



"Man with bilobular goiter. Artists rarely portray goitrous women." [From *A Simple Matter of Salt*; copy out of J. Brown, Jusupe de Ribera, *Prints and Drawings*, 1973]

dez begins her volume by posing this strange historical fact as a problem regarding iodine-deficiency disorders that have been endemic in the Cantabrian Mountain villages of Asturias.

Fernandez found that in the 1920s a highly influential Spanish physician, Gregorio Marañón, had deliberated over goiter prevention through the use of iodized salt but preferred the more ambitious approach of improving economic conditions of the poor nationwide. If implemented, his approach would have eliminated many specific nutritional deficiencies and other health problems, and Fernandez's findings about differences in the incidence of goiter according to socioeconomic level imply that it too would have been reduced. Neither strategy was adopted, however, and ensuing political developments prevented reconsideration until recently. In the Franco period, health administrators defined the problem of goiter as genetic (the result of inbreeding) and therefore not subject to public health measures, despite some opposition within the Spanish medical profession. Fernandez carefully documents the weakness of the genetic hypothesis with her own data and provides convincing evidence of the role of diet in the mountain communities. She points out, moreover, that shipments to the region of expensive medical technology from the United States to diagnose iodine-deficiency disorders were not accompanied by information on less costly preventive measures. The villagers themselves were concerned about the disorders but were unaware that

such measures existed, despite good access to medical care throughout the century. Finally, after Franco's death, the problem was officially addressed by regional prophylaxis in 1984.

Incorporating both policy analysis and reflective ethnography, *A Simple Matter of Salt* complements work by a number of other anthropologists concerned with health issues, especially L. S. Greene's analysis of endemic goiter in Ecuador (in *Malnutrition, Behavior, and Social Organization*, Academic Press, 1977). As have Latin American anthropologists, Fernandez emphasizes history as crucial on many levels, and she analyzes genealogies spanning seven generations to explore kinship, marriage, genetics, and land tenure. She also explores the cultural ramifications of the disease, contrasting an Asturian saying that one without goiter is not beautiful with the derogatory terms used to characterize those so afflicted and the concern on the part of the inhabitants of the afflicted villages with the disrepute in which they are held by outsiders.

Malnutrition is a phenomenon that has absorbed a great deal of attention, time, and money in recent decades, yet it continues to exist. The analysis by Fernandez is crucial to understanding why. The iodine-deficiency disorders that have been endemic in this part of northern Spain cannot be ascribed simply to underdevelopment, for the region is advanced in education, access to medical care, and connections to outside markets. Instead, these disorders can be characterized as diseases of political miscarriage and maldistribution of medical knowledge, as well as of regional prejudice and poverty. This work represents a new standard in studies of nutritional deficiencies on the community level and will receive wide attention.

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Evolutionary Disentanglement

The Comparative Method in Evolutionary Biology. PAUL H. HARVEY and MARK D. PAGEL. Oxford University Press, New York, 1991. vii, 239 pp., illus. \$70; paper, \$24.95. Oxford Series in Ecology and Evolution, 1.

The natural world displays a bewildering variety of organisms that appear uniquely adapted to a myriad of environmental conditions. In seeking to disentangle the basis for this diversity, evolutionary biologists commonly draw comparisons among taxa to formulate or test hypotheses. Yet the conclusions generated from comparative analy-

ses have often been weakened by their dependence on mere correlation and by the implicit assumption that phenotypic traits are molded and optimized by extrinsic selective forces arising within an environment. Two species exhibiting striking similarity in phenotype and occurring in matching environments would be interpreted to represent an equivalent response to a common selection factor, and few studies tested for the effects of other factors that could explain variation in the phenotype. Beginning in the late 1970s, Paul Harvey and associates published several widely cited papers that demonstrated the importance of history in explaining patterns of variation in several phenotypic traits among cross-taxa comparisons. These and other papers led evolutionary biologists to recognize the necessity of incorporating phylogenetic information in comparative studies. This reawakening to the importance of history has generated a confounding array of statistical and methodological procedures, and ecologists and evolutionary biologists now face analytical and methodological options that were not always dealt with in their training.

The Comparative Method in Evolutionary Biology, in offering a broad review of the field that places the various procedures into a evolutionary and statistical context, is thus timely. Largely an expanded version of several recent review articles by the authors, it presents a clear and concise account of the major advances forming the "new comparative method."

Harvey and Pagel begin with an overview of the comparative approach and espouse the need for a phylogenetic perspective in the study of adaptation. Appropriate comparisons may demonstrate previously unknown relationships among sets of traits and, when properly conducted, test hypotheses regarding their adaptive significance. Several classic examples are discussed to reinforce these points. Most comparative studies perform contrasts across a wide range of taxa that differ to some degree in a phenotypic trait (generation time, for example). Significant covariation between the trait and an environmental feature should indicate adaptive evolution. Herein, argue Harvey and Pagel, lies the weakness of the comparative method, which is part statistical and part conceptual. The varying degrees of relatedness preclude the use of species as independent data points and therefore inflate the true number of degrees of freedom; other assumptions of many common statistical procedures are also violated. The evolutionary biologist also faces a problem involving the appropriate method for disentangling the extent to which an observed association is a manifestation of

shared ancestry among rather than of independent evolution. Harvey and Pagel point out that explicitly incorporating a phylogeny in the analysis resolves these issues in several ways. First, an objective definition of adaptation is apparent by comparing ancestor-descendant pairs, namely an apomorphy ("derived character") that evolved in response to a particular selective agent. Second, identification of appropriate "control" and "experimental" groups for comparison is straightforward. Finally, including a phylogeny provides an alternative hypothesis (nonadaptation) for the comparative analysis. Further refinements for assessing the influence of history in the evolution of a trait are also available. Harvey and Pagel show that one group of analyses may infer the direction and rate of evolutionary change by characterizing trends along branches. Another set compares values across species to assess the concordance of variation in a trait with phylogenetic relatedness. In Harvey and Pagel's view, the role of comparative studies involves partitioning "the independent origin of character states" from "identity by common descent."

The next two chapters review in some detail the importance of understanding the influence of phylogenetic similarity among taxa and the methods used to estimate phylogenetic relationships. In chapter 2, Harvey and Pagel provide a clear discussion of the confounding influence of phylogenetic relatedness in interpreting patterns of adaptive variation in comparative studies. Ostensibly, variation in a character state that correlates more closely with phylogenetic relationships than with, say, environmental factors may be interpreted as evidence for phylogenetic effects. Yet there are many paths by which organisms may exhibit phenotypic similarity through phylogenetic relatedness, and terms such as "phylogenetic effect" and "phylogenetic constraint," which are increasingly used in comparative studies, remain vague. Harvey and Pagel posit three biological processes that may yield a phylogenetic effect: phylogenetic niche conservatism, phylogenetic time lags, and differential adaptive responses. The last category includes different responses to similar environmental factors, different responses to similar selective forces, and developmental constraints. Because each process poses unique problems for comparative studies, the authors conclude that the influence of each must be assessed.

Given the prerequisite of a phylogeny, Harvey and Pagel next discuss criteria for obtaining reliable estimates of both phylogenetic trees and ancestral character states. They conclude that only phylogenetic hypotheses embodied in a cladogram are suit-

able for subsequent comparisons. Furthermore, they suggest that maximum likelihood procedures or cladistic analyses based on parsimony and compatibility criteria are likely to arrive at the best approximation to the true relationships among taxa. Their brief discussion should prove valuable for individuals who are unfamiliar with the principles of phylogenetic systematics. Additional matters relevant to the construction of phylogenetic trees are also expounded, such as the use of molecular data, including models of molecular evolution; rooting of trees; and the incompleteness of some trees. Methods for determining ancestral character states for a specific branching structure are also reviewed. A major point implicit in this chapter is that all biologists must be cognizant of the methods and assumptions involved in producing cladograms. It should be emphasized that phylogenetic trees are hypotheses regarding evolutionary relationships and a degree of uncertainty exists with respect to the branching sequences. As these relationships are refined, the tree may be modified, with a concomitant change in the results of comparative analysis.

Chapters 4 and 5 are the heart of the book, for here Harvey and Pagel outline and elaborate on the analytical procedures available for testing hypotheses of character evolution based on discrete and on continuous characters. Each chapter begins with a discussion of the nonindependence of data points and the likely evolutionary scenario through which it occurs. Throughout these chapters Harvey and Pagel stress two key points: that different models and rates of evolution may lead to different patterns of phylogenetic similarity and that standard statistical procedures must be modified to accommodate the nonindependence of data points, particularly with respect to degrees of freedom and the probability levels for the associated test statistic.

Harvey and Pagel review three methods for performing comparative tests using categorical data when a phylogenetic tree is available. All involve tallying the number of independent character-state transitions within a branch of a phylogeny without regard to changes in other branches. The first method tests the hypothesis that change in one character, say lekking in birds, is independent of another, for example sexual dimorphism in body size, by a chi-square statistic. Harvey and Pagel demonstrate that this method may be enhanced by including a test for directionality of evolutionary change in discrete characters—that is, does change in one character affect the likelihood of change in another? Harvey and Pagel's major contribution is a previously unpublished statistical model that incorporates informa-

tion about branch lengths to calculate standardized scores, based on transition probabilities of character state change, that may be used in subsequent analyses, such as rank correlation tests. This is their preferred method. Its utility, however, depends upon the availability of both a cladogram and estimates of branch lengths (time since divergence from a common ancestor). A comparison of the methods reveals that the general statistical model with its use of branch length information achieves higher resolution of the correlation between two variables given a phylogeny. Nevertheless, the authors show that the previous methods form special cases of their general statistical model.

Many other comparative procedures have been proposed for the analysis of continuous characters. All attempt to estimate the association between two traits, for example body size and age at maturity, after removing the correlated influence of phylogeny. Chapter 5 sketches the essential characteristics and assumptions of nine such methods; arranged in order of perceived ability to disentangle the effects of phylogeny in testing adaptive hypotheses. The goal of these analyses is to remove the variation in a trait attributable to phylogeny and perform subsequent tests on the residual variation. As Harvey and Pagel show, most are rooted in nested analysis-of-variance or regression models and invariably employ a taxonomic classification as an estimate of phylogenetic relatedness. In the absence of a cladogram, these methods are often a useful first approximation to assess the appropriate taxonomic level for subsequent comparisons. Additional methods are examined that have the flexibility to use either taxonomic or phylogenetic information. Harvey and Pagel prefer the method of pairwise independent comparisons, and the most space is given to this technique. Independent comparisons directly relate all the information contained in the cladogram to test for the correlated evolution of two or more traits; several variants of this method are presented that include options for incompletely resolved phylogenies. Although the authors take care to explain the assumptions underlying each of the analyses as well as their weaknesses, little emphasis is placed on the heavy reliance of this method on the estimates of ancestral character states. These are point estimates and have an associated degree of uncertainty. How does one control for this uncertainty in a comparative analysis? After reading this chapter a biologist may have a better understanding of the methods but still lack information about the appropriate procedure. The chapter could have been strengthened by comparing the performance of each meth-

od on the same data set.

Harvey and Pagel complete their survey of comparative methods by demonstrating how the incorporation of phylogenetic information can reveal the selective basis underlying the functional relationship between two variables. Here they grapple with allometry: the regular change in one trait with a change in body size. After a lucid description of allometric relations and fitting allometric equations, Harvey and Pagel strive to demonstrate that the analysis of allometry is extended from a purely descriptive endeavor to one of elaborating the putative functional bases for the observed relationship.

These are exciting times in comparative biology. In just one year we have seen the publication of two books, Brooks and McLennan's *Phylogeny, Ecology and Behavior* and now Harvey and Pagel's work, that set forth a phylogenetic approach to the study of adaptation and evolutionary biology. The two complement one another, the former underscoring the contribution of phylogenetic systematics to understanding the influence of history to recent developments in ecology and ethology and the latter emphasizing the statistics of comparative analyses. Use of phylogenetic relationships among species in comparative analyses has invigorated the field. Harvey and Pagel's compelling survey of the powerful analytical techniques currently available for the study of adaptation in a phylogenetic context provides the basis for new and deeper insights into the of origin and maintenance of organic diversity.

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Recent Books on Instrumentation and Techniques

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