However, the number of 1990 nests/plot did not vary between groups (P > 0.05, Mann-Whitney U-test), supporting the contention that the number of nests established by birds in each of the three groups of plots during the 1990 breeding season were similar before manipulation of nest numbers in 1991. This also suggested that density and characteristics of vegetation used as nesting habitat were similar among the three groups of plots in my study area.

The median number of 1991 nests established by birds varied from 6.0 nests/plot in the removal group to 7.5 nests/plot in the supplemental group (Table 1). As with the 1990 nests, the number of 1991 nests/plot did not differ between groups (P > 0.05). Furthermore, the number of nests established by birds in each group considered separately did not vary between 1990 and 1991 (P > 0.05, Wilcoxon's signed-ranks test). Thus, despite a presumed absence of old nests in the removal group and an increase in the number of nests in the supplemental group, the number of nests established by birds in the 1991 breeding season in these two groups was comparable to that in the control group.

I conclude that the number of nests established by the breeding-bird community in small, even-aged plots is not affected by the relative density of old nests. Moreover, I do not believe that old nests act as a proximate cue to the suitability of a habitat for nesting birds in even-aged plots. Similarly, Erckmann et al. (1990) found little support for the old-nest hypothesis in nesting Redwinged Blackbirds using marshes in Washington. Other features of the nesting habitat, such as degree of vegetative concealment in the vicinity of nest-sites or distance of nests from edges, presumably are more relevant to nest-site selection by Gray Catbirds and coexisting species in even-aged plots (Yahner 1987, 1991).

The results of my study obviously depend on success at locating nests in the field. Because nest searches were conducted when vegetative cover was minimal or nonexistent, and because searches in each plot were done slowly and systematically, I am confident that most nests, or at least a similar proportion of the total, were found each year. That relatively few (5%) of the nests that were found or placed in 1991 were relocated in 1992 suggested that even if nests act as possible cues for nest-site selection, they would be effective for no more than two breeding seasons.

A criticism of my study may be that I did not focus on individual species. I considered all species concurrently for two reasons. First, unlike nests of colonial nesting birds (e.g., Red-winged Blackbirds, Erckmann et al. 1990), those of birds in even-aged plots were less common and more widely dispersed. This gave small sample sizes per species. Gray Catbirds, for instance, occupy discrete territories and seldom occur in densities of greater than one pair/ha (e.g., Nickell 1965, Yahner 1986). Thus, nests of all species were considered concurrently to provide adequate sample sizes for statistical analyses.

Second, even-aged plots in central Pennsylvania contain an assemblage of bird species that are adapted to similar brushy vegetation or edges (Yahner 1986, 1987, 1991). Therefore, if the number of nests remaining from the previous breeding season served as cues for nest-site selection by birds in even-aged plots, perhaps any nest placed in vegetation and relatively close to ground level could be interpreted by a variety of coexisting species as a measure of habitat suitability. For example, two abundant and coexisting species that nest in shelterbelts of farmlands in the midwestern United States, the Mourning Dove (*Zenaida macroura*) and the American Robin (*Turdus migratorius*), exhibit pronounced similarities in nest placement (Yahner 1982). This suggests that both species use similar cues in nestsite selection.

This study was funded by the Pennsylvania Agricultural Experiment Station and the Max McGraw Wildlife Foundation. I thank especially thank Tim Kimmel, Brad Ross, and Chuck Yohn for their tireless effort in the field. Also, field assistance from Greg Adler, Brian Burhans, Kelly Bryan, Dorothy Dateo, Gwenn Flickinger, Len Groshek, Mike Hock, Sean Joyce, Greg Matty, Lisa Murphy, Jim Olszak, Ron Rohrbaugh, Andy Ross, Ken Shugart, and Jen Shuman was appreciated.

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# **BOOK REVIEWS**

## CHRISTOPHER W. THOMPSON, EDITOR

The number of academically significant books in ornithology that are published each year increases more than 10% annually. In 1991, nearly 300 were published in English alone. One consequence of this information explosion is that it is increasingly difficult, time-consuming, and expensive for biologists to determine what books are being published, to obtain and evaluate the value of these books, and to do so in a timely fashion. To effectively manage this task, biologists must rely increasingly on publications that note or review recently published literature (e.g., book review sections of major ornithological journals, ornithological newsletters, and the Recent Ornithological Literature supplements to The Auk, The Ibis, and The Emu). This approach alone is woefully inadequate. To date, only 23% of all major ornithological books published from 1987 through 1991 have been reviewed at any length and for only an additional 13% has publication even been noted in either The Condor, The Auk, The Emu, The Ibis, the Journal of Field Ornithology, the Wilson Bulletin, the Ornithological Newsletter of the Ornithological Societies of North America, or the Recent Ornithological Literature supplements to The Auk. The percentage of books reviewed in any one source is, of course, much smaller. In addition, most book reviews are not published for at least two years-and sometimes much longer-after the book is published.

# AN INTERDISCIPLINARY APPROACH TO PARASITISM

A review of **Bird-Parasite Interactions: Ecology**, **Evolution and Behavior.**—Edited by J. E. Loye & M. Zuk. 1991. Oxford University Press.

The study of avian parasites has begun to emerge from the confines of entomology, arachnology and parasitology, to unite with population biology, evolutionary biology and behavioral ecology. How far does *Bird-Parasite Interactions: Ecology, Evolution, and Behavior* advance this emergence? One way to address this question is to recast it according to the organizing principles set out in Catherine Toft's introductory chapter. Do the contributions draw together the relationships between pathogenicity, ecological conditions and host characteristics from an evolutionary perspective?

The chapters tend to focus on the research projects of their authors, and therefore resemble a collection of related journal articles more than cohesive contributions toward a common goal. The best chapters integrate one discipline with another, observational studies with experimentation, and field with laboratory. They provide transitions from the realm of opinion and hypothesis to the domain of scientific discovery. The green

Therefore, I believe that the Book Review section of The Condor should serve three functions. First, it should review at length the books that represent the most significant advances and syntheses in ornithology, and that are likely to be of general interest to readers of The Condor. Second, these reviews should be published as rapidly as possible after each book is published. Finally, because it is neither feasible nor desirable to publish lengthy reviews of all ornithological books, the Book Review section should present a bibliography in each issue of all other ornithological publications of potential academic interest that have been published since the preceding issue of The Condor. Each bibliography will include annotations to book titles that are not self-explanatory, to give readers a useful notion of the content and potential utility of each book. For practical reasons, I only include literature in English. Despite trying to make this bibliography complete, I undoubtedly have omitted many significant publications. So that they can be included in future listings, I would be grateful if readers would inform me of omitted books, errors, and future publications in any language. Thank you for your help in this difficult task.

C. W. T.

vegetation that starlings weave into their nest decimates their mites, cutting the estimated daily blood loss of nestlings by about 20%. Preening defends pigeons against some damaging ectoparasites but not against others, which hunker down in the trenches between barbs clenching the barbules to avoid being swept away. At the other end of the spectrum, a few chapters resemble pilot studies. Most, however, lie in the middle ground; like most journal articles, they will be useful but not exemplary models for integrative studies of the future.

One general weakness is the inattention to the inherent virulence (i.e., level of pathogenicity) of parasites, an attribute that is centrally relevant to each of the major issues addressed in the book. Parasites that evolve toward mild coexistence with their hosts are poor candidates for regulating host populations, driving sexual selection or significantly altering host behavior. A few chapters directly assess the negative effects of parasites on host fitness, and a few others mention that the lack of information about virulence is a major obstacle, but the relevance of general theory about the evolution of virulence is found only in Toft's introductory chapter. Because most parasites of vertebrates are relatively benign, the hit or miss sampling of parasite species is likely to generate more misses than hits. That is, results may fail to conform to theoretical predictions, not because the theory is wrong but because the parasites' effects are too slight to satisfy the theory's underlying assumptions. This ambiguity may explain some of the discrepancies generated by tests of the Hamilton/Zuk hypothesis (Hamilton and Zuk 1982) which proposes that the negative effects of parasitism on host fitness may be generating the heritable variation upon which sexual selection can act.

This need to incorporate theory about evolution of virulence is well illustrated by some of the chapters in the ecology section of the book. The chapters on blood parasites tend towards descriptive tallies of different parasites and their pathological effects. These tallies and the chapters on endoparasitic insects reveal a great deal of variation in the effects of parasitism but inadequately address the central virulence question: Why is it that some of these parasites severely damage their hosts while the effects of others are minor or virtually undetectable? Their analyses of this question are restricted to variation in host resistance or imperfect coadaptation. Current theory, however, implicates the potential for transmission from immobilized hosts as a key factor favoring the more selfishly abusive parasite genotypes. Accordingly, vectorborne endoparasites of humans tend to be particularly damaging (Ewald 1983). Avian malaria and avian pox viruses may be severe in Hawaiian birds, for example, not just because the Hawaiian fauna has had little time to generate resistance; if selection on avian parasites is comparable to that on mammalian parasites, the avian malarias and pox-viruses may be severe at least in part because they are vectorborne.

Some of the chapters on ectoparasites integrate knowledge about harm to the host particularly well. The authors deserve a great deal of credit, but they probably were helped out a bit by the luck of the draw. Negative effects of ectoparasites are positively correlated with their tendency to be studied because larger, more abundant ectoparasites tend to be more harmful, obvious and accessible. The extension of this approach to endoparasites requires a more deliberate application of evolutionary theory about virulence. In this regard it is noteworthy that the strongest support for endoparasite-driven sexual selection comes from vectorborne endoparasites. But even within a single genus of vectorborne parasites, the inherent virulence of parasites can be extremely variable. If an epidemiologist were to assess the demographic impact of malaria on human behavior, ecology and evolution, for example, the conclusions would depend on whether the parasite was the often-lethal Plasmodium falciparum, or one of the other three Plasmodium species which have much milder effects. The most virulent Plasmodium species and subspecies tend to occur in areas where transmission is relatively continuous. In areas where opportunities for transmission are sporadic, the parasites tend to cause milder infections and are prone toward laten-

Recognition of such patterns allows a better understanding of which parasites are most relevant to which theory, but it also suggests a variety of ecological studies of avian vectorborne pathogens, particularly in light of the extensive variation in opportunities for transmission among avian pathogens. Comparative studies could assess, for example, whether vectorborne parasites are more benign when they are sporadically transmitted than when they are continuously transmitted, or when seasonal transmission is predictable as opposed to unpredictable.

This recognition also draws attention to alternative hypotheses. In the chapter on blood parasites and bright birds, for example, Marlene Zuk proposed that tropical residents should be brighter than migratory birds because year-round residency permits tighter coevolutionary coupling between parasite offenses and host defenses. Her data support this prediction. But if patterns of virulence among vectorborne parasites of birds are like those among malarial parasites of humans, those parasites infecting migratory birds should be relatively benign for two reasons. Their opportunities for transmission are more sporadic, and negative effects on mobility may be especially damaging during migration. The net effect is that severe pathogens may tend to be filtered out of migratory populations before sexual selection has a chance to act. Because benign infections are less powerful drivers of sexual selection, the brighter coloration of tropical birds could be explained by the evolutionary effects of migration on virulence rather than (or in addition to) the effects of migration on the tightness of coevolutionary coupling between host and parasite.

The contrasts between experimental and correlational approaches drawn in parts of the section on sexual selection are divisive rather than unifying. These two approaches are sometimes cast as alternatives competing with each other for scientific validity. To consider the "correlational approach" and "the experimental approach" as such alternatives is to ignore the history of science. Correlational studies and experimental studies are tools that need to be used jointly. Only in disciplines such as astronomy and paleontology, where key variables typically cannot be manipulated, should we be content to abandon manipulations of the variables implicated by the theory and its correlational evidence. Conversely, to imagine that experimental tests are more important than nonmanipulative studies is to ignore the reasons for the experiments-to understand the (correlational) patterns observed in nature. The pattern could involve the distribution of sexually selected characteristics across species, ages and sexes, that is, the pattern originally addressed by the Hamilton/Zuk hypothesis. Or, the pattern could be more specific: the brighter coloration of tropical species, for example, or the sometimes positive associations between parasite loads and bright coloration, not directly predicted by the Hamilton/Zuk hypothesis but nevertheless present in zebra finches and lizards, as described in the chapter by Burley et al. The appropriate emphasis is not on whether the correlational or experimental approaches are independently sufficient to test hypotheses. Rather it is to determine which experiments are critical to decipher the processes that generate the correlations.

Perhaps because the authors tended to focus on their own research programs, the book tends to bypass a more general question that may be on the minds of many ornithologically oriented readers. Why should we study the parasitism of birds? Is it just that we haven't cataloged the associations yet, or is it that bird/ parasite associations can foster new conceptual insights? The material in this book can be used to make a strong case for the latter. The life habits of birds offer new twists on established concepts and particularly tractable options for investigating familiar issues. The dependence of birds on nests, for example, facilitates quantification and manipulation of parasites that are (i) in the nest, (ii) in birds that predictably come to the nest, or (iii) in vectors homing in on the nest inhabitants. This dependence similarly facilitates study of antiparasite defenses, for example, with regard to the use of green vegetation in nests. The diversity of avian reproductive systems also offers advantages. Colonial nesting and reuse of nest sites may select for parasites that more ruthlessly exploit their hosts. If swallow bugs use their chick host so extensively that the bird dies, the bugs pay a small price so long as they can move on their own to a new nest. At the other end of the spectrum, a mite transmitted primarily from parent to offspring should evolve to become particularly mild (Fine 1975, Ewald and Schubert 1989). More generally, ectoparasites that are vertically transmitted from parents to chicks should be milder than horizontally transmitted ectoparasites, particularly those infesting colonially nesting birds. Ecologically this variation may result from variation in parasite density per host. Evolutionarily it may result from variation in relative sizes of parasite and host, and the evolved egg-laying predispositions of the parasite: Does it tend to lay few eggs or many eggs per host nest? The observability and manipulability of many bird/parasite systems provides valuable opportunities for investigating such ideas both correlationally and experimentally.

Beyond these particular reasons for spotlighting avian hosts, there is a more general historical reason. The incoming data on parasitism can be embedded in a particularly rich body of knowledge about avian behavior, ecology and evolution. The ectoparasitism of barn swallows, *Hirundo rustica*, presented in the chapter by Anders Møller is a case in point. Previously garnered knowledge about tail length as a sexually selected character (Møller 1988) dramatically enhances the scientific value of the association between mite densities and tail length. If females choose males according to tail length, then an association between mite densities and female choice must also be present. As Møller points out in his chapter, experimental manipulations will be needed to determine whether this association represents cause and effect. The two chapters on sage grouse, Centrocercus urophasianus, drive this point home: experimental reductions of ectoparasite densities among males did not increase their attractiveness to females in spite of a strong association between ectoparasite density of males and their selection by females under field conditions. The low ectoparasite density of chosen males may be an effect of some underlying characteristic of these males that drives female choice or the effects of ectoparasite density on female choice are not adequately simulated by the short-term experimental reductions.

In their introductions, Price and Toft emphasize the value of integrating ecology, evolution and behavior of bird parasites. Although the book that accomplishes this task is yet to be written, *Bird-Parasite Interactions* gives us some glimpses of what that book will be.— PAUL W. EWALD, Department of Biology, Amherst College, Amherst, MA 01002-5000.

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