BEHAVIORAL ECOLOGY

Why Animals Don't Lie

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A central problem for evolutionary biologists interested in animal communication is to explain why animal signalers generally are truthful. A male nightingale advertising for a mate reliably signals properties of his qualities through his beautiful song. By dressing in screaming black and yellow colors, the wasp reliably warns approaching predators (and us) of her painful sting. The trivial answer to the honesty problem is that it would not pay animals to respond to a signal unless they by and large benefited. If wasps never stung, no one would bothered to notice their striking colors. The color pattern would cease to be a signal. However, the more interesting question—the main theme of John Maynard Smith and David Harper's *Animal Signals*—is what keep signalers from cheating? What prevents, say, a poor quality male nightingale from claiming that he is of higher quality than he actually is?

In the book's preface (and again in its opening chapter), Maynard Smith and Harper tell us that they aim to bring order into the apparent chaos of theories and empirical results that currently characterize the subject of animal signals. At present, confusion extends over the distinctions among different types of signals, the precise meaning of various terms, and the interpretation of particular biological cases. The authors conclude their introductory chapter with a proposed list of definitions and terminology, which, they hope, will sort out some of the confusion that currently prevails in the literature. They use a limited number of fairly broadly defined signal types compared, for instance, with the highly detailed classification scheme suggested by Oren Hasson (*1*). The apparent advantage of the scheme they propose lies in its simplicity; we are uncertain, though, whether it will appropriate in all cases.

Animal Signals
by John Maynard Smith and David Harper

Oxford University Press, Oxford, 2004. 176 pp. $99.50. ISBN 0-19-852684-9. Paper, $44.50. ISBN 0-19-852685-7.

The book is concise and contains seven short chapters. After their introductory overview of what signals are, the authors offer three chapters that cover general theories on honest signaling as well as interpretations of some particular cases. They devote considerable attention to the handicap theory, made well know to a broad audience by Zahavi (*2*): signals are reliable because they are costly to produce or have costly consequences. Maynard Smith and Harper clarify and specify the situations in which the handicap principle properly applies as well as situations where other explanations are more appropriate. The authors, quite correctly, emphasize that there are several evolutionary routes to honesty, of which the handicap principle is only one.

Another class of signals that receives considerable attention from the authors is indices of quality—that is, signals whose intensity is causally related to the quality being signaled and which therefore cannot be faked. For example, the "back-arching" behavior of cats may be an index of size. The signal is reliable because the skeleton, muscles, and fur sets limits to how big a cat can appear during the display. Maynard Smith and Harper categorize a rather broad range of signals as indices. It is somewhat unfortunate that they chose not to distinguish between indices and amplifiers. According to Hasson (*1*), amplifiers resemble indices in that their reliability is caused by design rather than costs. However, an amplifier is not functionally related to the quality being signaled; instead the amplifier simply makes it easier for the receiver to assess that quality. In a bird species where females prefer males free from ectoparasites, for instance, a signal that makes it easier for the females to spot the parasites on the male's plumage or skin (say a contrasting color) would be an amplifier. Hasson discussed some key differences between indices and amplifiers(*1*), differences that in our view justify a distinction between them.

In their chapter on the evolution of signal form, the authors emphasize the importance of distinguishing between signal systems at an evolutionary equilibrium and evolving signal systems. Much confusion has prevailed because researchers have not clearly observed—or even been aware of—this distinction. For decades biologists have, for example, argued whether the handicap theory (*2*) or Fisher's runaway model (*3*) better explains the evolution of sexually selected traits. The former may describe the maintenance of signals at equilibrium, whereas the latter represents an evolutionary process; thus the two explanations are not directly comparable.

The problem of honest signaling seems especially challenging to our intuition when we consider contests, situations in which the contestants prefer different outcomes. In their chapter on signaling during contests, Maynard Smith and Harper explore some consequences of the contestant's shared interest in avoiding an escalated fight. They discuss badges of status. minimal-cost signals that indicate need, and aspects such as extended interactions, punishment, and the effects of the divisibility of a resource.

In the final chapter, the authors discuss signaling in primates and some other social vertebrates. Here we find several topics that border on other fields such as psychology and the evolution of language. The chapter provides some of the book's most entertaining examples and most thought-provoking suggestions. These include the evolution, through natural selection, of animal signaling into human language; that is, the transition in our past where genetic change was eclipsed by cultural change and history began.

Maynard Smith has inspired generations of biologists with his writing, and he certainly will continue to do so with this work with Harper. Through their admirable assessment of the current status of the field of animal signal evolution, the authors have developed a platform for consensus. Reading the book is a great pleasure, and anyone interested in animal communication will find it both useful and inspiring. Even though much of the literature the authors refer to relies on some rather difficult mathematics, most of their discussions are effectively conveyed in ordinary but precise prose. Their fascinating and intriguing empirical examples and natural histories are excellently suited to illustrate the theoretical problems they address. Although only future discussions will reveal how well Maynard Smith and Harper have sorted out the topic, we are convinced that *Animal Signals* will help clear up important misunderstandings and misconceptions.

Note added in proof: John Maynard Smith passed away Monday, 19 April 2004.

References

1. O. Hasson, *J. Theor. Biol.* 185, 139 (1997).
2. A. Zahavi, *J. Theor. Biol.* 53, 205 (1975).
3. R. A. Fisher, *The Genetical Theory of Natural Selection* (Clarendon, Oxford, 1930).

Behavior ritualized into a signal. The sky-pointing courtship display of the blue-footed booby (*Sula nebouxii*) seems to have been derived from flight intention movements.

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