def. of allometry: departure from geometric similarity - constancy in shape w/ change in size (isometry)

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ANALYZING BODY SIZE AS A FACTOR IN ECOLOGY AND EVOLUTION

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INTRODUCTION

An organism's size is perhaps its most apparent characteristic. The recent outpouring of studies on the influence of body size on all aspects of biology and evolution and the extension of the focus of such studies from physiology and functional morphology to ecological characteristics has resulted in a spate of books on the subject (17, 82, 99). As a result, the field of scaling, the study of the influence of body size on form and function, has rather suddenly become a prominent focus in ecology and evolutionary biology. [I prefer Schmidt-Nielsen's (99) term of "scaling" for this field over Gould's (35) "allometry," since the latter refers also to departures from geometric similarity; confusion of the two senses of "allometry" has further complicated an already confused literature.]

Because the study of body size was long relegated to a minor position in biology, standards within the field have tended to be lax and the literature is replete with papers of dubious methodology, analysis, and conclusions. Inappropriate comparison of different types of data is probably the most common error in the scaling literature (e.g. 42, 73); data plots often treat individuals and species as equivalent entities. Less obvious but just as erroneous is the common tendency to equate intraspecific trends with ontogenetic or evolutionary phenomena. In scaling studies, both the level of analysis and the kinds of data included must be carefully chosen if the results are to be meaningful. See Cock (22) for a clear and careful introduction to this topic.

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Allometric Models

The study of scaling is more an empirical than a theoretical science, but a number of attempts have been made to justify the assumption that size per se influences the form and function of organisms. Central to the concept of scaling is the idea of *similarity*—a null model describing the expected change of some variable with change in size. In general, three kinds of similarity can be distinguished:

PHYSICAL SIMILARITY Often scale alone determines the relevant physical variables; as Steven Vogel (personal communication) observed, "Reality is size dependent." Typically the similarity criteria are constancy-of-force ratios such as the familiar Reynolds (inertial/viscous forces) or Froude (inertial/gravitational forces) numbers (see 113). The relative importance of gravity, inertia, viscosity, and surface tension all change with an organism's size; charming qualitative treatments can be found in Boycott (11) and Went (117) and a more quantitative treatment in Vogel (113).

GEOMETRIC SIMILARITY For any series of objects whose linear dimensions differ only by a constant multiplier, surface areas are proportional to some characteristic length squared ($A \propto L^2$), and volumes are proportional to that length cubed ($V \propto L^3$). In biology, constancy in shape with change in size is termed *isometric growth* (or *isometry*), the usual null hypothesis in morphological scaling studies. Departure from geometric similarity is termed *allometry*. Measurement of volume is both inconvenient and imprecise; most scaling studies assume that the density of different organisms is approximately the same and so they substitute mass for volume. There is much confusion in the literature about what constitutes isometry, since the appropriate null model depends on the geometric variables of interest. Isometry is specified by the ratio of the dimensions of the variables; i.e. the expected slope of a plot of log area vs log volume (see below) is $A/V = L^2/L^3 = 2/3$.

FUNCTIONAL SIMILARITY Any pair of functionally related variables that depend on different aspects of the geometry of the object—lengths vs areas, lengths vs volumes, or areas vs volumes—must change as size changes. For example, surface-to-volume ratios (relevant in diffusive transfer, heat loss, and settling velocities) are proportional to $L^2/L^3 = L^{-1}$ and thus will change, given a change in size alone. Most theoretical models which purport to explain empirical scaling results are based on the maintenance of some functionally relevant variable constant over a range of size—often the prediction of a regular distortion of the organisms' geometry to counter the functional changes which would occur under geometric similarity. Functional similarity models underlie most of the scaling literature in ecology and physiology.

The oldest of such models is Sarrus' "surface law of metabolism." The history of the "surface law" is an object lesson in the seductive potential of scaling "laws." Despite the fact that its assumptions were never critically tested and the vast majority of the data was at variance with its predictions, the "surface law" was considered a fact until Kleiber demonstrated that mammalian metabolic rates scaled more nearly as $M^{0.75}$ (99). Discrepancies between the "surface law" and relevant data were glossed over, in large measure because of the satisfyingly "physical" nature of the theory. (Parallels with Lord Kelvin's rejection of Darwinism because physics "proved" the earth could not be old enough for natural selection to have operated are probably not coincidental; see 14.) All theoretical models which purport to predict scaling relations should be subject to careful testing; empirical scaling relations are "noisy," and the desire of biologists for laws of the same power as those in physics is remarkably strong.

Elsewhere (61) I have discussed the general areas of evolutionary and ecological scaling. Here I focus on appropriate methodology for studies of biological scaling and offer three examples of topics drawn from the ecological and evolutionary literature to illustrate the problems common in many of the controversies on scaling.

THE METHODOLOGY OF SCALING STUDIES

Virtually all work in biological scaling assumes a power function of the form $Y = a\,M^b$, Huxley's (47) "simple equation of allometry" where a is the scaling coefficient and b is the scaling exponent. In morphometrics, a power law relation is usually justified by noting that relative growth rates of different components of the organism will follow such a relation (35, 47, 96, 107), but it has also been derived from dimensional analysis and fractal geometry (43). When the variable of interest is an ecological or demographic parameter, such explanations do not seem tenable, but power law models are used in the ecological scaling literature despite the lack of a rationale for their appropriateness. The few attempts at a general justification for a power law relation (e.g. 2, 55) have been unsuccessful. Whether a power law reflects a basic biological truth, the underlying structure of the universe we are embedded in, or whether it is simply fairly robust at approximating a variety of data relations is yet to be determined.

For most of this discussion it will be assumed that a simple power law function applies to most biological scaling problems. This assumption underlies much of the literature on scaling, but for some problems, a curvilinear or bimodal scaling relation may be more appropriate (9; see Figure 1). In extreme cases, much more complex models are required (see (29) for an exemplary model). When scaling relations vary either during ontogeny or

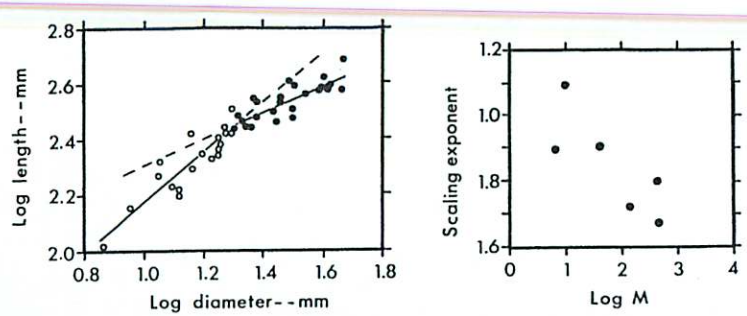

Figure 1 *(left)* Scaling of tibia length against tibia anterio-posterior diameter for bovids. Note that a single scaling relationship does not adequately describe the data across the full size-range studied. *(right)* The RMA scaling exponent for radius length as a function of radius diameter plotted against log median body mass for six families of terrestrial mammals. Note the systematic decline in scaling exponent with increasing body mass. Both figures redrawn from (9).

over a range of body sizes, alternative models should be explored. Examples of complex power law relations and discussions of appropriate statistics to dissect the relations can be found in (9, 19, 96).

Choice of Variables in Scaling Analyses

Virtually any variable can be (and has been) used in a scaling analysis, but not all variables are amenable to the regression analyses usually employed (see below). Care should be taken in the choice of variables. In particular, variables of the form A/B vs B or A vs B, where B is the sum of A plus another variable, should be avoided (4, 23, 52, 87–89, 107) since, if B is some measure of size, the scaling relations will be distorted and the correlation coefficient artificially inflated—a variable is always highly correlated with itself. This point is well made by Prothero (87), who shows that a regression of A/B vs B where A is a series of random numbers can yield correlation coefficients (in a somewhat artificial example) as high as -0.96. This practice is unfortunately all too common in the physiological scaling literature (see 80, 81) and can result in both false confidence in the strength of a relationship and the choice of an inappropriate regression model (see below).

Since biological data are noisy, if the range of size included in a scaling analysis is small (a range of an order of magnitude should be considered *minimal* in ecological studies), the probability is high that the scaling exponent and coefficient will be distorted by sampling error. In evaluating literature values, the study incorporating the larger size range should generally be given greater weight. Prothero (86, 87) recommends that the mass range considered should be reported as the log of the ratio of maximum to minimum size: $pWR = \log(M_{max}/M_{min})$. Such a convention would considerably ease the problem for the reader of estimating the range of size considered, but since

absolute size may also be a biologically important consideration, the value of M_{max} or M_{min} should also be reported.

It is common practice to estimate the scaling of a variable V as a function of body mass M by determining the scaling of the individual components of V (i.e. where $V = C/D$ or $V = C \times D$, determining the scaling of C with M and D with M), and presenting the scaling of V with M by algebraic manipulations of the scaling relations of the component variables. Such procedures are particularly common in the physiological and ecological literature, and they underlie Stahl's (109, 110) allometric cancellation procedure (see 87 and 104 for critiques of this practice). In the ecological scaling literature, Calder's (17) recent book relies particularly heavily on this approach. Such manipulations are valid if and only if the component variables are uncorrelated (116). If the covariance of the component variables is known, applicable correction factors can be found in (59, 116); direct determination of the desired relationship is preferable.

Fitting Data to the Allometric Equation

THE LOG TRANSFORM To estimate scaling coefficients and exponents from raw data, the simple equation of allometry is usually transformed by taking logarithms: $\ln Y = \ln a + b \ln M$. Although this procedure has been criticized (43, 102, 103), it is appropriate in the majority of cases (85) where the focus is "broad allometry" (103).

One rationale for log transforming raw allometric data is to normalize the distribution of the Y variable at any given value of M on the assumption that the values of Y at any given value of M are log-normally distributed (5, 6). This can be seen in a variety of data from both plants and animals (5, 6, 103, 119, 120). According to Harvey (41), interspecific data tend to be log normally distributed, while intraspecific data tend to be normally distributed. The assumption of log normality in the data structure is rarely specifically addressed in scaling studies.

A second rationale for performing a log transform is to equalize the variances of the Y variates across the range of the X variate. A log transform will equalize variances only if the variance of the raw variable is proportional to the square of the mean (13, 62). If the variance is directly proportional to the mean, then a log transform will yield a distribution whose variance is inversely proportional to the mean (13). Again, this consideration is rarely addressed in the scaling literature.

A log transformation introduces a systematic bias into estimates of the value of the scaling coefficient (6, 7, 108, 119). Regression techniques fit a line to the *mean* values of the y variables, but the mean of log transformed variables is the *median* of the original, log-normal distribution. Thus, without

orrection, values for the scaling coefficient (the antilog of the intercept of the egression line) will consistently be biased. The use of nonlinear or iterative east squares techniques to fit data directly to the allometric equation and to void log transformation of the data have been recommended (32, 33, 122, 123), but such techniques have been challenged (69). The simplicity and convenience of regression techniques with log transformed data have made hem the method of choice for most workers. Correcting for bias introduced by a log transformation of the data is simple and routinely applied in forestry (where power law relationships are used to estimate productivity), but it is rarely used in the scaling literature. The correction factor can be conveniently estimated from the standard error of log a (6, 10, 96, 108); this statistic is rarely reported, however, so the correction usually cannot be performed post hoc. Since the magnitude of the correction factor depends on the variance of the log transformed data and thus is unique to each study, published values for scaling coefficients must be viewed as suspect. The magnitude of this variance will depend on whether base e or base 10 logs were used; the nature of the log transform should be routinely reported.

Empirical analyses of the influence of body size on various aspects of morphology, ecology, or behavior are all ultimately dependent on a limited number of statistical techniques. Although a broad variety of statistical models and methods have been used in the past to clarify these relations, not all are equally powerful and some (despite continued popularity) are simply invalid. The critique of Donhoffer (28) is invalid (37, 90, 99)—if appropriate regression techniques are applied, the results are independent of the units involved. For simplicity, bivariate techniques and multivariate techniques are discussed separately.

BIVARIATE TECHNIQUES FOR THE ANALYSIS OF SCALING Although the biases introduced by log transformation of the raw data have been largely ignored in scaling studies, appropriate regression techniques to derive unbiased estimates of log a and the scaling exponent have been the subject of intense debate. The problem is to identify the "true" or "functional" (56) relation between the variables in the face of errors in the variables introduced by statistical noise and measurement errors. The different regression models in statistics differ in their assumptions on the nature of the relationship between variables, their variance structure, and associated errors (63, 71, 89). In the present context, Model I regressions such as ordinary least squares linear (abbreviated OLS regression for the remainder of this discussion) regression techniques assume that: (a) the error term (log ϵ) is normally distributed with a mean of zero and constant variance, (b) the distribution of log Y is normal at each value of log M, (c) the variance of log Y is constant

across the range of log M, and (d) log M is an independent variable, i.e. one whose values are known without error and are set by the investigator (see 105).

Values of M are never determined without error, and in many scaling studies these values are derived indirectly (from other scaling equations or secondary sources); such estimates are likely to have a large error term (see 22; p. 144). Attempts to circumvent this limitation of OLS regression by asserting that "body size is a primary *determinant* of numerous biological characteristics" (53; p. 151) or by recasting the definition of an independent variable as an "assumption in regression analysis of precision in the determination of the independent variable" (76; p. 37, and similar statements in 27, 82, 95) are invalid; neither causal relations or precision of measurement are at issue. The values of M are not set by the investigator; they are determined by the choice of data to be included in the analysis. Because OLS fits a line by minimizing the sum of squares of the residuals of the dependent variable (log Y) only, the "best fit" line will not be an efficient estimator of the functional relationship (56); the problem lies not in the technique, but in the fact that the underlying assumptions have been violated.

In Model II regressions such as major axis (MA) or reduced major axis (RMA) regressions, on the other hand, both variables are assumed to have an associated error term; there is no "independent" variable and the line is fit by minimizing the sum of products of residuals of both log Y and log M. MA and RMA techniques make different assumptions about the error structure and variance relations of the variables. If σ_m^2 is the intrinsic variance of log M, σ_Y^2 is the intrinsic variance of log Y, σ_λ^2 is the error variance of log M, and σ_ϵ^2 is the error variance of log Y, then MA regression techniques assume that

$$\sigma_m^2 + \sigma_\lambda^2 = \sigma_Y^2 + \sigma_\epsilon^2, \qquad 1.$$

while RMA techniques assume that

$$\sigma_\lambda^2/\sigma_m^2 - \sigma_\epsilon^2/\sigma_Y^2 = \text{a constant}. \qquad 2.$$

MA techniques are sensitive to the absolute scale in which the variables are measured and are not robust to rotation of the coordinate axes; RMA techniques are insensitive to scale and rotation (89). OLS, MA, and RMA regressions are all special cases of the "general structural relation" (56, 71, 89), itself a version of canonical variates analysis reduced to two dimensions.

The choice of regression model to use in scaling studies is not a trivial consideration, for the various techniques yield different results. OLS regression consistently yields the lowest values for the scaling exponent, while either RMA or MA may yield the highest value depending on the variance

ucture of the data; the differences between the three techniques decrease as
e correlation coefficient (r) increases.

Some (3, 52, 102) have objected to the use of Model II regressions in aling studies as sacrificing biological relevance to a statistical straitjacket; l, however, seem to misunderstand the techniques and, in particular, the gorous and nonintuitive definitions of dependent and independent variables biometrics. OLS regression is appropriate only when the goal is to describe e data set (in the same sense that a mean is a descriptor of normally stributed data) or to allow prediction of expected values given one of the vo variables. These are rarely the goals of scaling studies.

In general, Model II regressions are to be preferred (46, 48, 57, 60, 63, 71, 9, 93, 100, 105). Of the available techniques, RMA is least sensitive to ssumptions on the error structure in the data and is the least-biased estimate f the underlying functional relation (45, 89, 100). It has the particularly ttractive property that, if the errors are correlated, RMA *is* the functional elation (except when the correlation of the errors is precisely equal to the orrelation of the variables) (89). In a comparison of the efficiency of OLS, MA, and RMA in determining the functional relation in simulated data sets, McArdle (71) found that RMA was always more efficient than MA, and that RMA was more efficient than OLS when significant variation in the variables vas present. Appropriate tests for significance of differences between slopes letermined by RMA or between a slope and an expected value are given by 21, 45), but see (71) for corrections. The variance and standard errors of RMA estimators of the functional relation will be numerically equal to those for OLS regressions (22, 46, 71). Appropriate formulas for confidence intervals are given by (50, 71, 89).

The scaling exponent determined by RMA is equal to the exponent determined by OLS divided by the correlation coefficient (71, 89, 93). (Thus, the particular danger of regressing ratios mentioned above.) Laws & Archie (63) present examples where studies' conclusions are nullified or reversed by use of the appropriate Model II regression methods; further examples appear later in this paper. Effects of this magnitude highlight the importance of the proper choice of regression technique; needless to say, no scaling study has ever demonstrated that the data analyzed met the assumptions of the technique used. (Surprisingly, about 10% of the scaling studies published in the last three years do not even indicate the *type* of regression analysis used.) Readers should be particularly alert for correlations between exponents in scaling studies and their correlation coefficients; low exponents associated with low correlation coefficients should be a red flag warning of an inappropriate regression model.

A MENU FOR SCALING ANALYSES Cock's (22, p. 181) comment that "The standard of reporting and analyzing metrical growth data is still often deplorably low" unfortunately remains true 20 years later. Some conventions on appropriate analysis and reporting of data should be adhered to. Future studies should report characteristics of the data including:

1. the type of data (static, longitudinal, cross-sectional),
2. the range of each variable, their units, and pWR,
3. an estimate of measurement error for each variable,
4. the total sample size, and
5. the intrinsic and error variances for each variable (if available), or the results of the exploratory data analysis procedures recommended by (6). The variance of the errors associated with each variable may be determined in some cases using "instrumental variables" (60, 68, 71).

Descriptions of analysis techniques and results should include:

1. the log transform used (base 10 or base e)
2. confidence intervals for the scaling exponent and coefficient,
3. the standard error of the log transformed coefficient or a value of the coefficient corrected for bias due to a log transform,
4. the regression technique (OLS, MA, RMA) used, and
5. the correlation coefficient.

MULTIVARIATE TECHNIQUES FOR THE ANALYSIS OF SCALING An alternative allometric model was proposed by Jolicoeur (49) for data sets where no independent measure of size was available. The first principal component of the covariance matrix of log transformed data in a principal components analysis (PCA) represents a measure of size internal to the data set (49); the scaling exponents of the n dimensions in the multivariate analysis are equal to the loading of each dimension divided by $n^{-1/2}$. Jolicoeur's proposal has been expanded on (77, 107), and variants of the technique proposed (12, 78). This multivariate approach has been extensively used (e.g. 20, 64, 70, 92) where no independent measure of the size of the animals was available.

Critical tests of the technique have been performed by Jungers & German (54) and Shea (101), using both Jolicoeur's (49) PCA method and conventional regression techniques on bivariate data. According to Jungers & German (54), the size variable derived from PCA was not isometric with actual body mass, although PCA correctly rank ordered the scaling exponents of the variables. By definition, the squares of the coefficients for each dimension in the principal components analysis must average to one (22). The largest coefficient will thus appear to be positively allometric and smaller coefficients will be more negative; inclusion of another dimension *must* change the coefficients for all other variables (54). Reanalysis of Jungers & German's (54) results shows that the relative magnitudes of the PCA coeffi-

cients were very similar to those derived from bivariate regression analyses (24, 44). If the true exponent relating one variable to size can be determined, then the PCA coefficients may be appropriately scaled (101). Without inclusion of a size variable in the analysis or appropriate scaling after the fact, however, the scaling exponents derived from PCA will equal the traditional bivariate-derived exponents only by accident; extreme care should be used when results are taken from the older literature. If a measure of overall size is available, it should be included in the PCA analysis; care should be taken to exclude measures which are not size dependent, since they will grossly distort the analysis. Note that PCA assumes that the variables are linear and multivariate normal; PCA will yield undistorted results only when all covariances are approximately equal (106). An alternative PCA based on the correlation rather than covariance matrix is available (106). It is claimed to remove size from multivariate data more efficiently than Jolicoeur's method but is not so thoroughly explored.

EXAMPLES

The −3/2 Self-thinning "Law" in Plants

Yoda et al (121) proposed that competition in even-aged stands of plants resulted in stunting and mortality such that the average plant mass (m) and density of the stand (number of plants per unit area, N) were related by the power law function $m = kN^{-3/2}$ or $M = kN^{-1/2}$, where M equals the total plant mass per unit area (i.e. mN). The lines described by these functions were proposed to represent an absolute limit; as stands grew, the relation between density and biomass might follow any number of trajectories, but on reaching the limit defined by the above equations, all plant stands were proposed to track along the defined slopes. The "−3/2 law" (also known as the self-thinning rule) was soon applied by plant ecologists and foresters to situations beyond the original formulation, including mixed plant communities (34), ramets of clonal plants (85), marine macroalgae (25), and even phytoplankton in laboratory culture (1). The theoretical basis of the hypothesis as presented by Yoda et al (121) involved trade-offs between light interception and mechanical support. This explanation was soon realized to be flawed, but the self-thinning rule remained popular, and new theoretical developments based on the theory of elastic similarity (73, 74) were proposed (31, 118). [For a full historical development, see (115, 124); for a critique of elastic similarity, see M. LaBarbera, J. E. A. Bertram (unpublished ms)]. The fact that these theoretical explanations could not apply to, e.g. marine macroalgae, was glossed over, as were counterexamples to some of the more extreme applications of the "law" (e.g. 94, 98). White (118, p. 479) stated that "The *empirical* generality of the rule in its original formulation (Yoda et al 1963) is now beyond question . . .," while Harper (cited in 72, p. 234) referred to it as "the first basic law demonstrated for ecology."

The theoretical basis and evidence for the self-thinning rule have been critically reviewed (115, 124). Methodological problems abound. As Weller (115) notes, $M = kN^{-1/2}$ is the correct formulation if regression analysis is to be applied to the problem (as it nearly universally was) since plotting log m vs log N is equivalent to plotting (total plot biomass/number of plants) against (number of plants/total area). Since the number of plants appears in both variables, statistical properties are grossly altered and correlation coefficients artificially inflated. OLS regressions were the norm in these analyses despite the absence of any statistically independent variable, and no correction was made for the log transform despite the importance attached to empirical values of the thinning coefficient k in supporting theoretical expositions (e.g. 31). For a discussion of a (distressing) number of further methodological difficulties, see (115, 124).

Analyzing a total of 488 data sets using PCA to establish the slopes of the log transformed data, Weller (115) concludes that, although there is a clear relationship between stand biomass density and plant density, there is little support for a single rule describing this relationship in all plants. The exponent relating M and N is a function of the plant species and degree of shade tolerance, and different relations appear to apply to interspecific and intraspecific situations. The exponent is not a constant but rather a variable, one describing specific aspects of the plants involved and the biological situation. Using different methods, Zeide (124) comes to the same conclusion; "the law is neither precise nor accurate" (124, p. 532). But self-thinning is an empirical observation; should one conclude that the effects of competition among plants are totally random? In a separate analysis, Weller (114) demonstrates that 50% of the variation in thinning exponents can be explained by empirical scaling relations of shape and biomass allocation for the individual species involved; a significant proportion of the remainder is presumably due to other biological characteristics of the plants such as shade tolerance, moisture requirements, etc. Although plant ecology has apparently lost a "law," it would seem to have acquired a tool in the process–the thinning exponent has the potential of being a useful metric to compare plants in competitive situations, and those biological characteristics that influence its value (growth form, scaling relations, physiological characteristics) can be evaluated to determine their relative importance and to clarify the strategies that plants use in competition. The present situation, if less simple, is more satisfying.

Cope's Law

Cope's Law, the axiom that species within a lineage trend toward larger body size with evolutionary time, has been generally accepted in paleontology and

evolutionary biology (see e.g. 36, 79, 111). Most of the evidence in support of Cope's Law has, however, been anecdotal. Newell (79) outlined evidence that Cope's Law is applicable to some groups of forams, corals, bryozoans, echinoderms, brachiopods, and molluscs, but claimed that size increase in arthropods is rare and virtually nonexistent in most bryozoans, brachiopods, and graptolites. Newell (79) viewed Cope's Law as a potential source of evolutionary novelty and nonadaptive trends (via allometry)—in modern jargon, that Cope's Law might drive macroevolutionary trends. Such an association between small size and morphological novelties in salamanders has been recently documented (39).

Stanley's (111) influential paper argued that Cope's Law is better viewed as evolution *from* small body size rather than *toward* large body size; most higher taxa arise from relatively small, unspecialized ancestors (see Table 1 in 111), while their larger descendants tend to be more specialized (through scaling constraints). That adaptive breakthroughs occur primarily at small body sizes is confirmed by the observed Cambrian faunas; the first bivalves (58, 97) are less than a few millimeters in maximum dimension and the Tommotian-age shelly fauna (8) is characterized by small size.

The generality of Cope's Law or its inverse, dwarfing (evolutionary decrease in body size), are subjects of contention; for a discussion, see (61). Hallam (38) documents persistent trends toward larger size in 41 species or lineages of Jurassic bivalves and 19 of ammonites; 70% of these lineages double in size, and some increase by as much as four times. Chaffee & Lindberg (18) present data for size of 149 molluscan taxa in the Cambrian; maximum size certainly increases (from about 10 to over 50 mm), but it is unclear whether this represents an increase in size within clades of molluscs or simply an increase in the variance in size for molluscs as a group.

The best evidence offered to date to test Cope's Law is MacFadden's (67) restudy of the evolution of horses, one of the "classic cases" of Cope's Law. Body sizes of fossils were estimated from OLS regressions of log body mass vs the log of various osteological characters in the five living species of *Equus* (W_{min} = 27.7 kg; *pWR* = 1.28). Unlike the case of self-thinning in plants, the use of OLS regression in this study is perfectly appropriate; MacFadden's goal was to *predict* the body size of fossil equids from dimensions of the preserved bones. One might question whether MacFadden's confounding of intraspecific and interspecific allometry (use of multiple strains of *Equus caballus*) was appropriate, but the question in this context is not clear cut. [Parenthetically, MacFadden (67) devotes considerable space in this paper to a discussion of the higher coefficients of variation for body mass than for linear dimensions; this is exactly what would be expected (62) given the different dimensionality of these variables.]

Contrary to the common wisdom, 5 of the 24 species lineages that MacFadden (67) studied were characterized by dwarfing rather than an increase in body size, and those lineages that did increase in average size did not do so consistently through their history (Figure 2). Cope's Law in its strictest form does not hold, although size increase is pervasive. It is probably generally true that maximum size in a group tends to increase after the group's origin, but until further studies are published that follow the history of body size in all branches of well-defined clades, the proper form in which Cope's Law should be cast will remain unclear.

Scaling of Home Range and Population Density in Mammals

HOME RANGE McNab (75) was the first to point out that there is a regular scaling of home range size with adult body size in mammals. The scaling exponent he calculated using OLS (b = 0.64) was not significantly different from the scaling exponent of metabolic rate ($\propto M^{0.75}$), and McNab concluded that home range size was determined by metabolic rate. The RMA scaling exponent that I calculate for McNab's (75) data (b = 0.74) is even closer to the scaling exponent for metabolic rate than McNab's original value, but these exponents differ strongly from those in subsequent studies (see Table 1); the quality of the data McNab used must be considered suspect. Harestad & Bunnell (40) found that the home range of herbivores scaled as $M^{1.02}$ (RMA: 1.18), the home range of omnivores scaled as $M^{0.92}$ (RMA: 0.97), and the home range of carnivores scaled as $M^{1.36}$ (RMA: 1.51). Their interpretation—that home range increases more rapidly with size than does metabolic rate, reflecting a declining ability of the habitat to support a population as body size increases—is consistent with the corrected (RMA)

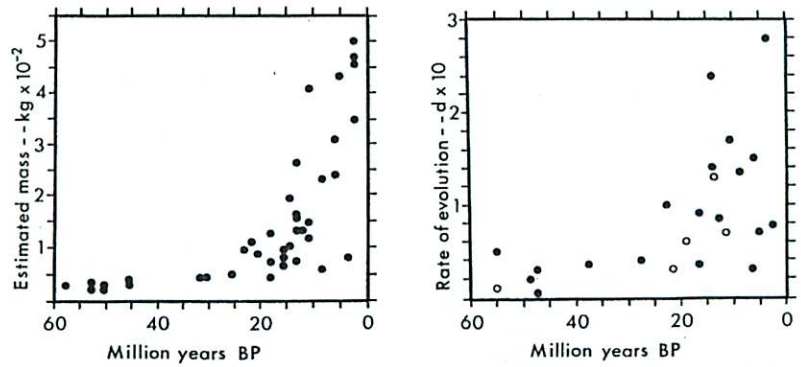

Figure 2 *(left)* Estimated body mass as a function of age for fossil horses. Note that size increase does not occur at a constant rate and does not affect all lineages. *(right)* Rate of evolution of body size change in darwins (*d*) as a function of age for fossil horses. Open circles represent species in ancestor-descendant pairs in which size decreased from the ancestral species. Both figures redrawn from (67).

scaling exponents. Mace et al (66) found lower scaling exponents within rodents: 0.97 for omnivores, 0.81 for herbivores, and 0.88 for granivores (all RMA slopes in the original), but sample sizes were small (3–14 species); these results cannot be statistically distinguished from Harestad & Bunnell's. Lindstedt et al (65) report a scaling exponent of 1.03 (RMA: 1.27) for a smaller sample of carnivores, but the 95% confidence interval that I calculate for the RMA scaling exponent (0.97–1.85) overlaps with the corrected Harestad & Bunnell value. Lindstedt et al (65) report differences in home range scaling between carnivores with habitats above 45° latitude (b = 1.08) and those below 45° (b = 0.94), but these differences disappear when the slopes are recalculated using RMA (1.22 and 1.20, respectively). The various studies of scaling of home range in mammals are summarized in Table 1. To a first approximation home ranges of herbivores scale as $M^{1.2}$, those of carnivores to a higher value, about $M^{1.3}$, and those of omnivores to $M^{1.0}$. For all mammals, home range scales approximately as $M^{1.4}$. Obviously, more data is needed to refine these estimates, but it is remarkable how well published studies agree when the appropriate regression model is applied.

POPULATION DENSITY Damuth (26) found a strong allometry in population density of terrestrial herbivorous mammals inhabiting a variety of habitats worldwide, with the number of animals per square kilometer proportional to $M^{-0.75}$ (RMA: −0.87). Multiplying the scaling relationship for population density times that for individual metabolic rate ($\propto M^{-.75}$ by his calculations), Damuth concluded that secondary production was independent of body size and that no mammalian herbivore species had an energetic advantage over any other on the basis of size alone. Unfortunately RMA yields a higher exponent for the functional relation of popultion density to body mass, thus negating

Table 1 Scaling of home range area with adult body size in terrestrial mammals. The scaling exponent, its standard error (SE), the correlation coefficient (r), the number of species (N) involved, the minimum body mass (W_{min}), and log weight range ratio (pWR) are given for each regression.

	Exponent					W_{min}		
	(OLS)	(RMA)	SE	r	N	(kg)	pWR	Source
Herbivores	1.02	1.18	.11	.87	28	.016	4.41	40
Carnivores	1.36	1.51	.16	.90	20	.005	4.17	40
	1.12	1.34	.20	.84	15	.07	2.90	65[a]
Omnivores	0.92	0.97	.13	.95	7	.016	4.10	40
All	0.65	0.74	.07	.87	26	.005	4.86	75[a]
	1.08	1.39	.12	.77	55	.005	4.96	40
	1.42	1.65	.18	.86	23	.030	3.37	112

[a] Recalculated from the data presented, averaging multiple entires for each species

Damuth's conclusion. (And, of course, adding the exponents for these two relations to get total population energy use is invalid without knowledge of the covariance of the variables.) Peters & Raelson (83) expanded on Damuth's (26) geographic data base, specifically focusing on differences in scaling relations with latitude. They found that a single relationship for all geographic regions was inappropriate; herbivore and carnivore densities differed in their scaling relations in different regions. Recalculating Peters & Raelson's (83) exponents using RMA, however, eliminates all significant differences in exponents. On a global basis, Peters & Raelson (83) found that herbivore density was proportional to $M^{-0.88}$ (RMA: −1.082), and carnivore (including omnivore) density was proportional to $M^{-1.15}$ (RMA: −1.32). For all mammals on a global basis, density was proportional to $M^{-0.86}$ (RMA: −1.09). From these relationships, they concluded that the average biomass per species of herbivore was proportional to $M^{-0.12}$, while that of carnivores was proportional to $M^{-0.15}$ (83); using RMA slopes, these values would be $M^{-0.08}$ and $M^{-0.32}$, respectively. Peters & Raelson repeat Damuth's mistake of adding exponents without knowledge of their covariances, but in a different context. Robinson & Redford's (95) estimate of the scaling of population density to body mass for a very small sample of neotropical herbivores (n = 6; b = −1.33) does not differ significantly from previous estimates even after correction of the slope (RMA: −1.55), nor does their estimate for neotropical mammals in general (b = −0.61; RMA: −0.91). Damuth (27) used a considerably larger data base (n = 467) to address the question of the scaling of population density in terrestrial mammals. His scaling exponent for herbivores, −0.73, is very close to the −0.75 reported in Damuth (26); both values convert to −0.87 using RMA. Damuth's (27) scaling exponent for population density of all mammals (b = −0.78; RMA: −0.98) differs markedly from Robinson & Redford (95), but these differences become insignificant using RMA to calculate the slopes. All of these studies are summarized in Table 2. Using an RMA regression model, the population density of terrestrial herbivores appears to be approximately proportional to $M^{-1.0}$, while carnivores show an apparently higher value, about $M^{-1.1}$. To a first approximation, the population density of mammals, regardless of trophic mode, scales as $M^{-1.0}$. Again, the agreement between published studies when the appropriate regression model is applied is remarkable.

A number of papers have addressed the question of the relation between population density and body size in birds (see 51 for references), but correlation coefficients for log-log regressions have been so low (r^2 = .03 to .27) as to make the exercise of questionable ecological significance.

A large body of literature exists on the scaling of other ecological parameters. For example, Garland (30) discusses the ecological cost of transport, daily movement distances, daily food consumption, etc; Calder (15, 16)

Table 2 Scaling of population density with adult body size in terrestrial mammals. (Conventions as in Table 1.)

	Exponent (OLS)	Exponent (RMA)	SE	r	N	W_{min} (kg)	pWR	Source
Herbivores	−.75	−0.87	.026	−.86	307	0.005	2.43	26
	−.88	−1.08	.035	−.81	108	0.01	5.40	83
	−1.33	−1.55	.39	−.86	6	2.4	1.22	95
	−.73	−0.87	.024	−.84	368	0.005	5.76	27
Carnivores &	−1.15	−1.32	.060	−.87	66	0.004	4.57	83
Omnivores	−.94	−1.11	.117	−.84	28	0.045	3.18	95[a]
Carnivores	−1.03	−1.14	.052	−.90	92	0.004	5.01	27[b]
All	−.86	−1.09	.032	−.79	174	0.004	5.80	83
	−.61	−0.91	.07	−.67	103	0.015	4.30	95
	−.78	−0.98	.027	−.80	467	0.004	5.83	27

[a] Calculated from the pooled "insectivore-omnivore" and "carnivore" categories in (95)
[b] Calculated from the pooled "mammals: insect-eaters" and "mammals: vertebrate-flesh-eaters" categories in (27)

discusses foraging time, efficiency, growth rates, litter size, and r and K selection; Peterson et al (84) discuss the allometry of population cycles. All of these works suffer from inappropriate regression models, addition or subtraction of empirical scaling exponents without knowledge of the covariance of the variables, or both. Swihart et al (112) measure the scaling of "time to independence" in home range use and relate this scaling to "physiological time" (reported as $\propto M^{-1/4}$), but their calculated slopes are all significantly elevated when recalculated as RMA slopes; their conclusions, and similar ones by Lindstedt et al (65) and Reiss (91), are thus highly questionable.

CONCLUSIONS

Some may argue that I have deliberately chosen examples from the literature where statistical conventions were weak and the conclusions thus vulnerable. Let me assure the reader that this is not true; I could have made these points just as well by reanalyzing data from the literature on scaling of production to biomass ratios, intrinsic rate of increase, reproductive effort, skeletal proportions, or (in a different journal) metabolic rates. Some may find it discouraging that many of the controversies in the literature are artifacts of bad statistics. I find it encouraging that reanalysis indicates that there are indeed robust generalities; in some ways this reanalysis is the ultimate in double blind studies, a rarity in any form in the ecological literature.

I do not argue for hegemony in statistical methods—I have no doubt that there are more robust techniques than I have recommended waiting for someone to exploit them. I do urge that all involved abandon practices (such as failing to correct for the bias due to a log transform and use of OLS regressions) that we *know* are inappropriate, and that future studies publish enough statistical information (or better yet, raw data) so that studies do not automatically become irrelevant as better techniques are developed. I freely admit that I have sinned in this regard, but redemption takes only a little thought and a few more keystrokes at the computer.

Scaling studies paint nature with a very broad brush; they are more akin to the gas laws of physics than to Newton's laws. They do not afford much precision in their predictions for individuals or perhaps even species, but the broad view—whether in space or time—is of interest in itself. Properly conducted, scaling studies can be one of our most powerful tools for achieving a broad overview of ecosystems and evolution.

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