Book Reviews

The Acquisition and Functions of Vocal Behavior

Bird Vocalizations. Their Relations to Current Problems in Biology and Psychology. Essays Presented to W. H. Thorpe. R. A. HINDE, Ed. Cambridge University Press, New York, 1969. xvi + 400 pp., illus. $13.50.

Hinde has two purposes in collecting this diverse set of papers dealing with bird vocalizations. One is to provide a tribute to W. H. Thorpe, who has done much to stimulate research with bird songs, and with whom most of the contributors have worked. The other is to "review some of the more important areas of advance" since Thorpe's book *Bird Song* in 1961. By no means all areas of active research with bird vocalizations are represented, and at least half of the papers are reviews only of the work of their authors and their students. But these are not important criticisms; the breadth of the collection is stimulating, the assortment is timely, and the book is a fitting tribute to Thorpe. Despite Hinde's instructive introductory prefaces to the book's six segments, however, it is too diverse to be reviewed as a unit, and must be considered topic by topic.

To begin, Marler offers a helpful guide for interpreting tonal quality in sonagraphic analyses. While sonagrams, used primarily to study the distribution of frequencies in time, have been essential to almost all modern work with bird vocalizations, few have probed far into how the characteristics of these records relate to the sounds we hear. Happy with a means of obtaining repeatable visible representations of some of the physical characteristics of sounds, most are satisfied to distinguish the signal from the noise. Marler now shows us how to understand much more, at least with respect to timbre of steady-state sounds. The discussion is well illustrated with sonagrams of pure tones whose frequencies are modulated at different rates and to different extents and which are compared with various bird vocalizations as analyzed with different frequency band filters.

Lorenz remarks in the foreword that the main concern of Thorpe's research has been with the ontogeny of behavior. Hinde reviews Thorpe's principal findings on the development of chaffinch song and discusses the "template" that birds are postulated to use as a model, approximating it through experience, of species-specific song. Among the predictions of the template postulate is that deafening a bird that has heard song but not yet sung should interfere with song development by decreasing its feedback for comparison with its model. Konishi and Nottebohm review the studies on acoustic isolation, tutoring experiments, and critical periods that underlie the template model, then summarize their research with deafening at different stages and show the predicted elimination of the effects of early hearing experience. They also show that some developmental processes are independent of auditory feedback, since deafening leaves frequency range, duration, and other properties of song relatively untouched.

A related postulate is that hearing song and some components of "subsong" during development increases the reinforcing effectiveness of song. Stevenson describes her experiments in which birds are provided with an operant that turns on playback of an adult song. Song acts as a positive reinforcer, whereas white noise does not, but control of the operant procedure by song reinforcement is very different from that produced by food reinforcement (for example, there is no high, steady rate of responding for song). The reinforcing value of song relates to at least two conditions for song-learning (prior hearing of song, and testosterone), but there are some indications that the natural situation contains other aspects that are also reinforcing.

Song-learning in other studied species is in most respects comparable to that of the chaffinch, but with interesting deviations in detail. Immelmann presents a very nice account of his work showing how the differences characteristic of zebra finches are adapted to that species' social behavior in its naturally irregular breeding season. Zebra finches not only get their "templates" very early in life, but also terminate song development at only three months of age. They hear and acquire song elements before they begin singing, then fix sequence, length, and rhythm while singing between their 40th and 80th days. They tend to imitate the song elements only of tutors with which they have a strong personal bond—and this is important, since the species breeds in mixed-species colonies. They are in close contact with related species soon after fledging, and may form pairs within such mixed flocks; thus they need to acquire the species-specific song while still with their parents and in the immediate vicinity of their nests.

The next three chapters explore physiological approaches. Brown reviews the use of vocalizations in assessing effects of stimulation and lesioning on neural function in avian brains. Although there have been few studies, he is able to challenge "older concepts of drives and centres" as overly simplified, and supports the view that the neural control of vocalization is not discrete but that "the controls of vocalization are the controls of sexual, agonistic, and other types of behaviour in which vocalization plays a role."

Andrew holds that vocal behavior cannot be explained in terms of such drives as fear, aggression, or sex. He finds that calls of young chicks may be just variants of a basic form, uttered during diffuse rather than intense attention; thus general physiological states may control their vocal behavior. After testosterone treatment a new set of vocal responses and concommitant behavior appears, as if a switch (the "testosterone mechanism," or TM) had been thrown, yielding also higher thresholds and less responsiveness to brief environmental changes. Neither the responses nor the TM are yet precisely defined, and, unfortunately, many of the experiments are too complex for easy interpretation. And although young chicks are practical subjects, they add an unwanted variable since their requirements of social behavior differ greatly from those of adults and are reflected in the use of their vocalizations. As controls they are not directly comparable with high-testosterone individuals, since these would typically

be adult, with different social needs and expectations. Yet Andrew's results are provocative, as is his proposed switch mechanism governing predispositions for many kinds of behavior.

Brockway studies not just the production of vocalizations, but also their influence (and thus that of social behavior) on the endocrine states of individuals. Tracing the role of vocalizations in integrating the behavior and endocrine responses of budgerigar sexual partners, she explores some quantitative aspects of vocal-endocrine feedback, and shows that one male call promotes ovarian activity and sexual behavior in females, whereas another is necessary for testicular activity in the males themselves.

The next seven chapters Hinde classifies as "functional" (Mulligan and Olsen, Hooker and Hooker, Falls, and Vince) and "evolutionary" (Crook, Lanyon, and Thielcke), but their topics are really much more diverse. They are, for the most part, the chapters most immediately concerned with social behavior. Whatever the developmental or physiological characteristics of vocalizations, clearly their fundamental *raison d'être* from the standpoint of natural selection is as carriers of information in mediating social behavior. Yet it is amazing how little detailed study has been allotted to the behavior of communicating animals by ethologists. Vocalizations and other displays have long been used more as indicators for studies of motivation, physiology, learning, phyletic relationships, and other characteristics than as interrelated, functioning components of patterns of communication. In many instances, including some in this book, this has led to incautious assumptions from inadequate behavioral information. It is encouraging, however, to see in several of these chapters keen realization of the need for more detailed behavioral studies, and a caution born of this realization. The process of communication and its roles in social behavior must be much more thoroughly investigated before the use of vocalizations as tools in other kinds of studies can be fully developed.

Partly as an attempt to interpret the significance of calls, Mulligan and Olsen present a preliminary analysis of their research on five sets of vocalizations used in canary courtship. The forms of the related calls within each set are shown quantitatively to be very stereotyped in most cases. The frequencies of occurrence of each call during 11 different forms of communicator behavior are analyzed, along with the behavior preceding and following the call. Each call is employed during about seven to nine different activities, although two of these usually account for half to two-thirds of the total usage of each vocalization. A change in the frequency of employment of each vocalization as the breeding cycle progresses indicates that each serves distinct functions. Further, the quantitative demonstration that each of the five sets of vocalizations is employed during several behavior patterns, and that the patterns of usage of each of the five sets are different, shows that each set carries different information. Mulligan and Olsen are not yet able to specify this information closely because, as they recognize, the behavioral categories used in recording data were chosen beforehand and were not fully appropriate. Nonetheless, their results are strongly suggestive and indicate directions for further research which can profitably use the methods they have developed.

Hooker and Hooker (Lade) studied the use of a set of vocal patterns employed by mated birds throughout the year in an intricate performance known as antiphonal duetting. They compare several African shrike species, each of which is like most other birds that duet in that they remain paired and on territory in a densely vegetated habitat throughout the year. Each adult pair learns together to group basic vocal components into several duet patterns, some of which are peculiar to them. Birds duet in crepuscular singing, in territory boundary disputes with neighboring pairs, in nest-relief ceremonies during incubation, and rarely in other situations. Unfortunately, it is not known what governs the choice of duetting pattern in different behavioral situations, at least partly because behavioral details are hard to see with the birds normally obscured by vegetation. Nonetheless, duetting remains of interest for other reasons. Each bird, for instance, appears to know the entire vocal pattern but to use only its part under usual circumstances. And the precision of timing in the answer of a bird to its mate is remarkable, whether the second bird employs visible clues (at close range) of the onset of the pattern, or responds solely to hearing it. The report of Hooker and Hooker is valuable in revising and extending Thorpe's initial calculations on auditory response times, and in demonstrating types of difference in duetting among closely related species.

Falls reviews his and his students' experiments with the playback of song to territorial white-throated sparrows. Their studies contribute significantly to our very fragmentary understanding of the responses made by recipients of vocalizations, albeit within the limits of playback technique. The recipient of playback of a recorded song does not find a natural situation; the behavioral feedback from his singing "challenger" is much more restricted than that from a real, conspecific individual, limiting the number of behavioral responses he will select. But he does respond, and at least the initial features of this response are quantifiable and interesting. Such limitations are recognized in these studies, and stimuli are restricted to song and modifications of it, excluding other components of the species' vocal repertoire. Behavioral criteria for responses are carefully specified, and two basic methods are used to minimize variables in assessing four measures of the strength of responses. The result is a convincing demonstration that three different functions of this species' song depend on different physical parameters of the vocalization. Some parameters are stereotyped for species recognition and some for individual recognition, and some are free to provide indication of differing probabilities of at least aggressive behavior by the communicator. Recipients appear to use the identifying information very efficiently; they do not respond to the different songs of most other sympatric species, and they come to respond less to the learned songs of their neighbors whenever these indicate a low probability of attack. There is one very nice demonstration of the importance of the context of song to a recipient: if the song of a neighbor is played from an unexpected location (for example, the opposite territorial boundary of the experimental recipient) it will elicit a much stronger response than if played from an expected site.

Vince gives a progress report and an annotated list of hypotheses on the function of the sounds made by hatching quail. She shows that synchronized hatching can depend on both acceleration and retardation of embryos, although the form of adjustment differs among species.

Crook obtained information on vocalizations of weaverbirds (Ploceidae) as a largely incidental feature of a broad comparative study. Although

recognizing about 14 different calls, his data permit detailed discussion of only four, in two groups. The "flight call" is apparently used only by gregarious species, and aids flock integration. Features of its employment are remarkably similar to those of calls I have termed "locomotory hesitance vocalizations" in distantly related, nonflocking tyrannids, supporting the view that the type of information being carried is important to diverse animals. The bulk of Crook's presentation, however, concerns short and long "songs," and "calls during nest-advertisement." During weaverbird courtship, song accompanies a male's approach to a female when he has strongly conflicting drives. The manner and circumstances of approach differ among species differing in both degree of colonial nesting and habitat. Solitary insectivores usually seek and court females away from the nest, with sex-chasing and song. But males of highly colonial species use elaborate visible display to attract females to their nests, then approach, with song or calls replacing it, only when the nest is entered. Crook provides a bold model correlating habitat, courtship type, and use of song or nest-advertisement calls that is consistent with his data and suitable for further testing. Yet the story is more complex, since males also sing when grouped on territories in the absence of females, and in some flock situations. The information in song may not be specific to partially inhibited sexual approach, and will richly repay further study. In fact, Crook identifies several important and exciting areas for research, including the apparently independent evolution of certain vocal and visible displays.

Lanyon's chapter on taxonomic uses of information about bird vocalizations usefully reviews studies characterizing allopatric populations and sibling species through comparisons of some of their vocalizations. But in contrast to Crook, Lanyon is little interested in the nature of each species' repertoire of vocalizations, and unlike Falls, with whom he shares dependence on field playback techniques, he overestimates what can be learned from the gross behavioral responses of birds to which he plays sounds recorded from other populations. A basic limitation of playback is its failure to permit a normal behavioral interaction to develop, and in testing phyletic relatedness it is not at all clear that initial responses alone are sufficiently informative. These responses are made even more difficult to interpret because Lanyon often accepts a grab-bag sample of a vocal repertoire, without knowing what information is carried by each type of vocalization. Vocalizations do not function solely to identify and proclaim territories; they are interdependent components of a species' signal repertoire, each carrying information to some extent different from that of the others and being used in information-rich and developing contexts. Yet Lanyon talks throughout about undefined "vocal characters" and "voice" as if these implied simple phenomena. He thus broaches one of the oldest and most obvious pitfalls of systematics, failing to consider the biological relevance of his taxonomic "characters" as a part of adaptive social behavior. Finally, he also casually assumes that vocalizations can provide little or no information useful to taxonomists at a suprageneric level. Hinde takes editorial exception (p. 263), noting that features of even species-typical songs are sometimes characteristic at the level of taxonomic families. In short, Lanyon's chapter points up the need for more thorough behavioral research if vocalizations are to be employed meaningfully in systematics.

The literature on various sorts of geographic variation in bird vocalizations is critically reviewed by Thielcke, who is keenly aware that research on this topic has usually been based on far too meager samples. Important hypotheses have not received rigorous testing, and Thielcke pleads that "far more precise data are indispensable." Still, the importance of studying the behavioral employment of the vocalizations that are to be compared among populations is not stressed. Problems arise whenever an observer fails to realize that different vocalizations of a species (for example, different forms of "song" as in the cited study by Ward on Carolina chickadees) are used differently and thus carry somewhat different information. The relative frequencies of such calls in different populations can be sampled only in fully comparable behavioral situations, often at limited periods in the annual behavioral cycle. In this regard, even Thielcke's proposed increase in the minimum suitable number of recording sites and number of individuals recorded per site remains inadequate. Behavioral studies of communication in each species are fundamental.

Man becomes the topic of the final chapters. E. A. Armstrong provides an essay on man's appreciation of bird song, now threatened by the loss of sites where one can find only natural sounds. A great naturalist, he is distressed that "man's desecration of his environment by noise is the most pervasive and gratuitous of his many outrages against nature." Then the last chapter, to my surprise because of its title "The aesthetic content of bird song," has some intriguing ideas on the origins of music, seeing evolutionary selection pressures similar to those dictating many characteristics of bird song. Hall-Craggs proposes that song may have arisen to facilitate communication over distances too great for conversation. She sees a rise in fundamental frequencies toward the range of greatest aural sensitivity, and greater concentration of energy around the main frequencies, as serving to increase carrying power. The addition of redundancy through repetition she sees as counteracting the increased interference to be expected with distance and then the development of rhythm as promoting efficiency of energy expenditure. Repetition leads her to consider the relative advantages of novelty and familiarity. Although she oversimplifies such behavioral concepts as territory and assigns only minimal functions to bird song, her chapter should be of interest to anyone concerned with the evolution of human communication.

That I have emphasized what I consider to be some of the failings of studies of bird vocalizations and harped on the widespread need for more study of communication and other social behavior should not be construed as an indication that this book is not valuable. On the contrary, it is an extraordinarily useful and appropriate sampling of a very active field of research, the relevance of which extends far beyond its avian subject matter. However one approaches the subject it is complex, and our understanding of it in all cases fragmentary. It is inevitable that researchers today will have different assessments of what constitutes the best approach to any of the problems involving bird vocalizations. Hinde has chosen well and edited well, and all of us studying animal communication and related fields are in his debt.

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