Signals and Responses

Animal Communication. Techniques of Study and Results of Research. THOMAS A. SEBEOK, Ed. Indiana University Press, Bloomington, 1968. xviii + 686 pp., illus. $20.

Modern studies of animal communication derive from both biology and linguistics. Animal displays were a major challenge to evolutionary theory, since their function as well as their origin had to be explained before a reasonable explanation of their existence could be given by natural selection. Darwin resolved both problems by showing that displays were probably communicatory and that communication could serve adaptive ends. The evolution of displays has remained of concern to biologists ever since, while studies of their causation became important with their use as experimental material by ethologists. One unforeseen but unfortunate consequence has been that studies of communication by biologists have concentrated on highly evolved signals and have rarely paid attention to the information that may be transferred by behavior whose main function is not communication.

The desire to understand and speak to animals is far more ancient than linguistics, and, from the start of the science, linguists have been ambitious to apply principles deduced from human languages to animal communication. A number of articles in the present volume are attempts by communications theorists to consolidate their recent gains along the new frontier of animal language.

It is striking that the articles which, like those of Hockett and Altmann, concern themselves solely with the establishment of principles are less successful in achieving that aim than some of the articles which describe the displays of a particular group. Wilson provides the most remarkable example of this in his account of chemical signals, which, thanks largely to his own work on arthropods, includes a variety of striking generalizations. Thus, to take only one example, a mixture of substances can be used to give specificity at close quarters, but not at any distance since its composition will change as dispersion proceeds. I was particularly impressed by the description of an ant alarm substance which when released induces true alarm behavior in an inner zone, where it is most concentrated, and serves as an attractant at greater distances and dilution. Not only can the dimension of such zones be measured, but their significance can be evaluated.

The same quantitative information is beginning to be available for vertebrates. It is possible to ask concerning the alarm substance released by an injured minnow, not only what response does it elicit, but over what distance and for how long. Thanks to Bremond, it is now known what are the exact characteristics which must be retained if an experimentally modified recording of the song of a European robin is to have the same effect on another robin as the song of a real territorial rival.

It would have been most instructive to read, even in a tentative and preliminary form, a classification of the types of responses that vertebrate displays have been demonstrated to evoke. Most discussions of displays still rest on qualitative descriptions of what appear to be their consequences, perhaps because in many cases these seem so obvious that further work is unnecessary. A threat display, for example, may be seen obviously to deter an attacker. The next step, that of determining exactly when such a display is ineffective or even promotes attack, is difficult but essential. Two approaches have been successful, neither of which is dealt with here at any length. The first, which provides a truly experimental situation by using models, has been fruitful since Lack first used stuffed robins to map robin territories. The other is the study of long sequences of interactions between displaying animals. It can usually be shown that, when a particular signal is given by one animal, certain responses tend to follow in another. It is difficult to demonstrate by such evidence that the signal causes the responses, since the responding animal may be responding to other, earlier acts or may itself be steering the whole interaction by its earlier behavior. However, the method is an essential one if normal communication is to be studied. One of the contributors, Altmann, has great experience with its use in the investigation of primate societies and might well have been asked to examine its advantages and pitfalls.

Such a discussion would also have made it possible to evaluate the estimated rates of information transfer, which are quoted in a number of contributions. These in some cases really measure only the correlation between coincident acts in the behavior of two displaying animals. Such correlation might be caused by an initial synchronization of the two sequences. In other instances, they accurately measure the potential rate of information transfer, without finally demonstrating that any transfer has occurred. The most interesting example of this is the communication of the location of foraging sites in bees. Discussions of animal communication have assumed that in bees information about the distance and the direction of food is always conveyed between workers by dances, as first described by von Frisch. Wenner summarizes his own work, which demonstrates convincingly that, although there is a remarkably close correlation between some features of the bee dance (including the sound signal discovered by Wenner, as well as the waggle movements) and the distance of the food source, this does not finally demonstrate communication. The vast majority of bees arriving at any source prove to be experienced animals who have visited the source before. They could therefore have found it by the use of their past experience, after identifying an odor characteristic of it on a returning forager. Inexperienced bees are recruited to a new site, but may well find it by detecting hive scent left there by other bees. However the controversy is decided, the very fact that it exists is highly instructive for students of animal communication. Clearly, an agreed code word can initiate a whole plan of campaign, but it would be very misleading to argue that such a code word communicated the plan. There can be little doubt that the interpretation of vertebrate communication will be complicated by similar but much more extensive use of past experience.

Another approach which can greatly clarify ideas about the content of animal communication is to consider more carefully the causation of vertebrate displays. A proper understanding of causation defines the potential infor-

mation contained in the display. Smith illustrates this in his interesting discussion of the calls of tyrannid flycatchers, in which he demonstrates that one call is given only during hesitation in locomotion. Once this is known, then the situation in which hesitation occurs allows quite specific deductions to be made, such as that "the approaching individual, because hesitant, is unlikely to attack." The subject deserves far more lengthy treatment in a book of this type. Two out of many possible examples may illustrate this. Reflexes indicating the state of postural tonus, such as tail elevation in dogs or the degree of limb extension, allow estimations of confidence in social situations. Orientation reflex components such as pricking of the ears can indicate how interesting a stimulus is, and protective movements such as ear flattening show at what distance it is thought to be dangerous.

Surveys of communication in different systematic groups form the main part of the book. Alexander surveys insect displays, and uses them to exemplify the way in which the signals of closely related species have changed in every possible parameter during evolution in order to be readily distinguishable. He also gives the clearest account of the causation of cricket calls I have yet read. It is interesting to compare Blair's chapter on reptiles and amphibians, which shows that many of the same selective pressures have acted on amphibian calls as on those of insects such as the Orthoptera. The chapter also can be recommended as an account of general amphibian behavior: to take only one example, I learned from it for the first time that defense of territories by fighting occurs in some anurans.

A number of the other vertebrate surveys are disappointing, despite the great experience of the authors. Tavolga devotes much of the short section on fishes to a discussion of a classification of communication into vegetative, tonic, phasic, signal, and higher levels, which seems irrelevant to real problems of communication. Hooker summarizes competently our knowledge of song learning, but touches on communication in birds only in passing. I was particularly disappointed that Altmann confined himself to what is basically an expanded bibliography of primate displays.

Tembrock gives a detailed and useful descriptive account of mammal displays, order by order. The section on marine mammals by Poulter differs from all the rest in that it consists largely of original observations. This is clearly useful, but out of place in a book that gives so little space to groups about which far more is known. We still have less knowledge of vocal communication in seals and dolphins than in dogs (let alone gulls or robins), and I remain unconvinced that much progress will be made by treating cetacean sounds as a language whose phonemes have the same specificity of meaning as those of human speech.

The final sections are concerned chiefly with human communication. Diebold gives a concise summary of the role of direction of gaze which shows that, in one field at least, quantitative experiments are both possible and valuable in the study of human nonverbal communication. He includes at one point, without further discussion, the intriguing statement that an observer can tell that he is being stared at even if the starer is not in his visual field. Otherwise, straightforward descriptive accounts of human communication are almost absent. Instead, attention is concentrated on the relation and the differences between human language and animal communicatory devices. The clearest position is that of Lenneberg, who argues for a "discontinuity theory," which states that human language is so different from primate communication that it is quite misleading to consider the first to be evolved from the second. Most of his discussion is, in fact, concerned with a different and quite acceptable thesis, namely, that it will be very difficult to establish when and how human beings began to talk. Those arguments which directly attack the belief of Kohler and others that it is now possible to trace the early evolution of many basic features of human language do not convince me. Thus Lenneberg states that human infants do not ordinarily imitate sounds. I would have thought it obvious both from observation and on a priori grounds that they do. What is more, if we can demonstrate why vocal mimicking evolved in some birds, then we are nearer to understanding how the same condition might have evolved in human ancestors before language appeared [see R. J. Andrew, *Science* **137**, 585 (1962)]. Readers may like to turn back to Hooker's account of vocal mimicking in birds and speculate for themselves.

Diebold raises, but does not resolve, another difficulty, that of demonstrating intention in animal communication. This problem will be clarified when the reinforcers are identified which can increase or decrease the frequency of particular displays. It will then be possible to identify those signals which the animal learns to use to regulate social interactions in the same way other operant responses are used to regulate more conventional rewards.

In conclusion, *Animal Communication* is a valuable book (as at the price it should be), but not an invaluable one. It mirrors accurately the present state of the subject. Most interest among anthropologists and psychologists concerned with communication centers around the establishment of general principles that will be applicable to animals and men. On the other hand, it is from the detailed experimental studies of communications in particular groups that principles can be seen to emerge. It would seem best that the study of animal communication should remain for a little longer a pursuit conducted within more established disciplines, and not attempt to find a premature independence.

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Vocalization

Bird Song. Acoustics and Physiology. CRAWFORD H. GREENEWALT. Smithsonian Institution Press, Washington, D.C., 1968 (distributed by Random House, New York). viii + 196 pp., illus., + 2 records. $12.50. Smithsonian Publication 4750.

A valuable extension of analytical methods into the study of animal sounds is made in this book. For the most part, studies of bird song have been concerned with variation within species or with behavioral aspects of these sounds. This book explores in detail an area long neglected but essential to a complete understanding of bird sound—its structure and production. It includes a synthesis of many papers, some not readily available.

Among the earlier suggestions about bird sound production which are supported are the dual-oscillator theory—that many birds can produce two nonharmonic sounds simultaneously—and the importance of the fundamental as a vehicle for coding messages, including the use of amplitude and frequency modulations. Among those refuted are