Book Reviews

A Study in Population Ecology

Ecological Isolation in Birds. DAVID LACK. Main illustrations by Robert Gillmor. Harvard University Press, Cambridge, Mass., 1971. xii, 404 pp. $12.

This is the third book (the other two being *Population Studies of Birds*, 1966, and *Ecological Adaptations for Breeding in Birds*, 1968) in a series on the population ecology of birds by a man who essentially originated modern avian ecology and who has greatly contributed to our understanding of general ecological principles. The present book explores the methods by which birds avoid or reduce competition with other species, a problem the investigation of which was pioneered by Lack more than 25 years ago. The study primarily consists of collation, summary, and review of existing literature, with all too rare touches of synthesis. The resulting volume thoroughly documents, for many groups of birds, the proportion of congeneric pairs of species that are ecologically isolated by (i) geographical range, (ii) habitat, and (iii) feeding habits, including size differences. That such patterns of isolation occur in birds has been known for some time, partly through Lack's earlier work. The unique feature of Lack's new treatment is that many studies, previously scattered throughout the ornithological literature, are now gathered under one cover. But if Lack's book is the index to the development of ideas about ecological isolation, it would appear that little progress has been made during the last decade or two.

Although the methods involved in the collation of data are straightforward, there are several weaknesses in the approach. First, Lack has limited his treatment to birds, although numerous examples of ecological isolation could be drawn from other groups that are more amenable to study. Any general theory of ecological isolation must comprehend patterns found in all groups. Second, the taxonomic constraints imposed by Lack (comparisons are made only within genera) produce artifactual biases. Lack admits many of these: few European passerine congeners are separated by feeding habits, because genera are morphologically narrowly defined compared to other groups; many species are isolated by range in the West Indies because species are named within superspecies groups; in North America, competition from warblers may limit the proportion of species of Paridae separated by feeding differences; and so on. A third, and more fundamental, limitation to Lack's approach is that his study is built upon a survey of effects, rather than upon direct attempts to elucidate the processes, of ecological interaction. I have some doubt that much insight into ecological mechanism is gained by examination of superficial patterns.

Within the limitations of his approach, Lack has provided many classical examples of ecological isolation. He has discovered some suggestive patterns of isolation, and has hinted at some intriguing hypotheses. The reader will find examples of character displacement in morphology, nest site, host-specificity of brood parasites, habitat, and feeding behavior. He will find that ecological isolation is seasonably variable and may disappear altogether in the presence of a superabundant food source (such as seasonal abundance of fruit for many insectivorous birds in the tropics); that carrion eaters are specialized on different parts of a carcass; and that individual oyster catchers are specialized on one of a variety of food resources, each of which requires a unique feeding technique. There is the suggestion that ecological isolation originates at the zone of contact between two species and spreads slowly through the population; and that the probability of species' being isolated by range, habitat, or feeding is determined, in part, by how recently contact between species has occurred. Differences in feeding are the hardest, and therefore the last, to be evolved. By demonstrating that frugivores are most often separated by range (fruits are much less diverse than insects and thus afford little opportunity for isolation by feeding), Lack has emphasized the potential value of frugivorous birds to the study of competitive interactions.

I was disappointed that species diversity is passed over briefly. Lack seems to accept the notion that species diversity reflects the diversity of ecological resources present in an environment, and cites the depauperate faunas of islands as positive evidence. (MacArthur and Wilson use the same superficial evidence to validate their widely accepted equilibrium theory.) Ecological isolation and species diversity are population and community consequences, respectively, of competitive interactions between species, and it is unfortunate that the most recent review of one aspect of this problem has largely ignored other, related aspects.

Lack has also failed to tackle many basic questions posed by ecologists in recent years: What percentage of overlap between competing species can be tolerated? What factors determine within- and between-habitat niche width? How do factors other than resources (climate, predators, and so on) influence the outcome of competition? What roles do local adaptation and gene flow play in determining the rate at which isolation is attained? Why are some species rare and local and others abundant and widespread? The burden of these omissions should not be placed entirely on Lack's shoulders. Ecologists have largely failed to properly consider most of these basic questions, concentrating on the easier task of describing superficial patterns.

The substance of Lack's book indicates many areas of theory in which our understanding is almost totally lacking, and prompts me to ask whether some ecological questions will ever be satisfactorily answered through present approaches. The elucidation of ecological mechanisms has been, and will be, severely hampered by several difficulties inherent in the study of ecological systems. First, mechanism on the population level is translated into pattern on the community level by an extremely complex array of interactions, through which most of the "information" contained in the interactions themselves is undoubtedly lost. Second, there are virtually no valid natural experiments in community ecology. Because several parameters

usually vary together, adequate controls for a single parameter are difficult to find. Third, it is nearly impossible to perform valid ecological experiments, except to gain pragmatic knowledge, because natural systems represent evolutionary equilibria and any manipulation upsets evolved balances. There is simply no time to wait for an ecologically interesting system to evolve into equilibrium with an experimentally altered environment. Fourth, attempts to build models of community interactions have been plagued with difficulties in verifying assumptions and premises and in eliminating alternative models that predict similar patterns.

Whatever the state of ecology as a science at present, David Lack has produced a thorough summary of one of its small, but more lustrous, facets that will be a springboard of patterns and ideas for the future. The book generally reads easily, except through some of the long series of examples and scientific names. Although Lack is somewhat guilty of the teleology which is rampant in ecology and which has engendered many ecological myths, he also displays the keen intuition about birds that has made him one of the foremost modern ecologists.

The book is attractively produced and it is handsomely illustrated by Robert Gillmor.

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Man

The Imperial Animal. LIONEL TIGER and ROBIN FOX. Holt, Rinehart and Winston, New York, 1971. xii, 308 pp. $6.95.

If a reader of the classical 19th-century novels that deal with the growth and structure of human families were, on the evidence they provide, to enumerate and describe the major features of human social existence (such as mother-child and sexual bonding and male contention for status) and further, to delineate the features common from one family to the next, the basic "biogrammar" of Lionel Tiger and Robin Fox would emerge. This comment is not meant to detract from the work under review but only to point out that *The Imperial Animal* has a strong line of common sense running through it and has been conceived in a humanistic tradition. This book shares with recent bestsellers by Desmond Morris and Robert Ardrey a view of man as a biological being possessing an evolutionary heritage. The effort by Tiger and Fox is unique, however, in that, in addition to attempting to extrapolate from the study of other higher primate species to man, it draws heavily on the combined knowledge of anthropology and sociology. Thus the authors have produced a document which presents a picture of the basic human, its needs and recurrent patterns of expression, that takes into account data provided by the study of mankind in many of its cultural manifestations.

Tiger and Fox's writing is interesting and lively. A tendency to depart from fact to weave a convincing argument from analogies bordering on poetic metaphor emerges from time to time, but the book is nevertheless an objective and a serious one.

One of the cornerstones of the book is the assumption that modern man has carried forward a heritage from the time when man was a seminomadic hunter living in small groups. Tiger and Fox argue that man is preadapted for certain forms of social interaction. That is to say, unless the environment he is presented with conforms in its essential parameters to the environment for which he was adapted 20,000 years ago, he may suffer emotional dislocations. To quote: "But this brain is still the old primate brain with an overlay of gray matter wrinkled into self-consciousness by the hunting transformation," and "the pitifully short time since we invented agriculture (about ten thousand years ago), and the even shorter time since industrialization began in earnest (perhaps two hundred years ago), should not blind us to the reality of our evolutionary heritage. In our economic behavior, as in so much else, we are still Paleolithic hunters." By contrast, in a recent publication ("Competitive and aggressive behavior," chapter 6 in *Man and Beast*, J. F. Eisenberg and W. S. Dillon, Eds., Smithsonian Institution Press, 1971) E. O. Wilson presents an argument which he summarizes by the statement, "There is every justification from both genetic theory and experiments on animal species to suppose that rapid behavioral evolution is at least a possibility in man. By rapid I mean significant alteration in, say, emotional and intellectual traits within no more than ten generations—or about 300 years." The viewpoints presented by Tiger and Fox on the one hand and by Wilson on the other bracket the dilemma of human sociobiology. We simply do not know, at present, what biological limits are present within the "wiring pattern" of man's brain.

In their zeal to relate man's present-day behavior to a past which man is apparently carrying forward into the present, Tiger and Fox develop criticisms of current aspects of Western society, such as educational systems, medicine, and international politics. Social criticism based on the assumption that man is preprogrammed for a certain type of stimulus input is certainly a valid approach, if we can reasonably demonstrate that man is indeed predisposed to live and act in a certain social milieu. It would seem that before such far-reaching recommendations as the authors make in their book are set forth, however, the limits of man's biogrammar should be more firmly established. The case presented by Tiger and Fox rests upon inference that is tenuous in some instances. There are certain attributes of man's behavior that are so consistent across cultures that one can only conclude that the authors must certainly be right in some of the generalizations they make. The question, then, is which ones. I do not believe that we have at our disposal the evidence to decide in many cases.

The Imperial Animal, in any event, is an interesting synthesis and a humane one. It is certainly far more successful as a discussion of human behavior patterns than any previous book written in this genre, and may be read with much profit by zoologists and social scientists.

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Historical View

Molecular Genetics. An Introductory Narrative. GUNTHER S. STENT. Freeman, San Francisco, 1971. xviii, 650 pp., illus. $12. Biology Series.

Question: What kind of introductory molecular genetics text is it that has no hurdles to exercise the student, that presents its "science" as a body of established knowledge too cleverly and definitively secured to be challenged, and that poses only one question for the future—and promptly declares that to be unanswerable? Answer: It is one written by a former geneticist who has previously declared his field to be dead.