

absence of viviparity or at least egg-retention in birds. And what drives research if not challenging mysteries? Moreover, the borderline between inventing adaptive stories and proposing hypotheses to generate testable predictions is not sharp.

The book presents new ideas at the research frontier, which is one of its many merits. For instance, Clutton-Brock argues that the potential reproductive rate determines which sex competes for access to the other sex, implying that if male potential reproductive rate is lower than female potential reproductive rate, females will compete for males'. What, then, is 'potential' reproductive rate?

'Potential' suggests something that is not realized due to constraints, but what exactly is that something? Access to mates and food supposedly should not constrain reproduction, but what about mating patterns such as monogamy: should an 'innate' reluctance or inability to mate with more than one partner count as a constraint?

The concluding chapter attempts to answer the five initial questions, or at least to point out current theoretical and practical difficulties in doing so. For take-home messages, this is a brilliant chapter. It ends with prospects for further theoretical and practical areas of research, as well as

some suggestions as to what we should avoid doing! I found Clutton-Brock's book stimulating and thought provoking, and strongly recommend it to anyone interested in breeding systems in general and parental care in particular.

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#### Reference

1 Clutton-Brock, T.H. and Vincent, A.C.J. (1991) *Nature* 351, 58-60

## Avoiding Phylogenetic Bias

### The Comparative Method in Evolutionary Biology

by P.H. Harvey, and M.D. Pagel, *Oxford University Press (Oxford Series in Ecology and Evolution, Vol. 1), 1991. £12.50 pbk (viii + 239 pages) ISBN 0 19 854640 8*

*Tell us how to reconstruct the past and we shall perform the comparative analysis with precision.*

With this sentence, Paul Harvey and Mark Pagel conclude their thought-provoking book. Whether or not the humor was intentional, it is a pithy and sardonic epigram on the dilemma facing research on adaptation. If only the True Cladogram of Life was at hand! Like a tiny, missing component without which a splendid race car will not run, this small absence stalls mighty ambitions. Why this is so should be obvious by now: if the reconstruction of evolutionary history is badly wrong, working on how that erroneous reconstruction 'happened' is pointless. Recognizing this, Harvey and Pagel emphasize that 'the key to comparative analyses depends on understanding the phylogenetic relationships among the sample of species being considered', but they are also eager to get to work, eager to use whatever 'phylogeny' is available.

Because their subject depends so crucially on correct phylogenies, the authors probably felt compelled to devote one chapter to a précis of systematics. Of course, an unbiased summary of so complex a subject in so small a space is probably impossible. However, the reader should read widely in the systematic literature before following the advice

given here on phylogeny inference. Neither author is experienced in producing phylogenies, and it shows in their uneven treatment of the issues involved, and in their reliance on a narrow spectrum of secondary sources. They seem oddly infatuated with DNA-hybridization data, but don't elucidate clearly the fundamental assumptions and problems with this essentially phenetic method. They leap nimbly over the non-additivity of genetic-distance data, the failure of the molecular-clock hypothesis, and are, on the whole, not skeptical enough of the highly peculiar results that often emanate from molecular data. They mention that maximum-likelihood techniques require simplistic and probably unrealistic assumptions about the evolutionary process, and that its estimation procedures are thus far unworkable for data sets of even moderate size, but cheerfully anoint it as the wave of the future. On the other hand, the methods actually in use by phylogenetic systematists (whose results, after all, are those on which most 'comparative' biology will rest) receive little mention or exegesis. For example, throughout the book they cite with approval studies that directly convert linnean classifications into phylogenies, even though such a procedure is perhaps the ultimate, damning evidence of uncritical work.

But systematics is not the focus of the book, and the authors, as consumers rather than practitioners, should be forgiven much. Indeed, the main point of the book, that history is crucial and essential in evolutionary biology, cannot be overstated. The authors deserve much credit for accepting and applying this long-ignored truth.

The main goal is to test explanations of convergent evolution; the more instances of convergence the better, and the stronger the test. In most examples cited, the scope of convergent events is limited to a single monophyletic group. This limitation suggests the possibility that devotees of the historical approach may be vulnerable to their own most cogent criticism - phylogenetic bias. A good example is Höglund's study of the association between lekking and sexual dimorphism in birds (as reported in this volume). If the comparison is limited to grouse and pheasants (Tetraonidae), a significant association is found. But if the data set is expanded to the 114 bird species for which Höglund had data, the significance disappears. How then to delimit such a data set objectively and naturally? If the hypothesis under test is the association between lekking and sexual dimorphism *per se* (as it must be if each instance is treated as an independent evolutionary event), then arguably the study should sample at random any taxa that lek and any taxa that are dimorphic (e.g. flies, frogs, etc.), not just one clade of birds that supports the hypothesis. Omitting other taxa amounts to a curious contradiction: statistical study of convergent adaptations requires unbiased sampling, but limiting the study to birds is certainly a bias, very like the sin this book hopes to expunge. Höglund's work shows that even within birds such circumscriptions unfortunately make a difference.

The chapters reviewing analytical methods for discrete and continuous comparative data are the most important in the book. The chapter on discrete data describes three ways

to evaluate associations between variates on a phylogeny, each more sophisticated than the last, and the continuous data chapter describes roughly nine methods, including some new ones. The methods range from using the linnean hierarchy as levels in a nested analysis of variance (a nearly worthless endeavor) to some rather sophisticated models. Some are nondirectional (i.e. two variables are merely correlated), while others specify direction (positive or negative correlation). In general, the more sophisticated the method, the better the data it requires (e.g. known phylogeny, known traits for all ancestors, known branch lengths of the phylogeny, etc.).

Harvey and Pagel summarize and compare these sometimes conflicting methods, but stop short of critically evaluating them. Although they interject warnings to the reader whenever the believability or as-

sumptions of perfect knowledge become too strained, they rarely heed their own warnings. Thus, I wonder what the authors thought, what they favored, how they resolved these conflicts. An additional chapter on allometry is sophisticated and welcome, but seems peripheral to the central topic: cladistic methods applied to evolutionary history.

Harvey and Pagel emphasize that all of these methods make assumptions, and presumably can fail quite badly under adverse circumstances. Readers should realize that whenever a method makes simplifying assumptions about the phylogenetic topology (and most do), the sensitivity of the results to violations of such assumptions is all but unknown at the present time. No doubt the realization that historical, evolutionary biology divorced from cladograms is impossible will be a powerful incentive to many workers to close that gap in the

next few years.

In summary, then, this volume is an excellent guide to a welter of sometimes conflicting techniques proposed to detect the action of natural selection on traits within supraspecific taxa. It is very up-to-date; several methods still in press are included. It is less of a discussion of the knotty issues underlying these methods, and not a very good summary at all of the systematics so fundamental to the entire endeavor. For all that, its faults are mostly those of the field as a whole at present. Certainly, this is a seminal, welcome and utterly mandatory book for anyone interested (pro or con) in the comparative study of adaptation.

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## Books Received

Review copies of the following books have been received. The appearance of a book in the list does not preclude the possibility of it being reviewed in *TREE* in the future.

Iain Brodie and Julian Doberski *Techniques in Ecology and Environmental Science. Set B: Aquatic Organisms and Habitats, Data Collection and Analysis* Daniels Publishing, 1991. £24.95 pbk (62 pages) ISBN 1 85467 081 6

Jonathan Cole, Gary Lovett and Stuart Findlay *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories* Springer-Verlag, 1991. DM 148.00 hbk (xvi + 375 pages) ISBN 0 387 97488 1

W. R. Dolling *The Hemiptera* Oxford University Press/Natural History Museum, 1991. £40.00 hbk (ix + 274 pages) ISBN 0 19 854016

Douglas Futuyma and Janis Antonovics (eds) *Oxford Surveys in Evolutionary Biology* (Vol. 7, 1990) Oxford University Press/OUP USA, 1991. £45.00 hbk (x + 314 pages) ISBN 0 19 506289 2

Janet Hayter-Hames *Madam Dragonfly* Pentland Press, 1991. £15.95 hbk (xii + 208 pages) ISBN 1 872795 20 X

C. G. N. Mascie-Taylor and G. W. Lasker (eds) *Applications of Biological Anthropology to Human Affairs* Cambridge University Press, 1991. £35.00/\$59.50 hbk (x + 252 pages) ISBN 0 521 38112 6

R. B. Myneni and J. Ross *Photon-Vegetation Interactions: Applications in Optical Remote Sensing and Plant Ecology* Springer-Verlag, 1991. DM 298.00 hbk (xvii + 565 pages) ISBN 3 540 52108 9

A. I. Payne *The Ecology of Tropical Lakes and Rivers* John Wiley & Sons, 1986. £25.00 pbk (viii + 301 pages) ISBN 0 471 93107 1

Gary A. Polis (ed.) *The Ecology of Desert Communities* The University of Arizona Press, 1991. \$49.95 hbk (viii + 456 pages) ISBN 0 8165 1186 1

Karen Pryor and Kenneth S. Norris (eds) *Dolphin Societies: Discoveries and Puzzles* University of California Press, 1991. \$34.95 hbk (vi + 397 pages) ISBN 0 520 06717 7

T. Salathé (ed.) *Conserving Migratory Birds* ICBP Technical Publication, 1991. £19.50 pbk (xi + 393 pages) ISBN 0 946888 20 5

James H. Thorp and Alan P. Covich (eds) *Ecology and Classification of North American Freshwater Invertebrates* Academic Press, 1991. \$59.95 hbk (xii + 911 pages) ISBN 0 12 69045 9

R. G. West *Pleistocene Palaeoecology of Central Norfolk: a Study of Environments Through Time* Cambridge University Press, 1991. £40.00/\$75.00 hbk (ix + 110 pages) ISBN 0 521 40386 5

Peter Westbroek *Life as a Geological Force: Dynamics of the Earth* W.W. Norton, 1991. £14.95/\$26.00 hbk (240 pages) ISBN 0 393 02932 8

## In the next issue of *TREE*:

- \* Methods for constructing evolutionary trees, *D. Penny, M.D. Hendy and M.A. Steel*
- \* Sex allocation in hermaphroditic plants, *J. Brunet*
- \* The Cambrian radiation of shelly fossils, *A.Y. Rozanov*
- \* Megapodes: origins, adaptation and reproduction, *D. Jones and S. Birks*
- \* Statistics, costs and rationality in ecological inference, *K. Shrader-Frechette and E.D. McCoy*
- \* Fisher's fundamental theorem of natural selection, *S.A. Frank and M. Slatkin*