

## **Animal Communication Networks**

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## BOOK REVIEWS

EDITED BY DAVID L. SWANSON

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**Antipredator Defenses in Birds and Mammals.**—Tim Caro. 2005. University of Chicago Press, Chicago, Illinois. 592 pp., 15 halftones, 130 drawings. ISBN 0-226-09436-7. \$38.00 (paper).

In this book, Tim Caro summarizes the massive literature on antipredator defenses of birds and mammals. He first considered writing about all animals but decided that this would be too much. He next considered limiting himself to mammals, but found that the crucial work he wanted to discuss was done with birds. The result is a fascinating book that compares and contrasts what we know about defenses in birds and mammals. The book has something to offer for almost any ornithologist. Here, I review the book's contents and major conclusions to highlight its remarkable breadth.

The book is organized along the sequence of interactions within a predator-prey encounter, starting with the ways prey avoid being found by predators and ending with defenses at the point of capture and consumption. This is a highly effective organizational scheme, though admittedly some defenses work at multiple junctures. The text starts with a careful definition of terms. The author points out that we often speak of alarm or warning signals without data demonstrating alarm or warning. The first chapter also discusses predator recognition, as recognizing predators is important to avoiding them. Predator recognition shows both strong innate tendencies and considerable learning.

The first defense against predators is to avoid being detected. This often involves morphological traits such as crypsis, countershading, or contrasting colors that disrupt the outline of the body. Female birds are likely to be cryptic when they perform nest activities alone and in species that suffer heavy nest predation. Mammals and birds also provide potential examples of countershading, disruptive coloration, and polymorphism, but no clear evidence that the observed patterns are effective in avoiding predation. The colors and patterns of bird eggs may be cryptic, but the potential for such a function is not well understood. The nests of birds show better evidence for concealment than do the eggs within them.

Animals can also change their behavior to avoid being detected by predators. These changes principally involve concentrating activities in times and places with few predators and reducing dangerous activities, notably foraging and reproduction. Birds often place their nests in relatively safe places and behave around the nest in ways that limit detection by nest predators. Risk of predation alters what, where, when, and how much birds eat. In contrast, reproductive suppression seems not to be studied in

birds. Caro suggests that adult birds rely less on behavioral mechanisms to avoid being detected than do adult mammals, and that birds mainly seem to avoid detection by aerial rather than terrestrial predators.

If predators detect potential prey, the prey may detect predators at a distance before the predators can attack. Caro devotes a chapter to vigilance and group size. Safety-in-numbers drives the well-replicated pattern of declining vigilance with increasing group size. Caro discusses why individuals do not "cheat" and avoid vigilance. The best-documented suggestion is that they would give up reliable personal information and be left with unreliable information generated by others.

Vigilance is affected by many factors besides group size, including age, sex, and dominance status. In addition, animals tend to be more vigilant at the edges of groups, with fewer close neighbors, and when farther from safety or in environments that can conceal predators. Adults with young often show heightened vigilance, though this is better documented for mammals than for birds. Caro emphasizes that these factors are often studied separately but probably interact in nature and pronounces, "Rather than demonstrate that a particular factor exerts an influence, it would be more profitable to reexamine its influence, taking many confounding variables into account" (p. 174). Across species, vigilance often depends on body size, attack rates, and how prey detect and escape from predators, but we are not good at predicting species differences in vigilance *a priori*. Caro also reviews sentinel behavior, including a reference unknown to me after a dozen years working on the subject.

Individuals who have detected a predator often give warning signals. Caro points out that the costs of giving warning signals seem to be very low in some situations and with some predators. He takes issue with the interpretation that callers lower the fitness of receivers in those cases where callers have higher fitness than receivers. Calls could be mutually beneficial in these cases. Deceptive alarms during foraging are a possible exception to this rule. Different calls may be associated with response urgency or escape tactic. Responses to warning signals develop rapidly in mammals though at the same time youngsters call too promiscuously and only gradually limit themselves to genuine threats. I suggest that these principles also apply in birds but have not been documented in the same detail as in mammals.

Prey also signal to predators that they are unprofitable to attack. Aposematic coloration is a clas-

sic example. Some birds, such as pitohuis, are known to be poisonous and many birds are strikingly colored. One possibility is that many birds signal their unprofitability through their plumage, with poisons being one aspect of unprofitability. Unfortunately, experimental evidence is decidedly mixed and we know almost nothing of the natural encounters from the predator's point of view. Animals may also behaviorally signal that they will be difficult to capture. Such signals are widespread in mammals and may be common in birds. Examples range from tail flicking by moorhens to singing by skylarks while being pursued by Merlins. In my opinion, many warning signals given to terrestrial predators could also function as pursuit deterrent signals.

When an attack happens, potential prey may benefit from being in a group because the attacker can only kill one group member, because group members detect the attack sooner, or because the predator fails to kill any group member. These benefits are unequally distributed across groups, including colonially nesting birds. Across birds and mammals, group living is more common in open-country species that rely on vigilance and escape to survive.

Prey may have morphological or physiological defenses against attack. The simplest defense is size. Escape flight in birds depends on both size and wing shape. Spines and quills are most common in medium-sized mammals but are apparently lacking in birds. Birds may defend themselves with beaks, talons, and spurs, though these primarily function in feeding and sexual selection. Some birds may employ malodorous defenses and eiders apparently produce especially repellent feces only during seasons when they defend nests. Questions abound for someone with a keen sense of smell and a strong stomach.

Caro devotes a substantial chapter to nest defense. Birds both harass and distract potential nest predators. Even though the costs of nest defense are rarely measured directly, nest defense shows many features that appear sensible from cost-benefit analysis in a life history context. Intensity of nest defense is greater for more valuable broods, whether these are larger or older. Differences between the sexes in nest defense are less clearly understood. Caro emphasizes that offspring may play a part by keeping silent while their parents are noisy.

Prey may mob a predator to encourage it to hunt elsewhere. Mobbing also conveys information to conspecifics and can lead to the cultural transmission of fearful responses. Although the definition of mobbing allows for solo efforts, a mob of one is not the same as a mob of many: mobbing behavior works best in larger groups. Mobbing is often important in colonial species and often birds of one species benefit by nesting with members of more pugnacious species. This association may be commensal, mutualistic, or even parasitic.

Even when an attack is well underway, prey can employ flight and "behaviors of last resort." Their flights can be to vegetation or into the air and may involve aerial maneuvering. Such maneuvering is affected by body weight and fat reserves. Even when

contacted by a predator, prey may scream or play dead. The evidence about fear screams does not definitively support any of the current hypotheses and perhaps these screams serve several functions.

Caro ends the book with a chapter on "Framing questions about antipredator defenses." He emphasizes that morphology and behavior act synergistically in defensive complexes. Caro believes that predators and prey species are rarely linked intimately enough to drive coevolutionary changes in each other, and this may help explain why antipredator defenses are imperfect. Caro asks ten pressing questions about antipredator defenses. Of these, five are questions about the actions of predators. The other five involve predator recognition, multifunctional defenses, and the interactions of morphology, behavior, and coloration. These questions flow from the detailed review in the first twelve chapters of the book.

In this book, Tim Caro acts as an authoritative guide to the literature. The tour shows many places that merit revisiting and many places where further work is needed. Commentary is limited. For the most part, the data speak for themselves and the author does not interrupt. He has, of course, done a huge job in lining up what studies speak, and in what order. Tables and figures often come directly from the original studies. Other tables summarize across studies. For me, these took some study because abbreviations were not always obvious and citations were given in numbered footnotes. This book is a marvel of care, organization, and production. The most serious error I noted was confusing which vigilance experiments used Dark-eyed and which used Yellow-eyed Juncos.

Who should read this book? Anyone with a research area involving birds or mammals could benefit from the context provided by this book. Anyone looking for a research area will find a gold mine of carefully weighed studies and fascinating natural comparisons, e.g., alarm calls of Australian passerines are not the high-frequency single tones we know from the Palearctic (p. 184). Furthermore, many will want their own copy to reference repeatedly. I am sure I will use this book week-in and week-out for years to come. I applaud Tim Caro for pulling together this massive synthesis and recommend the book wholeheartedly.—PETER A. BEDNEKOFF, Biology Department, Eastern Michigan University, Ypsilanti, MI 4817. E-mail: pbednekof@emich.edu

**Animal Communication Networks.**—Peter McGregor [editor]. 2005. Cambridge University Press, New York. 672 pp. ISBN 0-52-182361-7. \$130.00 (cloth).

In compiling recent research advancements and prospects in the expanding area of animal behavior, this volume presents a perspective that can increase our understanding of animal communication: communication networks. *Animal Communication Networks* is based on the fact that communication is an inherently social behavior, and that many signals used in communication travel farther than the average distance between animals. However, the wider social context is often ignored in studies of

animal communication and has rarely been considered explicitly. In adopting a network perspective, we are able to identify and explain communication behaviors that cannot occur in a dyad, such as the eavesdropping behavior of birds. The book covers several taxonomic groups (from insects to humans), and several types of signals (including visual, acoustic, and chemical). It also highlights disciplines that interact with the study of communication, such as psychology and physiology. *Animal Communication Networks* offers convincing evidence for the existence of communication networks presented by a diverse group of authors, including many prominent ornithologists.

The book is divided into four parts. Part 1 deals with communication behaviors, such as audience effects and eavesdropping, that involve three or more individuals and therefore fall outside of the traditional dyadic approach to communication. Part 2 explores concepts that are valuable to consider from a network perspective, such as predation and mate choice. Part 3 is grouped taxonomically, from crabs to humans, because characteristics specific to different taxa influence the properties of communication networks. Part 4 contains chapters that link communication networks to other disciplines in biology. Of the 26 chapters, each written by a different group of authors, 10 are specifically about communication in birds, including such topics as mate choice, male-male song contests, and nestling begging. In this review I will focus on these chapters and evaluate how this book may be useful to ornithologists.

In Chapter 2, Tom Peake discusses eavesdropping, focusing on the costs, benefits, and implications of eavesdropping behavior on signaling interactions. Because eavesdropping is a receiver behavior that is only possible in a communication network, I think this is an excellent way to begin the book. Peake makes convincing arguments about the occurrence and significance of eavesdropping with many examples drawn from the ornithological literature, and prompts researchers to take this behavior into account when studying animal communication. Chapter 3 deals with social eavesdropping and the acoustic signals of birds. It identifies potential costs and benefits of eavesdropping and uses information about how bird song transmits to explore how eavesdropping is best achieved. In this chapter, Torben Dabelsteen discusses how communication behavior can be made public, private, or anonymous, and how eavesdroppers should behave. Chapter 3 is short on data, but contains several suggestions for avenues of future research. Figure 3.3 highlights the results of an interesting study on the movement patterns of female Great Reed-Warblers (*Acrocephalus arundinaceus*), in which researchers found that females positioned themselves at equal distances from neighbouring males to listen in on vocal interactions. Apart from this example, much of the evidence used to support these ideas is experimentally based but not tested in a natural setting. This is a common thread in the book; most authors conclude their chapters with a statement of how natural, field-based research is needed to confirm experimental results derived from the laboratory or other artificial situations.

Ricardo Matos and Ingo Schlupp introduce the idea of audience effects in Chapter 4. They highlight that audience effects and eavesdropping are essentially opposite sides of the same coin, depending on the individual of interest. The authors begin by presenting useful, clear, workable definitions to introduce the topic. They include a section on human behavior that seems misplaced in light of the rest of the chapter, and was too short and superficial to be very informative here. Victory displays are the topic of John Bower's Chapter 6. He pools the available information on victory displays and interprets their functional significance from a network perspective. The main evidence he uses to illustrate victory displays is an observed increase in the winner's song rate after a contest in Song Sparrows (*Melospiza melodia*). However, in this case it is difficult to unambiguously distinguish a victory display from the interaction itself, especially when the signal used in the victory display was also used in the interaction (i.e., song), and it is not a display unique to winners of contests. Victory displays are virtually unexamined in birds, but Bower provides some insightful discussion to stimulate research on this topic. Part 1 ends by prompting researchers to incorporate eavesdropping into theoretical models and to look for evidence of eavesdropping in natural contexts.

In Chapter 7, Ken Otter and Laurene Ratcliffe present evidence to suggest that a communication network is a likely context for mate choice, because females are able to assess the widely broadcast mate attraction signals of multiple males. They focus on primary and secondary mate choice based on acoustic signals in territorial songbirds. They discuss how mate choice is achieved, comparing simultaneous and sequential assessment tactics, and how female movement can be used to infer sampling within a network of males. I think this chapter was one of the strongest in the book; it provided compelling evidence for female assessment using a communication network perspective. They included a section on habitat alteration that seemed out of place, but this did not detract from the overall strength of the chapter.

Nestling begging has traditionally been considered in a dyadic context, between the brood as a whole and the parent. In Chapter 9, Andrew Horn and Marty Leonard reveal how considering begging as a network can yield new insights into begging behavior and provide a model system to study the evolution of signaling. Data in the form of tables and figures were absent from this chapter, but overall the authors made a convincing argument for how concepts from communication networks can be applied to a variety of model systems previously considered dyadic systems. Section 2 concludes with a discussion of future challenges in studying a broader view of communication in model systems.

In Chapter 14, Marc Naguib combines current knowledge on strategies of vocal interactions in songbirds with concepts of territorial behavior and territorial settlement. Naguib emphasizes that singing strategies have evolved in a network environment, and thus should be studied from a network perspective. This chapter would be of interest to anyone

studying territorial songbirds, and outlines ideas to consider when conducting field studies. In Chapter 15, John Burt and Sandra Vehrencamp consider the dawn chorus of songbirds from a network perspective, which seems an approach likely to reveal the function of this behavior. They begin the chapter with an excellent figure outlining three basic network structures, which is a useful starting point for a reader unfamiliar with communication networks. In particular, they outline the results of their research on interactions between neighboring tropical wrens. They used a microphone array, a new tool for investigating networks, to examine the properties of interactions among four focal males. This chapter provides compelling preliminary data, uses informative graphs to illustrate key points, and provides a good amount of background information without being overwhelming. Section 3 concludes by posing important questions for future research: how many individuals are encompassed by a signal, and what is the extent of a network?

In Chapter 20, Ulrike Langemann and Georg Klump discuss perception and acoustic communication, arguing that the sensory abilities of the receiver are often overlooked. This chapter unites communication networks, psychophysics, and physics, but is not a stand-alone chapter. For a reader new to the communication network idea, this is not the place to start. The chapter is full of physics, equations, and detailed methodology. Using this approach, the authors provides new tools to study communication and perception, but these tools are not necessarily applicable to communication networks. Irene Pepperberg highlights the need to consider nontraditional forms of experimentation on cognitive aspects of networks and avian capacities in Chapter 24. She focuses her discussion on transitive inference, and offers insight as to how to test this idea in future studies. She cites specific examples from the literature that support, or at least prompt further investigation of, transitive inference, and concludes that birds demonstrate complex cognitive processing skills. This chapter has several ideas that parallel earlier chapters on eavesdropping with an emphasis on territorial songbirds. Although Pepperberg's chapter is compelling, I think Section 4 is the weakest part of the book. While the connections to other fields of study are potentially fruitful avenues for future research, these connections are at present only minimally developed. Thus, it seems premature to include these superficial discussions in the first edition of this text, and after three strong sections based on empirical evidence from the laboratory and the field, Section 4 was a rather disappointing way to end the book.

In sum, I would recommend *Animal Communication Networks* to anyone interested in discovering a new approach to the study of animal communication, and I think that it will be especially appealing to those involved in research on acoustic communication in songbirds. Although a few chapters seem inappropriate for the book, overall it is a well-written compilation of a new and exciting avenue of research in animal communication.—LAUREN P. REED, Department of Biological Sciences, University of

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#### BRIEFLY NOTED

Washington and Beyond: Birds of Washington State and Shorebirds of North America

**Birds of Washington: Status and Distribution.**—Terence R. Wahl, Bill Tweit, and Steven G. Mlodinow [editors]. 2005. Oregon State University Press, Corvallis, Oregon. 448 pp. ISBN 0-87071-049-4. \$65.00 (cloth).

This book represents the first comprehensive treatment of the birds of Washington State since the 1953 publication of Jewett et al. *Birds of Washington State* (University of Washington Press, Seattle, Washington). Its subtitle aptly describes the content of the book, which provides a current summary of the status and distribution of birds in the state. The book is limited to this focus for the most part; it is not a handbook to the birds of Washington State, like the recent Marshall et al. (eds., 2003) *Birds of Oregon: A General Reference* (Oregon State University Press, Corvallis, Oregon) is for the avifauna of the state's neighbor to the south. Like Oregon, however, Washington has an abundance of habitats ranging from marine and coastal environments to high desert, and also including temperate rain forests and mountains with Cascade and Rocky Mountain influences. This variety of habitats results in a large list of bird species documented for the state, and 483 accepted species are included in the book.

The contents of the book include seven introductory chapters, the species accounts, which comprise the bulk of the book, and some accessory materials following the species accounts. The first chapter describes the species account template and provides definitions for abundance and status classifications. Abundance and status are given separate classifications in this book, with abundance for regular species categorized as abundant to rare, and status categorized as resident, summer, winter, migrant, visitor, or vagrant. Irregular species are classified as very rare or casual, with the definition of casual being "not expected to occur again." There is no accidental status category, as there is in most books of this type, which may lead to some confusion within the casual category. Chapter 2 provides an extensive classification of habitat types and a detailed comparison of previous attempts to classify wildlife habitats within the state. Chapter 3 describes the creation of the excellent range maps included in the species accounts and Chapter 4 contains an overview of conservation issues for Washington birds. The conservation issues are treated by habitat types, and problems faced by Washington birds parallel those in the Pacific Northwest and Great Basin region in general, with some of the most pressing issues including clear-cutting of old-growth forests, fire suppression effects, loss of riparian habitats, and loss of coastal wetlands. The conservation chapter closes with a review of state and national conservation efforts related to birds, but does not include an explicit plea for amateur



ornithologists to become involved in these conservation efforts. Chapters 5–7 deal with a brief history of ornithology in the state, a description of data collection methods and sources of data for the book, and changes in the status and distribution of birds in the state since 1950, roughly the date of the last comprehensive treatment of the birds of Washington (Jewett et al. 1953), focusing on well-documented changes in populations. This latter chapter concludes that the species accounts “indicate or suggest that over one-half of the species currently known in Washington have changed in status or populations over the past 50 years” (p. 26).

These chapters are followed by the species accounts, which are split into “accepted species” and “other species,” the latter of which includes escapees and unsuccessful introductions, along with hypothetical species of uncertain origin. Species accounts for accepted species include status and distribution, habitat, remarks (e.g., taxonomy, identification, conservation concerns, need for future studies), and noteworthy records (e.g., early or late dates, out-of-range occurrences). Also included are distribution maps and a bar graph of seasonal timing within the state. Closing materials include an extensive bibliography, an appendix outlining habitats and habitat associations for regular species, short biographies of contributing authors, and an index of birds treated in the text. The book is effective in updating the status and distribution of birds in Washington State and will serve as an invaluable reference to both academic ornithologists and birders interested in the avifauna, and in avifaunal changes, of the Pacific Northwest.

**Shorebirds of North America: The Photographic Guide.**—Dennis Paulson. 2005. Princeton University Press, Princeton, New Jersey. 361 pp. ISBN 0-691-12107-9. \$29.95 (paper).

The increased attention devoted to shorebird research over the past 15 years and the release of the second edition of the U.S. Shorebird Conservation Plan (Brown et al. [eds.], 2001, Manomet Center for Conservation Sciences, Manomet, Massachusetts) has stimulated renewed scientific interest in shorebirds. Many shorebirds present identification difficulties, so this book fills an important need for researchers involved in survey work for conservation purposes, as well as for birders interested in delineating the different species. This represents the first comprehensive photographic guide to North American shorebirds and treats 94 species, including species that are rare or accidental in North America.

This book is an identification guide, not a book on shorebird biology that includes information on identification. The author states in the first sentence of the Introduction that “this is a book about shorebird identification” and the book does not stray from its intended purpose, so other literature is necessary to cover additional aspects of shorebird

biology. Photographic guides sometimes suffer from uneven quality of photographs, but the photographs presented here are uniformly excellent. In my opinion, this is one of the best photographic guides available, as it provides a wealth of photos for each species, illustrating seasonal, geographic, and age-related variation in plumage. Moreover, the author is one of the foremost experts on shorebird identification and his expertise is clearly evident throughout the book. The bulk of the book consists of species accounts for the 94 species, and the species accounts follow an introductory chapter. This introductory chapter includes information that is pertinent to shorebird identification, such as shorebird anatomy, plumage variation, molt, and a cursory treatment of behavior and vocalizations. A short section on hybrids with some accompanying photographs is a particularly interesting part of the introduction. Finally, very short sections on shorebird distributions, briefly mentioning differing migration strategies among shorebirds, and conservation, which includes a plea for amateur birders to become involved with local or large-scale shorebird monitoring programs that have recently been initiated in many locations, are included in the introduction.

The species accounts are arranged according to a template that includes plumage descriptions, subspecies designations, identification information, and habitat and range descriptions. No range maps are included along with these descriptions, and the author specifically refers the reader to other field guides for maps. However, I felt that thumbnail maps included in the species accounts would be useful and wouldn’t take up much space. The species accounts are relatively light on text, but heavy on photographs, and much of the important identification information is included in the figure legends. Comparing the text pages devoted to species accounts in this book with that in Paulson’s (1993) *Shorebirds of the Pacific Northwest* (University of Washington Press, Seattle, Washington) illustrates this approach nicely. As examples, dowitchers are covered in only four pages of text (excluding photos) in this book but take up 12 pages in Paulson (1993). Similarly, stints are covered in 14 pages of text in this book, but 31 in Paulson (1993). This text-light and photo-heavy approach allows for a lot of variation in plumage due to age, sex, season, and geography to be dealt with in a concise fashion in this book, and I found this to be an effective presentation method.

This book is an indispensable guide for shorebird identification and will be an exceedingly useful resource for scientists training field workers in shorebird identification. It will also likely serve as the primary shorebird reference for birders, and the book is portable and sturdy enough to stand up to substantial field use.—DAVID L. SWANSON, Department of Biology, University of South Dakota, Vermillion, SD 57069. E-mail: David.Swanson@usd.edu