Book Reviews

Issues of Allometry

Size and Scaling in Primate Biology. WILLIAM L. JUNGERS, Ed. Plenum, New York, 1985. xvi, 491 pp., illus. $69.50. Advances in Primatology.

The time is ripe for the publication of a book such as this one. There is a renewed interest in how and why size affects the brain, diet, locomotion, social organization, and growth of human and nonhuman primates. More than half a century has passed since the publication of J. S. Huxley's *Problems of Relative Growth*, yet the subject is far from fully understood even in our own order. The resurgence of interest in part must be credited to the 1977 publication of S. J. Gould's *Ontogeny and Phylogeny*: Gould is by far the most often cited author (and, as one might expect from such prominence, one of the most critically scrutinized as well).

Fleagle sets the tone for this 20-chapter tome by warning the reader to keep a naturalist's perspective. Scaling can become too far removed from real biology, with too much concern for data points and too little focus on the animals themselves. Fleagle's points are so well illustrated that his irresistible drawing of a male gorilla weighing over 100 kilograms holding a 65-gram mouse lemur finds its way onto the cover of the book. A clear example of his point is his scaling of the intermembral index of eight species of New World monkeys, which appears to imply some underlying biomechanical principle, but is also due to the fact that there are some fundamental locomotor differences between the small and the large species (fig. 12).

Fleagle introduces and many of the subsequent authors explore the three varieties of scaling: ontogenetic, intraspecific static adult, and interspecific. Ontogenetic scaling is surely the primary trajectory for future growth of all allometric studies, as Shea perceptively explains. It is transformations in ontogeny that lead to phenotypic differences between species and should be the primary focus for analyses of evolutionary mechanisms. Studies on growth are more scarce, unfortunately, so that only four of the chapters actually deal with the analysis of ontogenetic data. Most of the book is for adults only, either within or among species. Intraspecific allometry is more difficult to interpret, since the difference between small and large adult members of the same species may be merely a measure of sexual dimorphism, a reflection of different heritabilities of features, or even a developmental artifact. Interspecific scaling is the favorite: most of the chapters deal with it, some confined to relatively narrow taxonomic categories and others including the entire order. As Fleagle cautions, the pleasure of those high correlation coefficients in broad allometry carries the risk of blurring real adaptational differences. For example, scaling tooth size across all primates spans insect eaters at the small end and frugivores and folivores at the large end, obscuring differences.

As might be expected from the most encephalized members of the primate order, the scaling of brain weight receives special attention. Lande uses the relationship between brain weight and body weight to explain the quantitative genetics of ontogenetic, intraspecific, and interspecific scaling. The strengths of his model and the weaknesses of others are explored more fully by Wolpoff. Armstrong presents a very useful review of brain-body scaling and especially an explanation of how different parts of the brain relate to size. Martin and Harvey explore the evolutionary reasons for the different brain-body scaling coefficients at different taxonomic levels. They conclude that closely related species have low coefficients because selection is acting primarily on body weight. The scaling coefficients among more distantly related species (within an order or class) reach 0.75, which Martin and Harvey relate to the constraints set by maternal metabolic turnover.

Over a third of the chapters deal with limb proportions and other topics relating to primate locomotion. The primate order has a wonderful array of locomotor varieties including leapers, digitigrade and palmagrade quadrupeds, clawless climbers, arm swingers, and one habitual biped. As Jungers points out, the effort to make sense of this variability spans most of this century. Alexander places the subject in mammalian perspective by comparing limb lengths, limb diameters, and muscle masses in bovids and six primate representatives. The chapter by Jungers is perhaps the most useful in the book, with a valuable table listing wild-shot body weights of 90 primate taxa, a careful review of limb proportions within each family, and much more. Jungers finds a pervasive trend for the intermembral index to increase in size from small to large species, a trend he attributes to the biomechanical requirements of vertical climbing. Ford and Corruccini present an impressive analysis of proportions of eight species of New World monkey, with particular insight into the evolution of dwarfing lineages. Preuschoft and Demes explain why the arms of the brachiating lesser apes are long but not too long. Steudel reviews the problems involved in estimating fossil body weights on the basis of body proportions. Reviewing the energetics of locomotion, Heglund explains why large animals are more efficient and why mode of locomotion has surprisingly little effect on efficiency.

The scaling of tooth size to body weight is explored by several authors. Across the full range of primate species, cheek tooth area scales to body weight with an exponent close to 0.67 (expected for geometric scaling) according to Gingerich and B. H. Smith. Within a human population, Wolpoff finds the coefficient much lower (0.17 to 0.24 with sexes combined), as is expected from the quantitative genetic model developed by Lande (chapter 2). R. J. Smith gives some practical advice to those wishing to estimate body size of fossils from tooth dimensions and illustrates the potentiality for error (for example, a single specimen of *Ramapithecus* could weigh between 15 and 100 kilograms according to the method of narrow allometry).

Martin, Chivers, MacLarnon, and Hladik investigate interspecific scaling of gastrointestinal size and diet by defining the gastrointestinal quotient, which is analogous to the familiar encephalization quotient. Larson presents a wealth of new data on the ontogeny of the internal organs of six species of Old World monkeys to examine the developmental origins of adult intersexual and interspecific size differences. Cochard analyzes the ontogeny of the macaque cranium to explain intersexual differences. Bookstein describes and gives examples of his powerful cephalometric technique. Shea contributes a thoughtful discussion of ontogenic scaling with its implications for adaptive growth, functional cranial analysis, heterochrony, genetics, taxonomy, and evolutionary transformation.

Although most of the book is concerned with scaling of morphological variables, two chapters deal with mating behavior, sexual dimorphism, and body size. Clutton-Brock reviews the changing views concerning why polygynous species tend to have greater sexual dimorphism in body size than monogamous species. Leutenegger and Cheverud find that the variance in an absolute measure of body size dimorphism is explained primarily by the variance due to body weight of the species and only slightly by mating system, diet, habitat, or activity rhythm. Their quantitative genetic analysis reveals that sexual dimorphism can evolve most readily if there is dimorphism in genetic variance rather than dimorphism in selection.

The book contains many controversial views and even some mistakes in analysis and logic. Contradictions from one chapter to the next are common, for example, concerning the appropriateness of the reduced major axis. Some of the mistaken "allometricks" that W. A. Calder III warns against in *Size, Function, and Life History* are repeated. On the whole, however, the book is an excellent addition to the literature on size and its consequences among primates.

HENRY M. MCHENRY
Department of Anthropology, University of California, Davis 95616

Quantum Chemistry

The Quantum Theory of Unimolecular Reactions. H. O. PRITCHARD. Cambridge University Press, New York, 1984. xvi, 175 pp., illus. $49.50.

Intramolecular rate processes are in some sense the simplest molecular transformations, but the detailed theory of these processes involves many conceptual intricacies. The theory of gas-phase unimolecular processes has been under active development since the pre–quantum-mechanical 1920's, but it has recently taken on a new excitement due to the stimulation provided by new laser spectroscopic investigations of intramolecular vibrational relaxation and the search for mode-selective chemistry. The RRKM theory of unimolecular processes (named for Rice, Ramsperger, Kassel, and Marcus) has become widely accepted as an essentially correct framework. This theory treats the phenomenological rate constant as arising from a twofold competition in each microcanonical ensemble of energetically activated molecules between reactive events treated by transition state theory and deactivation processes treated by a strong (or modified strong) collision approximation. This conventional theory and the new insights obtained by the current explosion of interest in the nonlinear mechanics of intramolecular vibrational relaxation are not described in detail in this book, but they inevitably form a background against which many readers will judge it.

Pritchard describes a very attractive alternative to RRKM theory, namely a master equation approach. In this approach one deals in principle with state-to-state processes rather than microcanonical ensembles, although in practice coarse-graining approximations may be used to recover the microcanonical level of description. The basic entity of the master equation approach is the matrix of state-to-state rate constants. Pritchard shows clearly how the phenomenological rate constant is related to an eigenvalue of the rate matrix, and he shows how simple approximations to the reaction rates and energy transfer rates may be used to calculate the basic physical observables on which he concentrates, which are the rate constants for thermal reactions in small molecules and their temperature and pressure dependences.

What are the advantages of the master equation approach? It is a self-contained and general theory formulated in terms of transition rates between discrete states that may consistently be labeled with the most fine-grained information that is available concerning the quantal state. Any approach that tries to deal with mode selectivity will eventually gravitate to something very similar to what Pritchard has described here. State-to-state rate constants provide a more detailed picture of "what is really happening" than do microcanonical rate constants.

What are the disadvantages of the approach? Although we often want to allow for more mode specificity, we know that under most circumstances it is hard to observe, which supports the economical assumption that there is complete statistical mixing in each microcanonical ensemble. The master equation approach allows for the introduction of an almost unlimited number of parameters in the state-to-state rate constants; there is usually not enough information available to pin down all these rate constants. There are several possible responses to this difficulty, including reverting to the terser RRKM prescription or reverting to the simplest possible coarse-grained rate-matrix parametrizations for practical applications to most systems and giving a high priority to research aimed at obtaining the missing information for detailed treatments.

Pritchard makes about as strong a case as is possible for the second response; he has organized the material logically and has succeeded in making the presentation both more coherent and more elegant than the presentations in the original literature. In addition to making a strong case for the second response, he seems to reject the first response as unacceptable. He appears to have two primary reasons. First, he considers the idea of a transition state to be "a crutch" that often leads to "a considerable overelaboration of experimental results" and to which we should "resort" only if there is no other approach available. Second, he considers RRKM theory to suffer from fatal disabilities in that it sometimes predicts volumes of activation smaller than dissociative volume changes at high pressure. Many others, dating back to Wigner, consider a transition state to be a phase space hypersurface upon which one can build a well-defined economical description rather than an overelaborate one, although it is hard to use in a quantum mechanical world. I do not find Pritchard's references to volumes of activation to be an adequate reason to abandon RRKM theory. First of all, the volume of activation refers to a transition state species that is missing one degree of freedom, and it is very dangerous to compare it to real volume changes. Second, recent work aimed at incorporating internal frictional effects into the transition state theory of high-pressure reactions shows promise as a way to extend that kind of theory beyond its original validity limits.

Another problem with Pritchard's arguments against the idea of a transition state is that he errs in assuming that vibrational periods are independent of quantum number, which is true only for harmonic oscillators. On the basis of an argument that involves this error, Pritchard seems to conclude that the potential surface in the vicinity of the reactant's equilibrium geometry is more important than that in the vicinity of the transition state. Here again I disagree.

Of course, one doesn't have to be convinced that the first response is unacceptable in order to appreciate a clear and balanced treatment of the second one. Many of us are willing to use both