

## Toward a science of allometry<sup>1,2</sup>

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What makes a book -- a point of view, the sheer body of information contained therein, a superficial reiteration of the published literature, or a synthesis of knowledge? Although bound as a book, the treatise that Reiss presents does not warrant its hardbound nature. One expects at the least a synthesis of knowledge on allometric scalings (more thoroughly done by Peters, 1983) or a development of new theory (not yet done well by anyone). Neither emerges in this brief discourse; one would like either to improve matters or to forget the subject. Reiss says that allometry is as powerful as Mendelian genetics in interpreting patterns of nature. That may be true, but he fails to justify this belief and, consequently, fails to indicate how a study of allometry can be a science. With his concentration on the manipulations of allometric scalings to predict others, he misses the patterns of adaptations for which the technique is purportedly superior as an analytic tool.

To be an analytic tool, allometric relationships must have a mechanistic base. In genetics, the behavior of genes dictates the rules of inheritance. Most likely, although unfortunately not yet rigorously demonstrated, the morpho-physiology of organisms sets rules for the scaling on body mass, all else being equal, of metabolic rate and many dependent physiological and behavioral functions. Although the exact mechanisms governing the varied observed allometric scalings are controversial, one has to choose one basic law, analogous to independently inherited traits of Mendelian genetics, from which to derive predictions about the dependent physiological or behavioral traits.

Whether truly causal or not, basal metabolic rate is most widely chosen to explain the allometric scalings in other traits. Basal metabolic rate is a logical choice since the energy potential of an organism does dictate how much it can devote to reproduction, how fast it can grow, or how much space it must cover in a particular time interval in order to feed. Given a scaling for basal metabolic rate on body mass, whether this is 0.67, 0.75, or some other value, then the expected scalings for many other physiological, life-history, or behavioral traits are readily derived (e.g., see Maiorana, 1990). Reiss follows this general procedure in this book but he frustratingly uses a range of scaling values to predict values of dependent variables. The spread of the resulting predicted values renders testing them with observed natural patterns essentially impossible. He could have calculated a reasonable average value for the data he surveyed or pointed out that our current knowledge of actual values makes this impossible. As a result, what he has done is merely to provide an outline of how to proceed if we had such values to plug in. The book then is more a procedural guide than substantive science.

Reiss focuses exclusively on deriving a single scaling value (in actuality most often a range) for a particular phenomenon, such as age at maturity or home-range size. This level of analysis has been already well covered in many papers, reviews and books and thus seems repetitious here. What is needed more now are procedures for discovering whether the allometric relations vary among groups and, if they do, whether they make adaptive sense. I have attempted this for life-history traits of a guild of mammals (Maiorana, 1990) with some interesting results. Harvey and his associates have been exploring the existence of variable scalings for mammalian brain size on body mass (e.g., Pagel and Harvey, 1989) and I have done so more widely for terrestrial vertebrates (Maiorana, MS). I found that the relative body mass of the overall most derived lineages within a class influenced the scaling of brain size on body mass: those classes in which the derived subtaxa were small (reptiles, birds and the order Anura) had shallower slopes for the linear regression of log brain size on log body mass (0.61, 0.55, and 0.46, respectively) than did mammals (0.73), in which the most derived lineages are relatively large. Among all of these

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<sup>2</sup>The Allometry of Growth and Reproduction.

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terrestrial vertebrates, the values for the orders did not differ significantly from 0.67. For mammals, at the generic level, herbivorous taxa show lower scalings than nonherbivorous ones. I explain these varied patterns with the simple hypothesis that the scaling of brain mass with body mass follows a surface law, all else being equal. At the class level, historical factors shifted the scaling away from this expected value. If brain size has increased on the average over evolutionary time, more so in the overall more derived lineages, then the relative brain size of these more derived lineages can influence the slope, tilting it higher when they are large or lower when they are small. Genera, in contrast to classes, presumably reflect recent adaptive adjustments to ecological conditions. Taxa with high losses to predation decrease brain size at larger body sizes in order to enhance growth rate with the concomitant decrease in age at maturity and larger litter masses (see Maiorana, 1990).

Presumably every trait that depends directly or indirectly on metabolic rate is expected to show such adaptive variation. It is time to go beyond just reiterating that traits scale allometrically over some wide range. The real challenge and the real science comes in explaining that variation. Unfortunately, this aspect of the science is not easy because it demands large quantities of reliable data. Today, the gathering of raw data on animals in the wild, i.e., natural history, is not quite as prestigious as cutting up genes, but it may ultimately be more important for a true understanding of how animals evolve. A genetic basis for evolution is necessary but not sufficient for understanding the history of life; it fails to explain the patterns of diversity we see. A science of allometry can to a surprising degree do so if done correctly. At the moment most of what we have in the literature is based on scanty data, so when one attempts to get appropriate controls, to make all else equal, one is reduced to samples too small for statistical testing.

A different sort of procedural approach enters in the evaluation of home-range size. Like all patterns, the adequacy of allometric scalings depend on the adequacy of the data base, which is particularly bad in this case. A home range is hard to determine; it is one of the most variable of all traits since it depends on the quality of the particular home range, season, year, sex, age, etc. The obtained scalings reported in the literature may mean absolutely nothing, since they are not well controlled for taxonomic or even geographic location, both of which can influence home-range size appreciably and nonrandomly. Although the data base will always be poor, there are ways to use what meager data exist to test the hypotheses. Damuth (1981) did this in an innovative way. He showed that home-range size does increase disproportionately with body size in a guild of mammals. The explanation can now be pursued on other levels. Yet Reiss dismisses it without much comment and even suggests that it would not apply to carnivorous birds. Yet I believe it probably does. Damuth did not specify a mechanism for greater overlap of home ranges at larger body sizes, but I have done so (Maiorana, in prep.). It seems to apply to mammals, both herbivorous and carnivorous, and there is no reason to suspect that it will not apply to carnivorous birds as well; we just need the right sort of data to test it with birds, particularly more information on daily ranges.

Another poor section involves the question of optimal body size. In essence, this is not an evolutionary question but a morpho-physiological one, dependent on the 'niche' a species occupies, coupled with its basic body plan. But add in a geographic distribution that encompasses a wide range of temperature/moisture regimes or a complex social system, then there may not be a unique size optimum. Add in competitors and phagors, and the problem of defining the optimal size becomes even more difficult. Add in time, and this size may fluctuate as environments alter. As addressed by Reiss, without an ecological context, the question holds little interest. Although the interesting aspects of size diversity are not directly a part of a "science of allometry", those who address the question of "being the right size" hope to find insight into this poorly understood problem. Optimality arguments argue for convergence whereas divergence is a more relevant issue. Being the right size often means being different from one's neighbors in ecospace and time.

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