope is known to change with the taxonomic level of analysis; it is lower when only closely related species are compared. For example, slopes are often 0.2–0.5 among species within a genus, but slopes average about 0.66 for families within orders. Evolutionary mechanisms that assume varying patterns of selection acting on brain and body size have been advanced to explain the change in slopes. Although real changes in slope with taxonomic level may occur, we show that the changes observed in real data sets can arise as a statistical artifact, owing to the nature of error variation in the comparative data and to the methods used to estimate slopes. The result holds for regression, major-axis, and reduced-major-axis estimators of the slope. Before applying evolutionary interpretations to observed changes in slope with taxonomic levels, investigators should adjust for the effects of error on estimated slopes.

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