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BOOK REVIEWS

Marcy F. Lawton, Editor

Arkansas birds, their distribution and abundance.—Douglas A. James and Joseph C. Neal, illustrated by David Plank and Sigrid James Bruch. 1986. The University of Arkansas Press, Fayetteville. xii + 402 p.

It is a pleasure to review a first-class state bird book that the average environmentally-sympathetic citizen can admire and find useful. Obviously not a field guide and so stated, it nevertheless illustrates 70 species. Add on 18 habitat photographs in color and the beauty begins to show through. Arkansas' state bird, the Mockingbird, need not be on the cover, but why the Evening Grosbeak? I found very little wrong with the artwork though I did not particularly care for the Cedar Waxwing or the Swainson's Warbler.

Introductory material includes Dedication, Acknowledgements, Preparation of the Book, History of Ornithology in Arkansas, Arkansas Birds and the Environment, Arkansas Birds in Prehistory, and Finding Birds in Arkansas. The distribution, migration, and other life-history data for Arkansas' 366 species occupy the main 297 pages. Finally presented is a list of all known Arkansas specimens, a Bibliography, and an Index to Bird Names and Taxonomy.

The value of all this material to Arkansas ornithology seems considerably reduced by omitting migration dates, observers except in rare cases, and all but a very few references to *Audubon Field Notes* or *American Birds.* After years of summarizing the spring migration for the Central Southern Region for *American Birds,* and placing Arkansas records before a national birder audience, this reviewer is quite chagrined to find that the references do not even appear in the Bibliography. Also left out is the *Revised Edition of Alabama Birds* (1976), which contains about three times the information of the out-of-print first (1961), and includes Arkansas-Alabama banding recoveries not in the present text. Not only does the reader need this information for evaluating records, but the observer deserves credit every time it is due. Perhaps *Audubon Field Notes* or *American Birds,* where Bob Newman, Dan Purrington, yours truly, and others put these records, is now the only published source of this Arkansas information. Obviously the authors were very conservative on size of bibliography; unfortunate, since this reviewer believes that big, adequate, and useful bibliographies are usually a boon to students.

But, few completed tasks please everyone, for standards and abilities vary. With all the information on Arkansas birds and the adequate illustrations, it is by any standard a very useful volume. Such a big, important, difficult task has never been completed for many states and it is something to be cherished for a long time. We hope that it will make everyone in Arkansas more conscious and more appreciative of their beautiful birds and their part in a beautiful, more and more fragile, environment. Doug James, Joe Neal, David Plank, Sigrid James Bruch, Frances Crews James, and George Purvis and the many good photographers and birders can certainly say that they have helped make their fellow citizens much more aware of a beautiful Arkansas!—THOMAS A. IMHOF, 1036 Pike Road, Birmingham, AL 35218.

Foraging theory.—D. W. Stephens and J. R. Krebs. 1986. Princeton University Press, Princeton, NJ. 247 p.

Optimal foraging theory is a field which has received a great deal of attention and some criticism in recent years, and has been the subject of an inordinate number of reviews. *Foraging Theory* by Stephens and Krebs, however, is not simply another review of the field. Rather, it is more appropriately characterized as a field guide to optimization models employed to study foraging behavior, and is chiefly of value to those with at least some familiarity with foraging theory and some mathematical expertise.

The book is quite useful in clarifying and organizing these models. It does not attempt to review the empirical research on foraging behavior, and readers interested in recent studies should instead consult the symposium edited by Kamil, Krebs, and Pulliam (*Foraging Behavior,* 1987, Plenum Press, New York, 676 pp). *Foraging Theory* concentrates on models, especially economic models (e.g., marginal value theorem, risk-sensitivity). For this reason it is a little misleading to title the book "Foraging Theory." It is likely that the word "optimal" was not included in the title because the notion of optimality in foraging has drawn most of the negative responses that this field has received. In any case, readers should be aware that this book covers only part of the field of foraging behavior.

This is an important point, because the authors use this book as a forum to make a policy statement on how research in foraging behavior should be conducted. Stephens and Krebs essentially redefine the philosophy of foraging theory as an argument from design which is independent of any other measure of fitness. For example, they consider the number of reproducing offspring left by organisms adopting different foraging tactics to be irrelevant to how foraging decision processes evolve. While the recognition that behavioral ecology must move away from the "just-so story" approach is to be applauded, the engineering approach is only one way in which this can be done. In fact, the approach outlined in this book is only one of several which can be used to study the evolution of traits. For a discussion of other methods, see John Endler's *Natural Selection in the Wild* (Princeton University Press, Princeton, NJ, 1986).

Rather than placing the argument from design approach into a broader framework of evolutionary theory, Stephens and Krebs seem to feel that it is the only major approach to studying foraging behavior. As presented, the engineering approach cuts the field of foraging behavior off from the rest of behavior and biology. For example, given the approach described by Stephens and Krebs, researchers cannot reconcile data from ecology, population biology, and physiology with data collected on diet choice. The proper goal of foraging theory should ultimately be to allow researchers to integrate foraging behavior with other important aspects of the biology of an organism in order to achieve an understanding of the evolutionary consequences of different behaviors.

As far as evaluating its usefulness as an abstract of the field of optimal foraging, *Foraging Theory* is primarily useful for researchers already familiar with the field who desire an overview of the models, or a summary of recent developments. It does not stand on its own as an introduction to the field for those not versed in behavioral ecology, although it would be useful as an outline of the major theoretical advances for anyone delving into the literature for the first time. This was very apparent when I used *Foraging Theory* as the basis for a graduate seminar course; students unfamiliar with the jargon found the book heavy going.

The major failing of this book is that it summarizes and justifies what has been done to date, rather than providing any real insights into where the field should go in the future. This is a disappointment because foraging theory is currently at a crossroads, and new approaches are needed if the field is to continue to be productive.—CYNTHIA ANNETT, Department of Biology, University of New Mexico, Albuquerque, NM 87131.

The evolution of individuality.—Leo W. Buss. 1987. Princeton University Press, Princeton, NJ. xv + 203 p. ISBN 0-691-08468-8 cloth, 0-691-08469-6 paper.

This book is concerned with the evolution of multicellular organisms. How did differentiation of structure and function among the cells of organisms evolve? In answering this question, Buss covers a great deal of ground. Despite factual errors which some have discovered in his coverage, Buss's argument is of very great interest, for it provides an illuminating perspective on developmental biology, and suggests a unifying theme which cannot fail to be relevant.

Buss believes that once cells formed aggregated groups, some cells forced others within their group into "service functions," allowing the aggregation to reap the benefits of a division of labor. The case is like that of wasp colonies where some wasps force others to serve as foragers (Gadagkar and Joshi 1984). In both cases the advantages of "group living" are so great that it pays a "subordinate" to stay and help its relative, be it germ cell or queen wasp, reproduce rather than to leave and reproduce independently. On the other hand, if there is a chance of becoming the reproductive, it pays a mutant cell, as it pays a subordinate wasp, to try to do so even at the risk of the good of the group. Thus there is potential conflict of interest between an individual and most of its cells, analogous to that between an insect society and its nonreproductive members (West Eberhard 1975, 1979), and that between individual advantage and the good of a human society (Hardin 1968).

Organisms whose cells "can't do everything at once" are most likely to benefit from a division of labor among their cells. For instance, cells ancestral to metazoans could not maintain cilia while dividing. Thus cells in a group forming an otherwise ciliated spherical aggregate would benefit themselves by losing their cilia and dividing, forcing a pocket into the sphere's interior while enhancing the cellular aggregate's versatility and preserving its ability to move. This step yields a gastrula from a ciliated blastula and opens the way for further differentiation. This step requires, however, that the ciliated cells sacrifice reproduction for the sake of their relatives in the inner layer.

Buss views the developmental dance of successive inductions and differentiations as the record of successive enslavements of some cell lineages to fuel the proliferation of others. However, it must be remembered that even cellular lineages which have lost the ability to produce gametes compete to proliferate within an individual. The dreary tale of cancer suggests that competition between proliferating cell lineages is not necessarily good for the individual. How are the proliferative "instincts" of different cell lineages subordinated, or rather harnessed, to the good of the individual of which they are a part?

The attempt to reconcile individual advantage with the good of society has preoccupied prophets, philosophers, and political theorists throughout history and has brought forth some of the finest of human achievements. More recently, the conflicts latent within the seemingly perfect unity of wasp and ant colonies have shed light on the evolution of insect societies (West Eberhard 1979). Similarly, transposable elements, and genes capable of violating Mendel's laws, have reminded geneticists of potential conflicts between a gene and the individual which carries it (Crow 1979, Engels 1986).

As one might expect, a central theme of this book is how conflicts between individuals and their nongametic cells are resolved or suppressed. According to Buss, Weismann argued that immediate sequestration of the germ line solved the problem. If somatic variants cannot be passed on to future generations then selection on the soma favors the individual just as, if the queen is the only member of an insect colony which can reproduce, selection on the nonreproductive members of the colony favors the good of the colony, as expressed by its queens. As Buss notes, however, sequestration of the germ line is less prevalent than Weismann thought. It cannot be true in plants, or in animals such as corals and hydroids capable of reproducing by budding or fragmentation.

Even in animals, sequestration of the germ line is a derived characteristic. How were potential conflicts between an individual and its cells originally resolved? How did sequestration of germ lines evolve? How is it arranged?

True to his view of development as the successive enslavements of some lineages by others, Buss assumes that conflicts between individuals and their cells were "mediated" by force. For instance, a mother can diminish such conflicts in her offspring by controlling early stages of their development so as to encourage cells to serve their individuals. She can do this by suitably arranging messenger RNA and other matter in the fertilized egg. If the embryo develops within the mother, she can also dictate a pattern of unequal cell divisions. Similarly, a bee colony controls the division of labor among its young by the food its members give them (Seeley 1985). Buss argues that cellular differentiation occurs as early in animal embryos as ecological conditions permit, and believes that this reflects how effectively maternal control can prevent conflict between an offspring individual and its cells. Even under the most favorable circumstances, however, the mother's control of development is far from complete. There are limits to what she can put into the egg. Often the last stage in a mother's control is to direct the sequestration of the germ line so that selection on the soma favors the good of the individual. Differentiation among somatic cells can then be allowed to complete development without endangering individuality.

There are, however, less overtly forceful means for reconciling cellular interests with the good of the individual. In plants, rigid cell walls prevent the migration of cells from one part of the individual to another. Thus a "selfish" cell lineage cannot take over the reproductive organs of an entire plant, and can accordingly only parasitize the plant to a limited degree. Rigid cell walls, however, make it impossible to sequester a germ line: all stems contain cells capable of developing reproductive structures and many plants can reproduce "vegetatively." As a result, the good of each part of a plant is not fully identified with the good of the plant as a whole. Indeed, the concept of individual is less well defined in plants than in animals with sequestered germ lines. Neither genets nor ramets are as clearly individual as a mouse.

Syncytial fungi, where nuclei are not separated from each other by cell walls, are susceptible to parasitic nuclei, just as a pasture held in common is more subject to abuse than enclosed fields where each farms and benefits directly by taking care of his own. Buss remarks that such fungi protect themselves from undue proliferation of parasitic nuclei by arranging for all nuclei to divide simultaneously. One is reminded of the elaborate mechanism whereby all genes of a cell's genome divide simultaneously in direct correlation with cell division. Buss notes that when fungi form specialized reproductive tissues, these tissues and their surroundings are divided into cells with rigid walls as if to prevent selfish variants from taking over the reproductive organs. Moreover, when fungi fuse, elaborate mechanisms ensure the fair and even distribution of nuclei from each of the fusing partners.

Buss also remarks that all three kingdoms of organisms with cellular differentiation—animals, plants, and fungi—evolved from sexually reproducing ancestors possessed of the full panoply of meiosis. He thinks that sexual reproduction is a prerequisite for the evolution of multicellular individuals, for, given the susceptibility of primitive multicellular organisms to parasitic, heritable, somatic mutations, sexual reproduction offers the only chance of forming mutant-free offspring from parents carrying different parasitic mutants. Thus sex, individuality, and harmony meet, as long ago, and in a very different way, they met in the book of Genesis.

I think there is another reason why sexual reproduction is essential for the evolution of multicellular individuals. Sexual reproduction causes heritable variation among intracellular aggregates to far exceed that within each mitotically dividing aggregate. Where there is heritable variation between, but not within, groups the advantage of an individual is identical with the good of its group (Leigh 1983). Where there is any danger of cells migrating from one individual to another, increasing variation within, at the expense of variation among, individuals Buss finds, as one would expect, recognition systems which allow the identification and exclusion of foreign cells. In fact, sexual reproduction is doubly important to the evolution of individuality. Not only does sexual reproduction identify the advantage of a cell with the good of its individual; free recombination within sexual organisms also allows selection to identify the advantage of a gene with the common interest of the genome of which it is a part, which is to the good of the individual possessing that genome (Leigh 1987).

Clearly, the need to suppress conflicts between an individual and its cells constrains the variety of life cycles that can evolve. Buss discusses this subject. Unfortunately, the brevity of its treatment ruined its clarity. I hope Buss treats this topic more clearly in a later publication.

Buss ends his book by discussing evolutionary hierarchies. The biological literature is full of sermons on the virtues of hierarchical thinking, all curiously abstract in tone, a priori in attitude, and quite unproductive of concrete achievement. Buss has taken the trouble to consider how natural selection, which once acted directly on cells, now affects them according to their influence on the individuals of which they are a part. He shows how repeatedly analogous processes have occurred in the history of life. He brings his hierarchies alive in a wealth of fascinating, concrete detail, and in the process he brings an incredible variety of topics within the purview of a single perspective. He attaches meaning to the notion of evolutionary progress, and he may even have resolved that gorgeous enigma, the adaptive significance of sex. Such would be a suitable reward for his intelligent interest in organisms.

I will not presume to judge who must read this book, or whose shelf it must grace. For my own part, I find accounts of how individual advantage is reconciled with the good of a larger whole the most fascinating reading there is. Of all such accounts of reconciliation in the natural world, Buss's book is the most gripping, the most amusing, and the most stimulating I have yet encountered. Moreover, of all the books I have read, this one holds the most promise of reuniting the sadly divided strands of biological science.—EGBERT GILES LEIGH, JR., Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panamá.

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