A further problem is that in arguing from example, Ions is himself guilty of one of the main crimes of which he seeks to convict his opponents, namely, dogmatic generalisation based on insufficient evidence. He maintains a consistently fast pace but his bowling is loose and often aimed at the man

not the wicket: any decent umpire would have sent him off the field, but that would have deprived the crowd of considerable amusement.

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Animal communication in ethological research

John Krebs

The Behaviour of Communicating: An Ethological Approach. By W. John Smith. Pp. 545. (Harvard University: Cambridge, Massachusetts and London, 1977.) £13.65.

More than any other subject, animal communication has occupied a prominent place in ethological research throughout the past forty years. Lorenz's demonstration that displays of ducks and geese can be used as species-specific taxonomic characters trace phylogenies; Tinbergen's classic analyses of the motivational basis of displays in gulls; Thorpe and Marler's work on the ontogeny of bird song; and von Frisch's dancing bees are all justifiably recognised as pillars of ethology. In the past few years, although some of the emphasis has slightly changed, animal communication has still played a central role in ethological thinking, exemplified by G. A. Parker and J. Maynard Smith's application of game theory to ritualised

It is perhaps not surprising, in view of the voluminous and diverse literature, that no single person has, since Tinbergen with his Social Behaviour in Animals (Methuen, 1953), attempted the daunting task of reviewing the whole subject of communication. There have been notable collections of essays (Huxley's "ritualisation" symposium, Hinde's Non-Verbal Communication and Sebeok's Animal Communication). but W. John Smith is the first for nearly 25 years to write a comprehensive treatise. Comprehensive is the word: with over forty pages of references, Smith has done an admirable and scholarly job of bringing together the literature up to and including 1976.

Smith's own well known contribu-

tion to the field of communication has been to emphasise the distinction between the message contained in a signal (what it might potentially reveal about the communicator) and its meaning to the recipient(s). The meaning, measured by the response of the recipient, usually depends on the context. For example, a hypothetical call given by a bird whenever it moves may mean "I am about to attack" in one context, and "I am about to feed" in another. The book leans heavily on Smith's message-meaning distinction: after an introduction in which he clearly defines communication and states the problems he is going to tackle, there are six chapters (including a lot of descriptive examples) dealing with the structure and message content of signals.

The subsequent chapters deal in turn with the motivational basis of displays (a review of the traditional ethological work), the importance of context and the meaning of signals, ritualisation, ecological and other constraints on signalling systems, and finally a critique and reassessment of the display concept. In this final section, Smith points out that the usual preoccupation of ethologists with simple stereotyped displays (releasers) has led to an underemphasis on the possibility of complex grammatical rules for combining simple components into complex signals. Throughout the book, Smith provides numerous examples, many of them unpublished, which make interesting reading and act as an excellent diluent for the slightly heavy style of the more theoretical discussions.

In such a wide-ranging and thoughtprovoking book, it is hard to know where to begin in singling out points for discussion, but I will mention briefly a general feature of communication which I believe that Smith may have underplayed. Smith views communication as a cooperative venture between communicator and recipient; displays are acts "specialised to make information available to the recipient" (p69, p195) about the communicator's likely future behaviour, status, location, and so on. This standpoint is emphasised by Smith's statement that manipulation or intentional misleading is a "disturbing possibility" but not one that ethologists have yet discovered. (He inexplicably separates intra- and interspecific deceit—the latter is well known in, for example, Batesian mimicry.)

I would suggest that far from being a marginally possible aberrance, manipulation, or something very like it, is a central feature of much of animal communication. As Smith emphasises. signals can only evolve if there is an advantage to the recipient in responding, as well as an advantage to the communicator. But this is not to say that the benefits to the two are equal: and it seems inevitable that both participants in any interaction-be it between a territorial stickleback displaying to an intruder or a fledgling blackbird begging from its parentwill strive to get the maximum benefit. Viewed in this light, communicators are always trying to manipulate or persuade recipients, while recipients are increasing their sales-resistance. It is then not at all surprising that displays often provide incomplete information about the motivational state of the communicator (p201): it always pays to be poker-faced when selling a used car.

It also follows from my argument that many display interactions are concerned with assessment ("Is he really as confident as his threat indicates?"). The elaborate courtship nituals of many animals may have as much to do with assessment of the potential mate's fidelity and fecundity as with "helping male and female to cooperate in beginning copulation" (p300). This was brought home to me by the striking result of Erickson and Zenone (Science, 192, 1353-54; 1976). They showed that a male ring dove actually rejects a female who is too willing in courtship. This is a canny reaction: "precocious" females are forward because they have just been stimulated by mating with another male, and it supports the view that ring dove courtship involves assessment by the male of whether the female has already been fertilised. With the traditional ethological view of male courtship as a means of arousing the female to copulate, who would have foreseen that male ring doves would reject avian nymphomaniacs?

While I certainly would not claim that all intraspecific communication involves manipulation and assessment, it just might be useful to bear these ideas in mind when analysing court-ship and threat signals. Finally, let me emphasise that Smith's omission of the sort of discussion I have briefly outlined does not materially detract from his enormous achievement in synthesising and appraising such an important subject.

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