BOOK REVIEWS

Comparatively better

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The Explanation of Organic Diversity: The Comparative Method and Adaptions for Mating.
By Mark Ridley.
Clarendon: 1983. Pp.272. £19, $37.50.

THE use of cross-species comparisons to evaluate evolutionary patterns has been growing rapidly in recent years. And, as being explicit and numerical has become more respectable among systematists, interest in understanding the logical and statistical pitfalls of the comparative method has also increased. In *The Explanation of Organic Diversity*, Mark Ridley outlines a comparative method that is intended to take correct account of phylogeny. He illustrates its use by examining the distribution of two phenomena: precopulatory mate-guarding in arthropods and anurans, and assortative mating for size in a variety of phyla.

The first 41 pages of the monograph will attract the widest attention. Here Ridley presents a critique of previous approaches and an explanation of his own method. Previous workers have often engaged in statistical tests of association between a phenotype and an environment, using individual species as the data points. The problem with this practice is that the statistical tests presume that the species are independent, whereas they in fact are found in non-independent clusters in a hierarchical phylogeny. This clustering creates meaningless correlations: we may find that all bird species living on mountaintops have long tails, but fail to notice that they are a group of close relatives, and that the long tails were acquired only once, in their common ancestor.

Ridley joins the ranks of those — such as Clutton-Brock, Harvey, Baker and Parker — who are alarmed by the possibilities for statistical bias in using species as if they were independent entities. The method he proposes involves finding or constructing a phylogeny for the group under study and then, by minimizing the number of times that an independent origin must be assumed, inferring those points at which the phenotype has arisen independently. These independent occurrences are then taken as the individual instances in constructing a contingency table relating the phenotype to the state of the environment.

Although this method, also previously used by John Gittleman, is immeasurably superior to previous practice, it does not completely exorcize the statistical problems. In assigning positions of changes by minimizing the amount of change (a criterion that has acquired the unfortunate name of "parsimony", though Ridley mercifully avoids the term), one does not achieve an error-free assignment. If, for example, two sister lineages A and B both have their phenotype in a derived state P and both exist in environment E, we minimize the number of independent origins of P by assuming that it arose once, in the ancestor of A and B, which we assume also to have been in environment E. In truth, P may have arisen separately in the two lineages which themselves may or may not have entered environment E separately. The placements of changes in the phylogeny are thus subject to error, so that there is more statistical uncertainty than Ridley's test implies. I cannot persuade myself that the test is always conservative. In treating the inferences of placements of changes as if they were observations, Ridley's test does not entirely achieve statistical respectability even though it is a considerable step in that direction.

The monograph is written with clarity, considerable wit and a lack of false modesty. Without muddying the waters, Ridley is able to refute most of the arguments of those who criticize the comparative method. I was particularly relieved to see that, although declaring his method to be "cladism", he was able clearly to distinguish classification from phylogeny, something few systematists do. Cladism, which is always being confused with completely unrelated doctrines such as punctuationalism or even Marxism, is genuinely ambiguous on one point: whether it is a position on classification or a set of methods for inferring evolutionary history. Ridley uses Hennig's methods in the latter sense, explicitly disavowing any intention of taking a position on methods of classification. His dismissal of phylogenetic inertia is much less satisfying, however. The mysterious declaration that his methods could not cope with this inertia, coupled with his apparent lack of concern over such a state of affairs, leave me with the impression that I am in the presence of the truest of panselectionists.

The bulk of the monograph is a detailed examination of precopula and of assortative mating by size. For each of these a prediction is tested, using his methods, and the data and method are presented clearly. Ridley is frequently forced to use existing classifications as if they were phylogenies, but unlike many authors he is aware of the limitations of this practice.

If Ridley's monograph is able to persuade comparative biologists to abandon counting species as though they represented independent evolutionary events, it will have done noble work. But it would be unfortunate if Ridley's clarity and persuasiveness caused his methods to be taken as the last word on the statistical analysis of comparative data. ☐

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