PROBLEMS OF RELATIVE GROWTH

Julian S. Huxley

with a new introduction by Frederick B. Churchill
and an essay by Richard E. Strauss

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THE STUDY OF ALLOMETRY SINCE HUXLEY
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In looking back on Julian Huxley's work, and in particular on his emphasis on quantitative methods for the study of growth, it is easy to forget that the role of mathematics in biology remained a matter of controversy well into the twentieth century. Though mathematics had become an essential tool in physics and chemistry by the turn of the century, its acceptance by biologists was delayed for many years by a widely held philosophy of vitalism. Karl Pearson, the founder and first editor of the journal *Biometrika*, was both prophetic and optimistic when he said that "the day must come when the biologist will—without being a mathematician—not hesitate to use mathematical analysis when he requires it" (Pearson, 1901). But even as late as 1945, D'Arcy Thompson complained, "The zoologist or morphologist has been slow... to invoke the aid of physical and mathematical sciences... To treat the living body as a mechanism was repugnant, and seemed even ludicrous... Even now the zoologist has scarce begun to dream of defining in mathematical language even the simplest organic forms... In short, he is deeply reluctant to compare the living with the dead, or to explain by geometry or by mechanics the things which have their part in the mystery of life" (Thompson, 1945). It was in this context that quantitatively oriented biologists such as Huxley, Thompson, Minot, Robertson, Brody, and others developed and applied their early quantitative models of organismic size and shape.

The shape of an organism is a fundamental feature of its overall design, and an obvious aspect of the shape of an individual is that it often changes markedly, and in a continuous manner, throughout its ontogeny. Huxley's fundamental deduction about body form was his "law" of the constant differential growth ratio (Huxley, 1924), his finding that "the ratio between the intensity (or relative rate) of growth of the organ and that of the body remains constant over long periods of the animal's life." From this observation followed the principles...
and applications detailed in Problems of Relative Growth and his later publications. Huxley, however, was not the first to make, or even to quantify, the observation that morphological structures show a marked progressive change of relative size with increase in absolute size. As early as 1917, Thompson (1945) noted that all but the simplest organisms attain their adult form by differential growth in different directions. Pezard (1918, 1921) termed these changes heterogonic, while Champy (1924) described them as dysharmonic. Even Huxley's classical power function $Y = bX^k$ (his heterogony formula, now known as the simple allometry formula) had been used earlier (apparently unknown to Huxley) by Snell (1891) and Dubois (1898, 1914, 1918) to determine the cephalization coefficient (ratio of brain weight to body weight) in mammals. Lapicque (1898) and Klatt (1919) applied the same techniques to birds, and Hecht (1913, 1916) and Crozier (1914; Crozier and Hecht, 1914) applied them to fishes. These earlier applications, however, were entirely empirical or were based merely on dimensional analysis (assuming isometry), and Huxley was the first to derive the expression from biological principles of growth and to propose their general application to the dimensions of animals and plants.

Since Huxley's innovation of the allometry concept in the 1920s, a great deal of significant experimental and descriptive research has been added to it, so much more is now known about its physiological basis and general applicability (Brody, 1945; Le Gros Clark et al., 1945; Katz, 1980). Allometric equations are widely used in many biological disciplines to describe systematic changes in morphogenesis, physiology, adaptation, and evolution. Indeed, "allometry is perhaps the major principle regulating basic differences in form among closely related animals" (Gould, 1975).

The Biological Basis of Allometry

Early attitudes about Huxley's allometric model varied between two extremes: considering it to be a fundamental law of organic growth, of sufficient importance to potentially "explain the scale of being" (Quiring, 1941), and considering it to be merely a convenient statistical tool for summarizing data (Clark and Hersh, 1939). Current opinion about Huxley's model still varies, but not as widely. Although some biologists consider it to be a model of convenience (e.g., Smith, 1980), most recognize that it has at least a moderately firm basis in cellular patterns of differential growth (Katz, 1980; Gerhart et al., 1982; Atchley and Hall, 1991).

Huxley's derivation of the bivariate allometric model in Problems of Relative Growth was based explicitly on the process of specific or multiplicative cellular growth (Lumar, 1937; Reeve and Huxley, 1945; Medawar, 1950; Laird, 1965; Perkkiö and Keskinen, 1985). The allometric power function $Y = bX^k$ can be shown to be the solution of the differential equation relating the specific growth rates of two mensural traits $X$ and $Y$ with respect to time (Turner, 1978; Lande, 1985; Shea, 1985):

$$\frac{8Y}{8t} \cdot \log Y = k \frac{8X}{8t} \cdot \log X,$$

or

$$\frac{8Y}{8t} \cdot \frac{1}{Y} = k \frac{8X}{8t} \cdot \frac{1}{X}.$$

Thus, the allometric coefficient $k$ is equal to the ratio of the specific growth rates of $X$ and $Y$ (Reeve and Huxley, 1945); that is, $k$ is an index of the displacement in time of the growth process (or growth curve) of one trait in relation to that of the other trait (Laird et al., 1968). To the extent that the specific rates remain proportional to one another during growth, $k$ remains constant. Nonproportional rates will produce nonlinear bivariate logarithmic plots (i.e., nonloglinear plots), indicating that the allometric coefficient is either a continuous function of age (Creighton and Strauss, 1986; Lebeau et al., 1986) or is multiphasic (Strauss and Fuiman, 1985; Kluge and Strauss, 1985).

Huxley (1932) did note that there were several difficulties in applying his power function to studies of differential growth. Of the two most critical problems, he noted first that allometric coefficients are, at best, merely average values for large regions of the body form. If his concept of a growth gradient is really justified, we should expect a gradual and progressive change in allometric coefficients from point to point along the body. Identification of such gradients is primarily an operational problem, owing to the practical difficulty of finding a sufficient number of distinctive points within a body region among which to take measurements.

The second principal difficulty, and one that is not widely
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appreciated, is that the power function is only an approximate solution to the differential equations of time-dependent growth. Haldane pointed out to Huxley that a sum of parts growing at different rates with respect to body size cannot itself exactly follow an allometric relationship with body size (Reeve and Huxley, 1945). Lande (1985) elucidated the mathematical rationale underlying this statement and provided an expression predicting the amount of nonloglinear curvature in the allometry function resulting from this artifact.

In spite of these difficulties, allometry might have a reasonably sound theoretical basis if tissue growth were always a uniformly multiplicative process, but unfortunately even this is rarely the case. The physiological mechanisms of differential growth are only partly understood, and for certain aspects, such as competition among different structures and specific organ competence in relation to age, the data appear to be partly conflicting (Reeve and Huxley, 1945). In addition, many complex developmental phenomena, such as the de novo deposition of membrane or dermal bone by osteoblasts within the dermis, behave very differently from simple multiplicative growth and yet still seem to conform to the model of simple allometry. Despite these exceptions and theoretical difficulties, Huxley's expression of simple allometry remains the most general and meaningful expression of relative growth.

LEVELS OF ALLOMETRIC SCALING

Although the primary emphasis of Problems of Relative Growth, as its name suggests, was centered on relative changes in body form during ontogeny, there is a surprising amount of empirical evidence that morphological variation among individuals at comparable stages of growth, and even among populations and species, conforms well to the allometric model (Cheverud, 1982; Lande, 1985; Jungers, 1985). Huxley intimated these various levels of variation, but the terminology and the distinctions among them developed later (Cock, 1966; Gould, 1966).

Individual deviations in development, including slight differences in allometric growth gradients among individuals, produce phenotypic variation among individuals within a population. At any particular age or stage of development, Huxley's power function can be used to describe size-dependent variations in body form among individuals, which often conform reasonably well to patterns of loglinear variation. The resulting relationships, if they are described well by the allometric model, are called static allometries to distinguish them from ontogenetic allometries estimated from longitudinal data (measurements taken from the same individuals at several ages) or from variation among separate age groups. The static allometry of adults within a population depends on the variances and covariances of the traits, which can be expressed in terms of their initial values and growth increments (Lande, 1985). Such character associations are often fairly weak (Smith, 1981a) and have no necessary relationship to the average ontogenetic trajectory within a population, except in the biologically trivial case in which all variation among individuals corresponds exactly to different degrees of progression along a common developmental pathway. In fact, static allometric relationships often "cut across" average ontogenetic trajectories.

Although the distinction between ontogenetic and static allometry is important conceptually, in practice the two are often confused and discussed as though they were synonymous. Their analyses have often been assumed to yield similar results (Simpson et al., 1960), but, despite the general positive association often observed between them (Cochard, 1981; Cheverud, 1982; Klingenberg and Zimmermann, 1992), there is no reason to expect them to be perfectly associated. Cock (1966) and Cheverud (1982) have given theoretical and empirical examples of major differences between ontogenetic and static allometry; in fact, their actual values might be quite different even when they are positively correlated (Leamy and Bradley, 1982).

The term evolutionary allometry is used to describe allometric relationships among characters in closely related populations or species. Such covariances often result from secondary adaptations to evolutionary changes in body size (Rensch, 1959; Gould, 1966). Although, in its strict sense, evolutionary allometry refers to character covariances among individuals at corresponding ontogenetic stages in the population or species, the term is often used to describe variation among individuals at mixed stages, particularly when a large proportion of interspecific variation can be accounted for by allometric size variation (e.g., Strauss, 1984, 1985; Houck et al., 1990).

Most studies of evolutionary allometry have investigated the static character covariances among species assumed to be
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closely related (e.g., McKinney and Schoch, 1985; Strauss, 1985). The covariances among sets of species, however, might be very different from those within particular phylogenetic lineages, for at least two reasons: first, because covariances among extant species are insensitive to the directions and temporal sequences of phylogenetic character transformation (Donoghue, 1989; Martins and Garland, 1991); second, because species cannot be treated as independent observations if they are drawn from a common hierarchically structured phylogeny, as any traits held in common may be a result of common ancestry rather than, or in addition to, attainment due to independent adaptation (Felsenstein, 1985). For this reason one might also recognize a more restrictive kind of character covariance, phylogenetic allometry, describing variation within a single evolutionary lineage across time. Phylogenetic allometries can be inferred by parsimoniously “mapping” continuously varying character values onto phylogenetic trees and characterizing their covariances across time (Madison, 1991; Martins and Garland, 1991; Lynch, 1991; Strauss 1992a, 1992b).

Rieppel (1990) suggested that these three levels of allometry are closely interrelated. For example, any evolutionary change in morphology must be reducible at some level to a corresponding change in ontogeny, and the converse is also likely to be true. Evolutionary change also depends on heritable static variation of morphological traits in various ontogenetic stages, produced in turn by ontogenetic variation (Lande, 1979).

APPLICATIONS OF ALLOMETRIC SCALING

The concept of allometric scaling has had applications in three different biological arenas: morphology and morphogenesis, physiology, and ecology.

Morphological Scaling

There have been four interrelated applications of allometry in the study of morphology and morphogenesis (Atchley, 1983): (1) prediction of correlated evolutionary changes from the extrapolation of within-population covariances to interpopulational and interspecific covariances; (2) use as a “criterion of subtraction” (Gould, 1977) to correct for allometric effects in studies of shape differences among species; (3) use as an indication of taxonomic relationships; and (4) use as a tool for evaluating functional relationships.

1. The prediction of correlated evolutionary changes has been a primary application of allometry. As formulated by Gould (1975), the idea is that, if intraspecific allometry represents the correlated variability upon which evolution works, we should be able to determine the allometric rates of change of morphological traits following from changes in body size, if size alone is the object of selection. A caveat to such studies, based on the theory of quantitative genetics, is the demonstration by Lande (1979, 1985) that no necessary correspondence exists between patterns of static phenotypic variation within populations and evolutionary variation, even when selection acts only on body size.

2. Related to the use of allometry as a predictor of morphological change is its use as a parsimonious “null hypothesis” in accounting for observed patterns of variation among individuals. If it can be shown that the relative shapes or sizes of a structure in two or more species conform to an expected allometric dependence on body size, the dependence can then be subsumed in the more general explanation of size variation, and no special explanation (particularly one invoking adaptation) is needed to account for the differences in the structure per se (Gould and Lewontin, 1979; Sweet, 1980; Strauss, 1984). Perhaps the most striking examples are the analyses of antler size in the extinct “Irish elk” (Gould, 1974), and the reconsideration of horn size in titanotheres (McKinney and Schoch, 1985). In contrast, notable departures from otherwise consistent allometric trends may be of particular value in identifying and understanding functional adaptations. White and Gould (1965) and Gould (1971) considered methods for quantifying departures from expected allometry.

3. If the ontogenetic allometric coefficient for some morphological trait is characteristic of a population or species, there is no reason in principle why the coefficient might not be used as a “character” for assessing taxonomic relationships. Strauss (1992b) characterized the larval and juvenile-to-adult growth patterns of several species of pukeilid fishes and examined their utility as phylogenetic characters. While parsimonious trees constructed from larval allometries were congruent with comparable trees based on conventional systematic criteria, trees constructed from juvenile-to-adult allometries were in-
congruent with these, reflecting ecophenotypic convergence in body form rather than phylogenetic relationships. Much more needs to be done to assess the potential for using "dynamic" characteristics, such as ontogenetic allometries, for phylogenetic inference.

4. The application of allometric models for evaluating functional relationships dates in principle at least back to Galileo (Galilei, 1954 edition), who elaborated upon the idea that the dimensions of terrestrial organisms should be dictated by the physical demands of holding up and moving the body against the force of gravity. The analysis of scaling relationships in locomotion has been a particularly active field for the past twenty years (Sleigh, 1974; Wu et al., 1975; Rainey, 1976; Alexander and Goldspink, 1977; Pedley, 1977; Norberg, 1981; Norberg and Rayner, 1987; Biewener, 1983, 1990).

McMahon (1973) first proposed that terrestrial organisms, including both plants and animals, exhibit elastic similarity rather than geometric similarity. Whereas the simple allometric model rather vaguely predicts that body proportions should change in some simple fashion with size in all organisms, McMahon's model concerns terrestrial vertebrates, particularly mammals, which are subject to gravitational forces that affect both posture and locomotion. The model is therefore much more specific, predicting, for example, that the length of weight-bearing elements should vary by the two-thirds power of their diameter. Hence, if the long bones of mammalian limbs are of a constant density across species and comprise a constant fraction of body weight, their lengths and diameters should vary as the one-fourth and three-eighths power of body weight, respectively.

McMahon (1975), Alexander and his colleagues (Alexander, 1977; Maloiy et al., 1979; Alexander et al., 1979), and Biewener (1983) studied such allometric regularities in the limb proportions of mammals. They found that the model of elastic similarity holds very well for the long limb bones of bovids (cattle, antelopes, and their relatives), but that the predictions do not seem to hold nearly as well for the limb bones of other mammalian groups. In fact, Biewener concluded, from his study of thirty-two species of land mammals, that the diameters and lengths of the long bones scale almost as predicted by geometric similarity (or isometry) rather than elastic similarity. Similarly, Prothero (1992) applied an idealized geometric model of mammalian body form (consisting of cylinders of specified length and diameter, representing three body regions: head and trunk, forelimbs, and hindlimbs) to morphometric data on a variety of mammals, and concluded that a model of simple isometry adequately fits the mammalian data over a substantial weight range. It must be kept in mind, however, that isometry in this context is a null hypothesis, which can be falsified but not necessarily corroborated by the data. Because the conclusion of geometric similarity is at odds with a large number of morphometric studies of terrestrial vertebrates demonstrating fine-scale allometric variation within and among species, it may be that the measurement and modeling of gross head, trunk, and limb lengths, across species ranging from mice to elephants, are simply insufficiently resolved.

Physiological Scaling

An extensive literature has developed during the past half-century concerned with the demonstration and analysis of physiological and energetic scaling (Hemmingsen, 1960; Kleiber, 1961; Stahl, 1962, 1967). More recently, biologists have undertaken integrative studies that seek to provide formal, functional explanations for these scaling regularities, particularly in the context of the ecological roles and demands of organisms (Peters, 1983; Calder, 1984; Gittleman, 1985, 1986; Reiss, 1989). A now-classic example is McMahon's demonstration (1973) that the scaling of metabolic rate and the rates of heartbeat and breathing can be derived from criteria of elastic similarity that are characteristic of the locomotor system of terrestrial vertebrates. McMahon's work also emphasizes the importance of dynamic rather than static loading principles in the functional design of the muscular and skeletal systems of tetrapod vertebrates.

Ecological Scaling

As noted above, the allometric power function is the solution of the differential equation relating the specific growth rates of two traits, $X$ and $Y$, with respect to time. By analogy, the same time-dependent equations may describe the growth of populations as well as of morphological traits. Turner (1978; Griffiths and Sandland, 1982) generalized the allometry of relative population growth by modeling it by means of the conservative and non-conservative Lotka-Volterra kinetic equations; he found the fit to the non-conservative model in general to be
relatively better (in relation to the number of parameters in the model) than that for the simple allometric model. Antonelli (1985) showed that Huxley's model holds for logistic growth as well. Such models can be used, for example, to study the allometry of population cycling (Peterson et al., 1984) or the ecological scaling of herbivory with primary productivity (Cyr and Pace, 1993).

STATISTICAL ISSUES AND THE FITTING OF ALLOMETRIC MODELS

There has been a great deal of concern about the uses and abuses of various statistical techniques, because statistical regression procedures are so widely applied in allometric studies and the resulting allometric coefficients are often used for comparing relative growth patterns among different traits or taxonomic groups. Calculating the position of a line of best fit through a scatter of data is subject to at least three critical problems: (1) the use of linear versus non-linear regression methods (and the associated problem of logarithms); (2) assumptions about the "error structure" of the data, which in turn determine the particular form of regression to be used; and (3) the non-independence of points representing individuals or species. The spectrum of choices that need to be made for an empirical study of allometry confronts the biologist with "a confusing plethora of models and options" (German and Meyers, 1989).

Linear versus Non-linear Regression

There is a variety of ways to estimate allometric coefficients (Simpson et al., 1960; Kidwell and Chase, 1967; Manaster and Manaster, 1975; Siem and Saether, 1983), but with very few exceptions studies of bivariate allometry use standard least-squares predictive regression. After conversion of the two variables $X$ and $Y$ to logarithms to linearize Huxley's model, the slope coefficient of $Y$ on $X$ is a direct estimate of $k$. Although typically unimportant in allometric studies, the $Y$ intercept (or an equivalent adjusted mean, adjusted to a value of $X$ other than zero) is often of value in studies of relative shape differences between groups (Bookstein et al., 1985).

There is a significant statistical problem, however, with the fitting of the log-transformed, linearized version of the allometric model, a problem that was pointed out by Zar (1968). The linear regression finds the "best-fitting" line that minimizes the sum of squared deviations (residuals) of the data from it, but the residuals that are minimized are the transformed residuals, not those of the original data. This introduces a systematic bias into the calculations, with the result that the regression may provide only crude estimates of the "true" parameters (including the allometric coefficient), and the approximation is frequently poor. There are two ways in which this bias can be overcome: by using a correction factor to counteract it (Sprugel, 1983) or by using an iterative nonlinear regression procedure to fit a curvilinear function to the original rather than the transformed data. There are three classes of techniques in current use for fitting data to nonlinear functions (Glass, 1969): the Taylor-series expansion method, wherein successive corrections to parameter estimates are made until the solution converges; the gradient methods; and Marquardt's procedure, which combines the best features of the first two techniques. All of these have been used at one time or another in the fitting of allometric models.

The decision whether to use a linear or nonlinear procedure is not a trivial one, and there are criteria other than statistical fit to consider. For example, loglinear models are particularly amenable to descriptive analysis in cases in which the trajectory proves to be irregular or polyphasic. Inflection points, representing potential shifts in allometric growth patterns during development, are much easier to detect with linearized plots than with nonlinear ones. It is often beneficial to use log-linear plots in an exploratory way to examine the structure of the data, followed by "confirmatory" statistical fitting to derive the best possible statistical estimates of the parameters of the model.

Regardless of the method used to fit the allometric model to empirical data, it is worth emphasizing that three kinds of information about the regression procedure are needed: estimates of the parameters; estimates of the uncertainty of the estimates; and a statistical measure of goodness-of-fit. When the third item suggests that the model is an unlikely match to the data, the first two items are probably worthless. Unfortunately, many researchers never proceed beyond the parameter estimates; they deem a fit acceptable if a graph of the data and model "looks good," an approach known sardonically among statisticians as "chi-by-eye."
**Error Structure**

Whether linear or non-linear, the standard least-squares predictive regression models (so-called Type I procedures) assume an “independent” $X$ variable, measured without error, and a “dependent” variable $Y$, subject to sampling “error,” which includes both measurement error and individual biological variability. However, because in morphometric studies $X$ is seldom without measurement error or biological variation, the regression estimate of the allometric coefficient $k$ will be biased downward. The magnitude of this bias is a function of the amount of error in $X$ (Cock, 1966).

Due to this bias, many authors have proposed the use of regression methods that allow for variation in both variables (Type II procedures), such as major-axis regression, reduced major-axis regression, or linear functional regression (Teissier, 1948; Kermack and Haldane, 1950; Ricker, 1973, 1984; Kuhry and Marcus, 1977; Rayner, 1985; Mattfeldt and Mall, 1987; Hofman, 1988; Pagel and Harvey, 1988, 1989; Jolicoeur, 1990; Jolicoeur and Ducharme, 1992; Kimura, 1992). All of these simultaneously minimize the vertical and horizontal deviations from the allometry line, but differ in their assumptions about the relative errors associated with the two variables. Each method assumes a particular value for the ratio of error variances, and an incorrect assumption will cause systematic bias in the corresponding estimate of the slope. The various forms of regression are nearly equivalent when the characters are very highly correlated, as with most ontogenetic data, but can be dissimilar in slope when the characters are only weakly correlated, as for the static allometry, "which is that evolutionary changes occurring in the past are likely to be inherited by present-day descendants. Thus the species within one genus, for example, are more likely to resemble one another than they are to resemble species in other genera, due simply to their common ancestry. Statistically, they do not represent independent data points, which violates an important assumption underlying regression models (as well as most other statistical procedures). In the same way, genera within taxonomic families are likely to be more similar to each other than are genera from different families, and so on. Of course, taxonomic groupings such as genera and families (and even species) can be coarse and arbitrary; but given a phylogenetic tree specifying more refined relationships among species, taxonomic dependence is likely among all branches emanating from a given node.

Felsenstein (1985) provided one possible solution to the problem of taxonomic dependence. Given a phylogenetic tree, differences between sister taxa derived from a common node will have evolved independently of differences elsewhere on the tree. Given a bifurcating tree (with two sister taxa emanating from every node), there will be $n - 1$ independent comparisons, where $n$ is the number of extant species. If the tree is not fully resolved, other solutions are possible (Grafen, 1989; Harvey and Pagel, 1990; Martins and Garland, 1991).

**NON-LOGLINEAR ALLOMETRY**

Despite the wide application of Huxley's model of simple loglinear allometry, a survey of the literature of allometry reveals many examples of bivariate scaling that do not conform to simple allometry. Such exceptions are generally of two kinds: cases of *polyphasic loglinear allometry*, in which ontogenetic trajectories can be divided into loglinear portions representing different portions of the life cycle; and *complex allometry*, in which ontogenetic trajectories are curvilinear on a log-log plot.

**Polyphasic Loglinear Allometry**

The existence of allometric trajectories having two or more loglinear phases was first noted by Huxley (1932) in the relationships between the lengths of the chelae and carapace in fiddler crabs, as well as in the mouthpart dimensions of ants, beetles, and other insects. Many other examples have been described since then in the size-scaling of morphological and physiological data (e.g., Teissier, 1937, 1960; Gould, 1966;
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Phillipson, 1981; Hamburger et al., 1983; Peters, 1983; Schmidt-Nielsen, 1984; Strauss and Fuiman, 1985; Creighton and Strauss, 1986; Guerrant, 1988; Forbes, 1989; Lauder and Reilly, 1990; Reilly and Lauder, 1990; Brooks, 1991; Strauss, 1992b). An early, now-classic example is that of Wilson (1953), who developed a scenario hypothesizing evolutionary pathways in the development of caste polymorphism in ants, wherein diphasic and triphasic patterns represent transitions from monomorphism to caste dimorphism. Many other kinds of non-loglinear developmental trajectories have been described, including those accounting for ontogenetic attainment of sexual dimorphism and for the reorganization of growth patterns in the transition of larval stages to juvenile and adult forms. The inflection points separating the loglinear phases are often associated with such critical developmental periods during ontogeny (Kluge and Strauss, 1985). Various techniques have been proposed for determining the inflection points of polyphasic functions (Somerton, 1980a, 1980b; Forbes and Lopez, 1989).

To determine the extent to which various morphological structures might follow such polyphasic trajectories and lead to expressions of sexual dimorphism in vertebrates, Brooks (1991) formulated a hierarchical set of ontogenetic-trajectory models under the assumption that juveniles, mature females, and mature males each possessed growth patterns that could be characterized by simple allometry, but that attainment of sexual maturity is correlated with “instantaneous” shifts in the pattern of allometric growth. The “null” model is that of simple allometry, in which female and male allometric patterns for some morphological trait are merely extensions of the juvenile pattern; males and females would exhibit sexual dimorphism in this case only if one sex grew to a larger size than the other. A second model describes the case in which one sex continues along the juvenile trajectory, while the other undergoes a shift in allometric growth patterns such that it diverges from the juvenile trajectory. This would typically result in sexual dimorphism even if both sexes grew to the same body size; sexual monomorphism could result only if males and females grew to “compensatory” sizes, exhibiting the same relative size of the trait, that is, the same “shape,” at different body sizes. Three other models are also possible by allowing both males and females to diverge from the juvenile trajectory. The simplest of these results is when males and females diverge in the same way at the same body size. This is a four-parameter description that, like the null model, produces sexual monomorphism unless one sex grows to a larger size. If males and females diverge in different ways at either the same size or different sizes, three loglinear segments are needed to characterize the variation.

The purpose of formulating these alternate descriptive models is to be able to best characterize the ontogenetic allometric pattern for a morphological or physiological trait. This is a statistical problem that can be solved by fitting the various models to a set of data, allowing the point of inflection to be estimated by the data, and deciding which of them best describes the observations (accounting for the number of parameters) in terms of producing the smallest residual variance. Brooks applied these models to test the widely held belief that, in continuously growing vertebrates, sexual dimorphism arises from allometric changes in males at the onset of maturity while females continue along the path set by juvenile growth. In fitting the models on a character-by-character basis to cross-sectional morphometric data for four fish species, however, she found that different character complexes grow in different ways; that divergence from juvenile allometry occurs as frequently in female traits as in male traits; and that elaboration of a trait in one sex does not guarantee that this sex is the one that diverges from the juvenile allometric pattern.

Complex Allometry

It may often be the case (possibly more often than realized) that the allometric coefficient is itself a continuous function of body size, so that an allometric trajectory appears as a curvilinear function on a log-log plot. Laird (1965) and Wingert (1969) observed such patterns of “complex allometry” and attempted to model them using Gompertz and logistic time-dependent growth curves; in both cases they observed satisfactory fit. Turner (1978) and Griffiths and Sandland (1982, 1984) attempted to describe complex allometry based on the Lotka-Volterra equations, and also observed adequate empirical fit. None of these models, however, provides a practical test of the null hypothesis of simple allometry.

Jolicoeur and his co-workers (Lebeau et al., 1986; Jolicoeur and Pirlot, 1988; Jolicoeur, 1989) argued that the Gompertz and logistic models are inadequate for describing morphological growth because both lack flexibility at the upper bound,
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neither is constrained to pass through the origin, and the inflection points of these sigmoid-shaped curves are fixed at arbitrary levels. They instead proposed a modified version of the Pütter-Bertalanffy model, which was originally derived from physiological assumptions about metabolic growth, and from this time-dependent model derived an expression for complex allometry. Jolicoeur (1989) also derived from the Gompertz model a companion expression, which he observed to have better empirical fit to several data sets, and documented a number of cases in which the model of complex allometry provided significantly better fit than that of simple allometry (Dawood et al., 1988; Jolicoeur, 1989; Cabana et al., 1990). The only other application of Jolicoeur’s model was by Strauss and Altig (1991), who failed to find significant evidence of complex allometry in the growth of tadpoles.

MULTIVARIATE ALLOMETRY

Perhaps the single most significant advance in the analysis of allometric variation has been the generalization of Huxley’s bivariate model to one encompassing three or more variables simultaneously. Huxley’s model involves the two idealized metric traits, X and Y. Although X and Y in principle can be any measurable features of an organism, the “independent variable” X is typically chosen to be some measurement that reflects (i.e., is assumed to be a proxy for) the overall size of the body (such as total body length) or of the section of the body being studied (such as cranial length, or total head plus thorax length). In examining the allometry of organ weights, Huxley (1924, 1932) used X to represent total body weight minus the organ weight Y.

A significant problem with such bivariate analyses is that the allometric coefficient is a function of the particular size-variable selected. For example, in studies of human dental allometry the allometric coefficients derived when body mass is used as a measure of body size differ from those obtained when cranial length or skull length is the reference dimension (Smith, 1981b). This is true even when the various size measures are highly correlated with one another. For this reason the selection of an appropriate size variable has been said to be “the fundamental and frequently neglected problem confronting all studies of allometry” (Jugers and German, 1981).

A great deal of energy has been expended in discussions of the appropriate size measures to apply in particular studies or with particular groups of organisms. However, the approach that has generally proven most fruitful has been to use a composite measure of body size, reflecting the average value of a suite of traits measured for each individual. Following Sewell Wright (1932), such a composite measure, when it is discovered from (or fitted to) the data rather than defined a priori, is called general size (although Bookstein [1989] refined the terminology considerably). The use of a general-size measure, which estimates the “robustness” of an organism, is preferable to the use of particular measured traits for at least two reasons (Strauss, 1987): because individual characters are generally statistically “noisier” than composite traits, exhibiting more individual or random variation that is averaged out in the composite; and because any particular character is likely to be allometric with respect to general body size.

Composite traits may be of two kinds: simple (unweighted) sums or averages, or weighted sums or averages. A simple average is merely a special case of a weighted average in which each measured character is weighted equally; if the character is weighted, it is typically weighted by its own value, thus giving more weight to longer than to shorter measurements. A simple average might be an arithmetic mean of the raw mensural data or an arithmetic mean of the log-transformed data. In the latter case it is equivalent to the geometric mean of the raw data, which again gives more weight to longer measurements than to shorter ones. When the mensural data for an individual consist of distances among sets of morphological “landmarks” (specific anatomical points that are assumed to be homologous, or at least comparable, among individuals; Bookstein et al., 1985), a measure of general size that has some desirable statistical properties is the centroid size of Bookstein (1991), the sum of the squared pairwise distances among landmarks.

A significant benefit of all such composite measures is that they can be calculated independently for each individual without considering the rest of the sample (Strauss and Bookstein, 1985). Paradoxically, this is also their primary disadvantage in allometric studies. Because there is no information about allometric variation in the form of a single individual at a single time, the forms of all individuals within a sample or population must be used to characterize relative changes in characters during growth. The desire for a composite measure of body size taking ontogenetic allometry into consideration has been
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satisfied by the application of multivariate statistics (Bookstein, 1989). The primary tools for this purpose are factor analysis, originated by Wright in the 1920s (Wright, 1932, 1954; Teissier, 1955, 1960; Baker, 1954; Hopkins, 1966), and principal component analysis, applied to the characterization of allometric size variation by Jolicoeur (1963a, Jolicoeur and Mosimann, 1960).

The input for each analysis is the same: a matrix containing information about the covariances among all measured variables, values that characterize the associations among variables in terms of the original scale of measurement. (Note that correlations are computed by removing information about scale of measurement, which also removes information about relative rates of change; thus, correlations are not generally useful in allometric studies.) The covariances are calculated using the log-transformed data to linearize any allometric relationships among the variables. The two techniques differ primarily in that factor analysis (in the sense used here) is a “confirmatory” procedure, based on the fitting of an explicit model to the data and invoking various assumptions about the nature of the error components, whereas principal-component analysis is “exploratory,” simply identifying the major patterns of variation within the data. Thus the principal-component approach will correctly identify a size component only when size variation is the major source of morphological variation in the data. Various modifications of principal-component analysis have been suggested over the years to ensure its performance for multiple groups and for specific kinds of data (e.g., Burnaby, 1966; Humphries et al., 1981; Somers, 1986, 1989; Rohlf and Bookstein, 1987; Airdoli and Flury, 1988a, 1988b; Thorpe, 1988).

Regardless of the computational details, there are four important conceptual points about these methods. First, in the multivariate approach, size is viewed as an explanation of the measured data rather than a characteristic of them; as size increases, it “causes” the measurable traits of an organism to become larger together, each at its own allometric rate. In the language of factor analysis, general size is a latent variable that can only be estimated, not observed. Second, the result of either factor analysis or principal-component analysis is a function that is a linear combination of the original measured variables: in other words, a weighted sum that can be calculated for each individual from the coefficients of the function, which are simply the weights for each variable. If the weighted sum were divided by the number of variables, it would be a weighted average. The important point is that the formula providing the weights is not known in advance of the data analysis, but rather is derived from the data. Because the linear combination specifies the position of a straight line or vector through the geometric space defined by the variables, the factor or component is often said to be a size vector. The vector is assumed to account completely for allometric variation, which can be described by the direction of the line. The weighted sum (or average) is a score (or projection) of an individual on this axis, which provides a measure of its general body size. Third, the factor or principal component provides information not only about multivariate size, but also about multivariate allometry. The unscaled coefficients (also called loadings or direction cosines) are regression coefficients, and thus are estimates of the rates of change of individual characters with a change in general size (Leamy and Bradley, 1982; Lande, 1985). For this reason they are often called multivariate allometric coefficients. Fourth, just as there has been much argument about which particular univariate measure might best represent body size in an allometric analysis, there has also been much discussion about the appropriate multivariate measure. In terms of allometric models, the primary point of contention is whether, in studies of shape variation among different groups (such as populations, species, or ecological assemblages), it is desirable for a measure of general size to reflect allometric shape differences (Sprent, 1972; Mosimann, 1970; Mosimann and James, 1979; Humphries et al., 1981; Bookstein et al., 1985; Somers, 1986, 1989; Sundberg, 1989).

An interesting aspect of the application of multivariate allometric coefficients is that the information about relative bivariate growth is not lost among the multivariate coefficients. For any two characters, the ratio of their coefficients is proportional to the coefficient $k$ in Huxley's function (Jolicoeur, 1963b). The pairwise coefficients are simply rescaled by an appropriate constant of proportionality, chosen so that the overall rate of change is defined as isometry (Hills, 1982; Shea, 1985).

There are a number of uses for multivariate allometric vectors, once they have been estimated, and these can be classified into single-group and multiple-group applications. For a single group, it may be of interest to test statistically whether...
the observed vector differs significantly from an idealized vector of isometry. This is the multivariate extension of the test for whether a single bivariate allometric coefficient \( k \) differs from unity, the value corresponding to isometry. Two related tests have been used for this purpose. Asymptotic procedures (i.e., assuming infinitely large sample sizes) for testing hypotheses about the directions of vectors for populations were developed in the mid-1960s (Anderson, 1963) and were the basis of Jolicoeur's (1963b, 1984) tests for allometric data. These are powerful statistical tests but are based on the rather rigorous assumption that the population from which the data have been sampled is distributed according to a multivariate-normal distribution. An alternate procedure is to examine directly the angular deviation between the observed allometry vector and a vector of isometry (Kohn and Atchley, 1988). Bryant and Meffert (1988) developed a fairly robust "bootstrapping" (randomization) procedure to determine indirectly whether the angular deviation is significant.

Procedures similar to those used for single-group tests can be used to determine whether, and to what degree, the multivariate size vectors for two groups differ in orientation (Reymet et al., 1984). This is a very important test, because the assumption of parallel size vectors underlies the various procedures for discovering "size-invariant" or "size-free" shape differences among groups (Burnaby, 1966; Humphries et al., 1981; Rohlf and Bookstein, 1987); if two or more groups differ significantly in their multivariate allometries (i.e., if their multivariate growth patterns are sufficiently different), the shape differences between any two individuals will depend on how large they are.

An important recent application of multivariate allometric size vectors is that used by Zelditch (1987, 1988, 1989) in testing for the existence of "secondary factors" expressing morphological integration during rodent development. Zelditch used a confirmatory factor-analysis procedure to test whether various alternate developmental models, based on embryonic tissue origins or geometric or functional covariances, fit several sets of morphometric growth data any better than the null model of allometric growth. Although she failed to find evidence of such integration, possibly due to low statistical power resulting from small sample sizes, her work has established a context for examining patterns of secondary covariation that should be pursued with other organisms.

Huxley's *Problems of Relative Growth* is a classic work in the best sense of the term: scholarly, insightful, and elegantly written. It can be favorably compared to the influence of Darwin's *Origin of Species* in that many, perhaps most, of the current problems in organismic morphology were suggested or predicated in some way by Huxley.

A great deal of innovative and critical work in relative growth and form has been accomplished in the past sixty years, some of it by Huxley himself after the publication of *Problems of Relative Growth*. This later work has clarified and extended Huxley's basic models of allometry and growth-gradients to much wider arenas, has anchored his descriptive work more firmly in the cellular processes of growth and development, and has extrapolated the allometric model to the realm of multivariate statistics—made practical only with the advent of modern digital computers. Due to the current widespread interest in developmental patterns, however, particularly with regard to heterochronic changes in such patterns over evolutionary time, Huxley's work remains a valuable reference and is cited perhaps as much today as it ever was. *Problems of Relative Growth* demonstrates the persistent problems confronting morphologists as they struggle to explain the tremendous diversity of organic forms.


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