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BOOK REVIEWS

CHRISTOPHER W. THOMPSON, EDITOR

SPERM COMPETITION: A BROAD VIEW OF MALE PATERNITY EFFORTS

Sperm Competition in Birds. Evolutionary Causes and Consequences.—T. R. Birkhead and A. P. Møller. 1992. Academic Press, New York. 292 pp. with illustrations by David Quinn. $80 hardcover (ISBN 0-12-100540-2); $44.95 softcover (ISBN 0-12-100541-0).

All but the newest comers to avian behavioral ecology can remember when over 90% of birds were decidedly monogamous, and the few exceptions were readily explained in terms of ecological factors. The discovery that female Red-winged Blackbirds (*Agelaius phoeniceus*) mated to vasectomized males laid fertile eggs (Bray et al. 1975), followed by biochemical evidence of multiple paternity and maternity in monogamous species (Gowaty and Karlin 1984, Gavin and Bollinger 1985, Joste et al. 1985), muddied the mating system waters and gave new life to the study of bird reproductive behavior. Careful studies of the behavior of extra-pair copulation (EPC) in color-banded birds (references in Ford 1983, Mock 1983, Birkhead et al. 1987, Smith 1988), additional biochemical evidence that a species' social mating system is not necessarily equivalent to its genetic mating system (Westneat 1987, 1990; Westneat et al. 1990), and the discovery of complexities such as polygynandry in the Dunnock (*Prunella modularis,* Davies 1985, 1991) required reassessment of mating strategies and redefinition of mating systems. *Sperm Competition in Birds. Evolutionary Causes and Consequences* comes on the crest of this wave.

Contrary to implications of the title, this book is more than a study of spermatozoa frantically beating their way up the oviduct in a race to the egg. Birkhead and Møller use the term in a much broader sense, to encompass all the morphology, physiology, and behavior concerned with male aspiration for paternity. The implications of sperm competition extend to mating systems, sexual selection, and sociality, with important evolutionary consequences. Using the same term in both the broad and narrow sense is not particularly problematic for most of the book. However, several switches between the two uses in the first few chapters leaves one wanting terms that clearly distinguish between paternity efforts and competition among sperm cells within the female reproductive tract.

This broad view of the diverse and creative ways in which males strive for paternity is instructive for those outside as well as inside this particular sub-specialty of behavioral ecology. For bird researchers, chapter 3, on avian reproductive physiology, is informative, well-referenced, and more detailed than most ornithology texts. In chapters such as 4 (sperm precedence), 5 (pair copulations), 6 (extra-pair copulation behavior), and 10 and 11 (costs and benefits of extra-pair copulations for males and females), the authors review current knowledge of paternity effort and suggest the types of data needed to test the key hypotheses.

The book suggests that many bird behaviors, including male song, the dawn chorus, territoriality, sociality, and even parental care evolved largely in response to sperm competition. Although some may be skeptical of this sort of "sperm competition is everywhere" view, it can only serve to broaden our traditional views of bird behavior. Finally, few bird researchers will fail to appreciate natural history tidbits such as these: heads of Greater Flamingo (*Phoenicopterus ruber*) females remain totally submerged throughout copulation; one species (we are not told which) has copulated over 1,000 times per clutch; and the Australian Blue-billed Duck (*Oxyura australis*) has a phallus at least 10 cm long, which he trails in the water after copulating.

Chapter 7, on mate guarding, is detailed, comprehensive, and investigates several alternative hypotheses for the proximity of mates during the female's fertile period. Chapter 8 examines frequent copulation as an alternative to mate guarding in species in which it is not possible for males to guard their mates effectively. This otherwise interesting chapter could be stronger on the female perspective. Although higher rates of copulation solicitation by females suggest that females control pair copulations, the chapter is mainly an argument for why males should copulate frequently and neglects to ask what is in it for the female. Petrie (1992) has recently offered one satisfying answer: it is an effective way for females to prevent their own mates from engaging in EPCs.

It is surprising that there are so few studies designed to test the presumed costs and benefits of EPCs. Chapters 10 and 11 are excellent reading for those wanting thesis topics: the current information, multiple hypotheses, and suggestions for distinguishing among them are laid out clearly.

Most of the book's weaknesses can be explained in terms of its primary strength: this is a new and rapidly developing field. Data are simply not available to allow firm conclusions about many of the ideas presented. For example, there is virtually nothing known about sperm precedence in wild birds. Consequently, chapter 4, on sperm precedence and mechanisms of sperm competition, consists mainly of data from insects and domestic birds and could have been included in chapter 3. The latest molecular technique, using DNA microsatellites (Ellegren 1992, Queller et al. 1993), is just now beginning to be used for birds, and so is not mentioned (chapter 12). Given that DNA analysis of paternity is essential to evaluating the outcome of sperm competition, it is surprising that less than one page is devoted to DNA techniques, especially considering the space devoted to topics such as reproductive systems and copulation behavior. Finally, references to the au-

thors' unpublished manuscripts can be frustrating when the data or arguments are not presented in detail in the book. Generally, though, thorough treatment of the relevant conceptual issues compensates when particulars are wanting.

Although *Sperm Competition in Birds* succeeds in reassessing avian mating strategies, we still lack precise ways of defining mating systems, and the book falls short of clarifying the relationship between mating systems and sperm competition. Birkhead and Møller suggest that the mating system and/or opportunities for mate choice determine whether females copulate with more than one male during a breeding cycle (p. 17). An apparent contradiction appears later: "mating systems determine only the type of social bond, and not the sexual relationships between individuals" (p. 244). Most would agree that the number of mates defines the mating system, and not just the converse.

There are now estimates of extra-pair paternity in wild populations of over forty bird species (Table 12.2). In light of genetic data that frequently indicate the genetic mating system departs from the social mating system, particularly in the case of social monogamy, it is time to start specifying to which mating system, genetic or social (sociographic, Gowaty 1981, Wickler and Seibt 1983, Gowaty and Bridges 1991), we are referring. Quantitative descriptions of both social (e.g., percent of population showing polygynous versus monogamous bonds, percent of each sex engaging in multiple copulations) and genetic (e.g., percent of genetically polygynous males or polyandrous females) mating systems should be the rule. Although most emphasis is still on extra-pair paternity in socially monogamous species, it is necessary to quantify accurately the variation in (genetic) reproductive success in other social mating systems, in order to test evolutionary hypotheses.

Given that sperm competition in the broad sense (paternity effort) is intimately entwined with mating system evolution, understanding the evolutionary causes of sperm competition requires a look at factors important in mating system evolution. Ecology, especially resource defensibility, has been considered the single driving force in the evolution and development of mating systems for nearly 25 years (Verner and Willson 1966, Orians 1969, Emlen and Oring 1977). The relationship between sperm competition and mating systems presented (p. 17) mirrors traditional views of mating system evolution: ecology determines mating system determines opportunities for sperm competition. But surely this view is overly simplistic. The ways males respond to sperm competition also influence the mating system; the arrow points both ways. For example, males adopting territoriality as a form of paternity guarding restrict their own opportunities for EPCs (p. 27). Also, in multibrooded species with brood overlap, mate-guarding males may be unable to guard their mates effectively while the female is laying the second clutch (Weatherhead and McRae 1990). In this situation, males may reduce parental care to the second brood, which, in the presence of male-biased tertiary sex ratios, could provide an avenue to serial polyandry (Middleton 1988).

Gowaty and Bridges (1991) have suggested that the growing number of species known to exhibit discrepancies between the social and genetic mating systems require rethinking traditional hypotheses about mating system evolution and maintenance. If it were true that socially monogamous and socially polygynous species were characterized by similar gametic contribution ratios (Gowaty 1981, Wickler and Siebt 1983, Gowaty and Bridges 1991), the ability of males to monopolize resources may have limited influence on the genetic mating system. As new views and definitions of mating systems come about, we may be required to move away from ecological determinism in favor of more complex, coevolutionary models of mating system evolution.

Sperm Competition in Birds inspires the sense that the field of sperm competition and mating systems is rich and exciting, rapidly developing, and full of opportunity. If researchers follow the lead taken by Birkhead and Møller, the field will grow from the foundation laid here to an understanding of the many provocative issues raised in this important book.—KRISTINE JOHNSON, Department of Ecology and Evolutionary Biology, Rice University, P.O. Box 1892, Houston, TX 77251.

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REVIEW OF BIRD MIGRATION

Bird Migration.—Thomas Alerstam. 1990. Cambridge Univ. Press, Cambridge. vii + 420 pp. PB: $34.95, ISBN 0521-4482-20.

This is an English translation of a book published in Swedish in 1982. In the Preface to this edition, the author states that some twenty references to work published during the 1980s were added, so this is essentially the same book as the Swedish edition. The book is thus substantially dated at the time of publication, but this is not so much of a problem as it might seem. Much of the book is descriptive and that information has not been the subject of a lot of recent revision.

The first 226 of the 391 pages of text are devoted to a description of the earth's climates, wind and current patterns and how these are generated, and detailed discussions of the patterns of migration in the various types of birds (birds of wetlands, open water; those that feed on terrestrial plants, fish, insects, seeds; birds of prey). There is much interesting detail in these chapters and in some cases the examples are used to discuss general migration concepts (e.g., redshanks illustrate leap-frog migration). As might be expected, the vast majority of examples are drawn from Old World species. For North Americans this might seem to be a drawback, but I found it most interesting to read about the European systems and try to think of parallels and differences vis-à-vis migration patterns in the Western Hemisphere.

Following this section is one that outlines methods of studying migration and then discusses various aspects of the mechanics of migration, viz., flight speed and altitude, soaring flight, fat as fuel for migratory flight, weather and wind. The final section discusses orientation and navigation. The main areas absent from the book are discussions of the physiological control of migration and the genetics of migratory behavior; there is relatively little on the ecophysiology of migration.

The book's main strength is that it brings together a vast amount of information in an authoritative and readable account. It is the best such compilation available. In a sense, this is also its weakness. It breaks no new conceptual ground, and tends to enumerate the information and various views on issues rather than critique and synthesize. References to primary literature are provided sparingly and unevenly. The sections on orientation and navigation are the ones most affected by the lapse between original publication and translation because this area has seen more research activity.

With this book and two more recent volumes that fill in some of the gaps and recent advances (Gwinner 1990, Berthold 1991), the reader could have at hand a very thorough review of the whole field of bird migration.—KENNETH P. ABLE, Department of Biology, State University of New York, Albany, NY 12222.

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ARE CHICKENS REALLY BIRDS?

Genetics and Evolution of the Domestic Fowl.—Lewis Stevens, 1991. Cambridge University Press, Cambridge, UK. 306 pp., HB: $89.95, ISBN 0-521-40317-0.

Traditionally, avian geneticists working on wild birds, and poultry geneticists seem to live in different scientific universes. The latter are steeped in the traditions of animal breeding and are mainly interested in artificial selection, whereas the former come mainly from the field of evolutionary biology and concern themselves with processes of natural selection. Yet there are so many features which link the two disciplines. Both are trying to understand the genetic architecture of the bird and its response to environmental and genetic alterations. It is a pity, therefore, that there is so little overlap between the literature in the two areas. Un-

fortunately, this book does nothing to bridge this gap. It is written primarily for agriculturalists, veterinarians and poultry breeders. Within this context the first nine chapters of the book outline at an introductory level the basic concepts of Mendelian and quantitative genetics and their relevance to inherited traits in the domestic fowl. These chapters are essentially an update of F. B. Hutt's classic 1949 book *The Genetics of the Fowl.* The final three chapters introduce more modern ideas of protein evolution, immunogenetics and gene cloning. The book is competently written but I found some of the basic concepts, such as linkage, to be poorly explained and, in general, handled much better in most introductory textbooks.

From the viewpoint of the professional ornithologist, the book has some interesting ideas but the reader must seek out the relevance. The author seems unaware of the broader implications of poultry genetics to avian genetics. For example, clutch size and egg size variation have been widely discussed in the ornithological literature in their evolutionary and genetic context. Poultry breeders too are interested in the genetic and environmental causes of egg and clutch size variation; and much of the research in this area tells us some of the ways in which selection has influenced or could operate in this variation. The author seems unaware of this, but there are several lines of research reported in the book which may interest ornithologists studying evolutionary processes. The work of Fairfull and Gowe on selection on egg, clutch and body size surely is important for those ornithologists working on questions of trade-offs and the relationships between body size and clutch and egg size. It is about time that both ornithologists and poultry scientists recognized that domestic fowl are actually birds!

I feel that Stevens has missed an opportunity to bridge the gap between ornithology and poultry science, but if we as avian geneticists ignore his book, we are just as guilty of ignoring research which is of relevance to our discipline.—FRED COOKE, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada.

A USER'S GUIDE TO CHICKADEES

The Black-capped Chickadee. Behavioral Ecology and Natural History.—Susan M. Smith. 1991. Cornell University Press, Ithaca, NY. xi + 362 pp. HB: $46.50, ISBN 0-8014-2382-1; PB: $17.95, 0-8014-9793-0.

The genus *Parus* is a monophyletic group of more than 50 species of small cavity-nesting passerines, well-represented in North America and the Old World. Their abundance and tolerance of humans have made them popular subjects of reproductive and behavioral studies, and their subdivision into ecologically and morphologically distinct subgenera makes them ideal for comparative studies. North America's best known parid, the Black-capped Chickadee (*Parus atricapillus*), is certainly one of the most-studied birds on Earth.

In this readable and authoritative book, Susan M. Smith, whose first published work on Black-capped Chickadees appeared more than a quarter century ago, has summarized the extensive literature and her own intensive research on the species. The result is a largely successful synthesis, accessible to the layperson and undergraduate, yet useful to professionals as a review of a vast and unwieldy literature. The model for the book appears to be Britain's New Naturalist series, which has successfully produced data-rich popularizations for decades. In particular, *The Black-capped Chickadee* will be a companion and in some respects successor to C. M. Perrins's widely-cited *British Tits* (Perrins 1979).

This book will be extraordinarily useful to beginning researchers contemplating a study on a species of chickadee. In minutes the state of knowledge on any subject can be obtained. The phenological organization of chapters will tell a student what can be studied in the time one has available. And for one who has no problem in mind, Smith offers a multitude of suggestions. Additionally, an early chapter on study techniques, as well as results presented throughout the book, will suggest how to do the project. Finally, conceptual development is limited to a level understandable to undergraduates, so the student will appreciate why the study is or is not interesting to ornithologists.

Obviously, a book that is so attractive to beginners may not be as enticing for knowledgeable veterans. Indeed, there are places where the link between chickadee phenomenology and current theory could be more substantial. Nonetheless, Smith's assessment of existing knowledge is critical and thought-provoking, with frequent references to authoritative works on specific subjects. Moreover, so much work has been done on this and related species that almost every section will provide a fresh perspective for workers unfamiliar with parid biology.

There are ten chapters. The first is a brief summary of natural history, something of an abstract in that the entire book is a detailed summary of natural history. Chapter 2 is an introduction to simple study techniques. Chapters 3 and 4 treat foraging and communicating, respectively. The next three chapters describe the annual cycle, and are followed by two more function-defined chapters on physiology and population dynamics. The reason for this arrangement is not obvious, except that the physiology chapter (8) focuses on surviving in cold weather, the season covered in Chapter 7. The final chapter suggests avenues of future research.

Chapter 1 provides a brief overview of natural history, but also tackles the thorny problem of species-level relationships. Without invoking a particular species concept, Smith mentions the splitting of *P. montanus* (the Willow Tit of Eurasia) from *P. atricapillus,* and thoroughly reviews cases of hybridization with the Carolina Chickadee (*P. carolinensis*), but not with the Mountain Chickadee (*P. gambeli*) (Howe 1985). She favors the view that mixed song-repertoires are indicative of interspecific song-learning and not introgression, leading to the conclusion that the Carolina and Black-capped Chickadees are indeed distinct species, a view supported by recent biochemical studies. The chapter closes with a detailed section on subspecies, which seems anachronistic until one realizes that measurements are provided to facilitate sexing birds in different parts of the vast range of this species.

In her techniques chapter, Smith argues that color-

band combinations probably do not bias the fitness of chickadees, and cautions against invasive procedures such as laparoscopy. A good review of the unreliability of plumage characters for sex determination is followed by a seeming endorsement of discriminant function analysis, although the 90% accuracy of that technique is certainly not adequate in my opinion. She reveals that Black-capped Chickadees, which unlike most parids do not readily use nest boxes, do find them somewhat more acceptable if they have been filled with sawdust. This chapter is decidedly low-tech, not mentioning molecular techniques that are now routinely performed by undergraduates or even sound recording and analysis.

Chapter 3, on food and feeding, provides a stimulating summary of recent work on foraging and caching behavior in chickadees, with some additional information from Great Tits (*P. major*). There is a rudimentary discussion of optimal foraging theory, but recent complications are not mentioned. Sherry's work on the relationship between size of the hippocampus and caching ability is described in more detail.

Chapter 4 (communication) not only provides a complete catalog of vocal and visual displays, which will be useful for anyone attempting to understand the behavior of these birds, it also gives a taste of the cutting edge of acoustic research on chickadees. This includes individual and dialectal variation in "*gargle*" calls, constancy of frequency ratio in "*fee-bee*" songs, and combinatorial qualities of the "*chickadee*" vocalization.

The middle three chapters divide the annual cycle into early and late breeding seasons and the nonbreeding season. These 133 pages are perhaps the most valuable but also the least enjoyable part of the book. The phenological sequence separates subjects that might be treated together, e.g., clutch size and reproductive strategies, but is perhaps the most efficient way to present such a large amount of information. In Chapter 5 clutch size is reviewed, but without mention of David Lack's ideas; Smith favors the emerging view that each clutch is optimal in size for its parents. Chapter 6 covers hatching, provisioning of young, and dispersal. Heritability estimates for Great Tit dispersal distances are reported, without mention of van Noordwijk's refutation of the methods used to calculate them. The chapter closes with a thorough review of brood size manipulations in European tits, which provide "clear evidence of the cost of reproduction." Although nonparids are not mentioned here, it is still a good introduction to the empirical side of this question.

Group-living in the nonbreeding season is the focus of Chapter 7. Chickadees form pairs as they enter winter groups, the size and age structure of which varies with local food abundance. Group territoriality is common where food is evenly distributed, but local concentrations of food (feeders or deer carcasses) cause frequent intrusions and territoriality breaks down, as it does when natural conditions are unusually stressful. Smith's main focus in this chapter, however, is group composition. This is her bailiwick. Her ability to see beyond paradigmatic social structures has given us both sparrow underworlds and flock-switching chickadees. Here she gives the most detailed description and justification of her reasoning available. She now identifies three categories of mobile elements: dominant wanderers (evidently prospectors for rich food sources), visiting migrants, and flock switchers. Switchers are subordinate birds that are members of several social groups at once, until they insert near the top of a dominance hierarchy by pairing with a high-ranking bird that has lost its mate. Other high-ranking birds do not move up to fill this vacancy, or if one does, its place is taken by a switcher. If a switcher loses its new mate, it will not pair with another switcher, it will resume switching. This complicated system is written off by some skeptics as an artifact of the unlimited artificial food available in Smith's study area. This may be true, but switching has now been recorded elsewhere, and even if provisioning has "caused" this phenomenon, the way the birds respond to the artificial situation is of great theoretical significance. After all, we subject birds to a variety of artificial conditions to learn what their physiological limits are, why not do the same with sociality?

Smith treats thermoregulation and weather-dependent foraging in "Surviving the winter" (Chapter 8). Winter residency in cold and snowy climates produces special challenges for small birds, which chickadees meet in numerous well-studied ways. Interestingly for a social species, group roosting is not routinely practiced, but hypothermia is, according to one American study and another on the Willow Tit. Conflicting data on hypothermia from Alaska suggest that this phenomenon is not completely understood yet. Also barely mentioned is heat stress, which may be the reason territorial defense decreases as the spring advances.

The chapter on survivorship and population dynamics proceeds through anecdotal material on predators, theoretical approaches to alarm-calling (it is still unclear whether callers are helping or misleading their flockmates), the use of alarm calls to gain access to food, and the impact of parasites and interspecific competition, before revealing that we have no knowledge of age-specific survival in North American chickadees (J. Howitz, D. Dahlsten, and A. McCallum could correct this situation by publishing results of their long-term studies). Smith introduces unpublished data showing that breeding numbers have been stable over a 10-year period in her western Massachusetts study area, which appears representative of the species and genus. (She evidently locates nests but does not band young or assess nesting success.) Several European species have marked density-dependent dynamics, but once again no data are available for America. The situation might be different if Black-capped Chickadees used boxes more readily, and if House Wrens (*Troglodytes aedon*) did not destroy box nests so readily.

The dual nature of the social system makes questions about population regulation two-headed as well. Smith considers a variety of possible controls of breeding numbers and concludes that territoriality does regulate densities, provided poor survival has not depressed numbers below the regulated level. Winter flock sizes appear related to food abundance, with local and regional movements taking individuals, mostly young birds, from areas of low to areas of high food availability.

Smith closes with numerous suggestions for future research, most at the master's level or below. This represents more of a wish list, things that she and others, including me, would like to know about chicka-

dees, than conceptual problems that can be particularly well-addressed with studies of these birds. Some of the latter, in which the attributes of Black-capped Chickadees augur well for ground-breaking results, include (1) caching behavior and its relation to overwinter survival and social relations, (2) physiological and social aspects of winter survival, (3) effects of Tufted Titmouse range expansion on chickadee population dynamics, (4) cultural transmission of predator recognition, (5) the truthful and deceitful use of alarm calls, and (6) geographic variation in these attributes across the broad latitudinal (Alaska to New Mexico) and longitudinal (Atlantic to Pacific) range of the species.

A glossary of the jargon that is second nature to professionals but largely incomprehensible to lay readers, plus parenthetical explanation of terms and concepts in the text, make this an unusually "user-friendly" book. The book is richly illustrated with black-and-white photographs, line drawings, and an abundance of graphs and tables. Line drawings (creditably executed by Smith herself) on each figure indicate the species of parid that provided the data, a handy characteristic for the browser.

The Paridae are subjects of an immense literature, and Smith has cited it extensively. Nearly half of the more than 560 references treat North American chickadees, mostly *P. atricapillus*, and another 50 treat European chickadees, especially the Willow Tit, which was once considered conspecific with the Black-capped Chickadee. The Great Tit literature is also liberally sampled. Smith has not overlooked any important published work on chickadees that I can think of, but she has omitted reference to some good theses, e.g., Munzinger (1974), Howitz (1981), Howe (1985). Nonetheless, the reference section is a trove of citations.

In summary, *The Black-capped Chickadee* is a useful synthesis of published material. It does not break new ground conceptually (although many of Smith's papers do), nor is it a monographic treatment of single population, e.g., Koenig and Mumme (1987). It does provide immediate and easy access to virtually everything known (as of 1990) about one of America's best known and most easily studied birds. Every college library should have a copy, as should everyone who teaches ornithology. No one interested in sociality can afford to ignore Chapter 7. Many others will find some or all of the book useful. I hope this successful blending of the popular and technical will inspire other experts to do the same for their species; it's a great story, well told.—D. ARCHIBALD McCALLUM, Department of Biology, College of Charleston, Charleston, SC 29424.

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