

BOOK REVIEWS

MARCY F. LAWTON, EDITOR

Culture and the evolutionary process.—Robert Boyd and Peter J. Richerson. 1985. The University of Chicago Press, Chicago. viii + 331 pages. \$29.95.

In science, one often hears that theory is underdetermined by data. This is a polite way of saying that scientific explanations outrun the evidence which inspired them or, more darkly, that we don't really know what we're talking about. Sociobiology is not controversial because it provides genetic explanations for some behaviors of social insects. It is controversial because it provides underdetermined genetic explanations for some behaviors of human beings.

The logic justifying such explanations, from "natural origins," appears impeccable. Humans, who are cultural beings, arose from non-human, non-cultural animals. Thus the capacity for culture must have organic origins. In particular, that capacity must have arisen under the influence of natural selection, just as all our phenotypic properties must have arisen. This guarantees that however culture works in detail, it must usually enhance genetic fitness. "Usually" because in our post-neo-Darwinian world, genetic drift must be given its due.

Unfortunately, attempts to reconcile cultural phenomena with evolutionary theory have failed at least in part because sociobiologists have attempted to apply models from population genetics to data that have been collected under a set of assumptions radically different from those of biology. Thus, sociobiologists are faced with the problem of trying to explain one sort of phenomena with a theory devised to explain phenomena of another sort.

What has been lacking has been a means to link the theoretical structures in the two domains—social science and evolutionary biology—so that phenomena difficult to explain in the former are clarified in terms of theoretical concepts provided by the latter. The establishment of such theoretical links, however, is usually a complex "coevolutionary" process.

It would be something of a tour de force to meet these challenges head on and succeed. *Culture and the evolutionary process* almost achieves this. To the extent that it falls short, it does so because no single work could possibly complete the coevolutionary process needed, nor encompass the full range of theoretical links required to harmonize such disparate domains as population genetics and social science.

The operative thesis of this remarkable book is that culture can be viewed as a system of inheritance. This in itself is not new, but the book is distinguished by its use of the thesis. Boyd and Richerson recognize the need for reconciliation rather than reduction (in the territorial imperative sense) of sociobiology and social science. The goal of the book is thus limited to an exploration of the logical relationships between culture as a transmission system and neo-Darwinian processes of genetic evolution.

The means of exploring these logical relationships is to develop a collection of models Boyd and Richerson call the "dual inheritance theory." This involves tracking the evolution of the joint distribution of genotypes and phenotypes, where the latter include cultural traits. Sophisticated techniques from theoretical population genetics are used to build the models; and considerable ingenuity is required, since cultural transmission is often very different from genetic transmission. In all, some three dozen models are developed which provide an impressive tool kit for investigating the joint evolution of genotypes and phenotypes. Whether the book succeeds in human sociobiol-

ogy is almost irrelevant, because the technology it presents should find much wider application.

This book is by far the clearest, most readable account of mathematical models in population genetics that I have ever read. The assumptions and strategy for each model are clearly laid out before any equations appear. Derivations of many points are contained in "boxes" which can be ignored or referred to later. The authors frequently follow their equations with very readable verbal explanations and build complex models from well-motivated modifications of simpler ones.

The early chapters set up the basic thesis by analogy to genetic transmission, with the differences between genetic and cultural transmission stressed. Many of the models show that these differences can lead to surprising dynamic behavior of potential significance in explaining features of culture that resist sociobiological interpretation.

Although empirical data from the social sciences are used to motivate the models, the book makes no attempt to provide compelling conclusions on the nature of human culture. Rather, it presents a series of interesting conditional statements which put the theoretical model-building activity on firm ground. If culture is an inheritance system and if the assumptions of dual inheritance models hold (even approximately), then the conditions under which culture could originate in a non-cultural species can be understood.

The authors define culture in a way that makes it possible to build models of cultural inheritance: "Culture is information capable of affecting individuals' phenotypes which they acquire from other conspecifics by teaching or limitation" (p. 33). This information can be transmitted vertically (e.g., from biological parent to biological offspring), obliquely (e.g., from teacher to child), or horizontally (e.g., among peers). The mechanism by which this transmission occurs is called social learning, to distinguish it from individual, trial-and-error learning.

In many of the models, social learning is important because the cost of evaluating which behaviors to adopt is often too high relative to the benefit of adopting the behavior. Imitation of successful individuals, "cultural parents," or "models" is a cost-effective, heuristic strategy for developing a cultural repertoire. As with all heuristic procedures, imitation is not foolproof. Successful individuals exhibit many traits, and not all of them are indicators of success.

Boyd and Richerson identify and model five kinds of forces once the features of the cultural transmission process itself are modeled. Cultural transmission models are given for dichotomous and quantitative cultural traits with n cultural parents and vertical, oblique, or horizontal transmission. The net result is a general equation expressing the cultural analogue of Hardy-Weinberg equilibrium. For quantitative traits both a blending inheritance model, in which individuals average the trait value of n cultural parents, and multifactor models, in which n cultural parents with m cultural traits each, are derived. Cases in which the mathematical form of cultural transmission is symmetric or asymmetric to genetic transmission are considered. The main difference between the two is that cultural transmission includes the inheritance of acquired variation.

The five forces investigated are guided variation, direct biased transmission, natural selection, frequency-dependent biased transmission, and indirect biased transmission. Guided variation is a force generated by the coupling

of learning and cultural transmission. The offspring learns the behavior of its cultural parent(s) and modifies what it acquires according to a learning "rule" which is assumed to approximate a goal (e.g., a fitness optimum) contingent on local environment. This force shifts the mean of a population of offspring behaviors toward the goal. The most significant feature of guided variation as a force is that, unlike natural selection, it is independent of the amount of variation present in the population. This force will operate only when the environment is not too variable.

Directly biased transmission results from the cultural offspring evaluating behavioral traits directly on the basis of the intrinsic properties of the traits. Since the bias itself is a form of predisposition to adopt certain cultural variants, it depends on the amount of cultural variation already present in the population. The strength of guided variation and direct bias depends on the cost of estimating which cultural variant is favored in the local environment. When these forces are weak, cultural variation can be maintained in a population and natural selection can operate to change the frequency of variants. When genetic and cultural transmission are asymmetric in form, selection on cultural variants may not optimize genetic fitness.

Frequency-dependent bias occurs when individuals imitate common or rare variants disproportionately to their frequency. Indirect bias occurs when an indicator trait affects a cultural parent's "attractiveness" for some other trait. Under some circumstances, these forces are shown to lead to processes analogous to biological processes, e.g., cultural group selection and a cultural runaway process due to correlated characters similar in form to Fisher's sexual selection runaway process.

The specific conclusions to be drawn from the models are various, depending on how likely the particular assumptions hold true. It would be pointless to discuss them without a detailed account of the models themselves. Suffice it to say that the full range of intriguing dynamics recently under intensive investigation for purely biological models can be shown to occur under some conditions, as well as additional behavior due to the inheritance of acquired characteristics and novel modes of transmission possible for cultural traits.

Culture and the evolutionary process presents a remarkably clear philosophy of scientific theories that follows the work of Richard Levins. Philosophers of biology will be interested in tracing the consequences of this view through the book, in addition to evaluating the issues raised by the models themselves and their implications for sociobiology. The audience which stands to gain the most, however, are behavioral biologists. The models developed may ultimately prove more useful to students of bird song and habitat choice than to social scientists. Boyd and Richerson have done the best job to date of explaining and motivating the complexities of theoretical models in sociobiology for a wide scientific audience.—JAMES R. GRIESEMER, Department of Philosophy, University of California, Davis, CA 95616.

The Florida Scrub Jay: demography of a cooperative-breeding bird.—Glen E. Woolfenden and John W. Fitzpatrick. 1984. Princeton University Press, Princeton, N.J. 406 p. Cloth: \$45, Paper: \$14.50.

"Good theories come and go. Great data are forever."
Monte Lloyd, 1975

The authors of *The Florida Scrub Jay: demography of a cooperative-breeding bird* must have had this dictum engraved on their data sheets as they scoured the oak scrub of the Archbold Biological Station during the decade beginning in 1969. And the results of this ongoing investi-

gation into the behavioral ecology of *Aphelocoma c. coerulescens* are testimony to the fact that it's a good motto to live by.

Simply put, Glen E. Woolfenden and John W. Fitzpatrick have collected the single best set of life-history information available for any cooperative-breeding bird, indeed, one of the best data sets available in vertebrate population biology. In doing so, the 1985 winners of the American Ornithologists' Union's coveted Brewster Award provide an unusually lucid glimpse into the complex interaction between data collection and theory construction in science.

Long-term study of the Florida Scrub Jay, a disjunct member of the more widespread Western Scrub Jays, was born in the heyday of the sociobiological frenzy over altruism. In 1969, five years after W. J. Hamilton's two-page bombshell on the evolution of altruism by kin selection, Glen Woolfenden discovered eight Scrub Jay nests on the Archbold Biological Station in Lake Placid, Florida. Six of those nests were attended by non-breeding, adult helpers. Were the helpers altruists? Could their behavior be explained by kin-selection theory?

Although it rapidly became obvious that Florida Scrub Jay social structure and behavior were consistent with kin-selection theory, field observation of the population soon led the authors to suspect that kin selection was neither a necessary nor a sufficient explanation for helping at the nest. In this species, which is restricted to ever-diminishing habitat, competition for breeding status under stable, saturated conditions seemed to be the critical constraint on social organization.

One of the reasons for the authors' shift in emphasis away from the question of kin selection has been their discovery of several types of direct benefits helpers enjoy as a consequence of their behavior. One of the most conspicuous of these benefits for male Florida Scrub Jays is territorial inheritance by dominant helpers. A less conspicuous benefit pinpoints the extraordinary value of long-term studies in advancing our understanding of the evolution of social systems.

By 1978 Woolfenden and Fitzpatrick had documented territorial inheritance by dominant male helpers. In this book they report that subordinate males may also help themselves to acquire territories. Because male helpers defend territory borders, families with several males can enlarge their holdings. The consequences of such expansion are twofold. First, large territories abut more neighboring territories. As neighbors die, subordinate helpers from large territories do not have to go far from home to fill newly vacant breeding slots. Second, in families with large territories, a subordinate male can also establish his own territory by budding, i.e., carving off a fragment of the territories he helped enlarge. Either way, the subordinate male can become a breeder without having to risk long-distance dispersal.

This kind of subtle but direct benefit is apparent only in light of a long-term demographic study. Indeed, long-term study of survival and reproductive success is also critical to our understanding of the role kin selection may play in the evolution of cooperative breeding. In the case of Florida Scrub Jays, however, the data strongly suggest that enhanced inclusive fitness really is an indirect effect of social organization, rather than a shaping cause; and Woolfenden and Fitzpatrick argue correctly that the direct benefits of helping do away with the need to consider helpers altruists.

There is another sort of subtlety about *The Florida Scrub Jay*. It is the authors' unusual success in avoiding typological thinking while articulating demographic patterns within the population. Unlike most books, in which examples or case histories are used to support a particular argument, for instance, Woolfenden and Fitzpatrick use case histories to highlight departures from the mean. A

good example can be found in the description of territoriality.

Whether or not they have helpers, breeding pairs of Florida Scrub Jays almost always form monogamous, territorial pairs. However, on five occasions the authors have seen multipair territories. Woolfenden and Fitzpatrick use case histories to describe the particulars of these exceptional groups, noting that they "suggest evolutionary pathways that may have been followed in the development of the more complicated communal breeding systems of other birds, and especially of other jays" (p. 162).

It is the careful documentation of departures from mean population behavior that allows the reader to begin to appreciate the surprising range of variability displayed even in a population in which saturation places severe constraints on pathways to breeding status. It remains a puzzle whether such natural variation is especially characteristic of New World jays, or whether long-term demographic studies of the other cooperative breeding birds will also reveal unexpected within-population behavioral plasticity.

When it comes to theory building, however, the authors are less interested in the origins of behavioral plasticity than in the ecological factors that select for mean social organization. To this end, Woolfenden and Fitzpatrick draw heavily from their demographic information to generate a model for the evolution of cooperative breeding. The model is an algebraic expression of the idea that habitat stability and saturation can result in the evolution of cooperative breeding. Although not a new notion, the model is carefully constructed with a clear expression of assumptions and predictions. Thus, Woolfenden and Fitzpatrick have used great data to construct good theory. Their model is well-suited for application to other species in order to provide a strong test of current ideas about how selection shapes avian cooperative breeding systems.

The Florida Scrub Jay: demography of a cooperative-breeding bird, is a classic contribution to ornithology and a paradigm for future studies. To paraphrase another ornithological organization—Woolfenden and Fitzpatrick do Scrub Jays right.—MARCY F. LAWTON, Department of Biological Sciences, University of Alabama in Huntsville, Huntsville, AL 35899.

BOOKS RECEIVED

An annotated bibliography of literature on the Spotted Owl. Land Management Report No. 24. R. W. Campbell, E. D. Forsman, and B. M. van der Raay. 1984. Ministry of Forests, Province of British Columbia.

115 p. \$7.50. Source: Queen's Printer, Victoria, BC, V8V 1X5, Canada.

The atlas of bird distribution in New Zealand. P. C. Bull, P. D. Gaze, and C. J. R. Robertson. 1985. The Ornithological Society of New Zealand, Inc. P.O. Box 12397, Wellington, New Zealand. 296 p. \$30 NZ.

Birds of Nahanni National Park, Northwest Territories. G. W. Scotter, L. N. Carbyn, W. P. Neily, and J. D. Henry. 1985. Special Publication No. 15 of the Saskatchewan Natural History Society, Box 1121, Regina, SK, Canada. 73 p. \$7.00.

Birds of Rio Grande Do Sul, Brazil. Part 2. Formicariidae through Corvidae. William Belton. 1985. Bulletin of the American Museum of Natural History, Vol. 180, Article 1. 241 p. Paper cover. \$16.70.

Birds of the Texas Coast Bend. J. H. Rappole and G. W. Blacklock. Texas A&M University Press, Drawer C, College Station, TX. 126 p. \$19.50.

Conservation of tropical forest birds. A. W. Diamond and T. E. Lovejoy, eds. 1985. Proceedings of a workshop and symposium held at the XVIII World Conference of the International Council for Bird Preservation. ICBP Technical Publication No. 4. 318 p. \$18.50. Source: ICBP, Huntingdon Road, Cambridge CB3 0DL, England.

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The western bird watcher: an introduction to birding in the American West. K. J. Zimmer. 1985. Phalarope Books/Prentice-Hall Press, Englewood Cliffs, NJ. 278 p. \$10.95 paper, \$19.95 cloth.