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 bother 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 keeps signalers from cheating? What prevents, say, a poor-quality male nightingale from claiming that he is of higher quality than he actually is?

Animal Signals
by John Maynard Smith and David Harper

Oxford University Press, Oxford, 2003. 176 pp. $99.50. ISBN 0-19-852684-9. Paper, $44.50. ISBN 0-19-852685-7.

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 be appropriate in all cases.

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 known 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 set 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.


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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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 contestants' 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

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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 on Monday, 19 April 2004.

References

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BIOMECHANICS

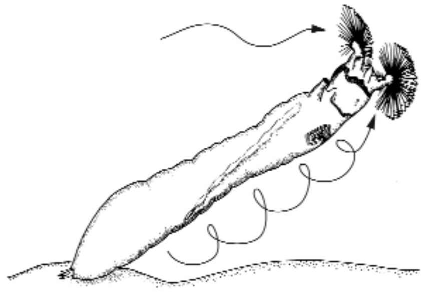
Life Among the Formulae of Physics

Julian F. V. Vincent

Comparative Biomechanics
Life's Physical World
by Steven Vogel
Princeton University Press, Princeton, NJ, 2003. 592 pp. $60, £39.95. ISBN 0-691-11297-5.

I generally go by the maxim that, in pursuit of objectivity, I never read any books I am asked to review. But in this case, I have to disappoint you—this review is about as subjective as I ever get. I tried skim-reading Steven Vogel's *Comparative Biomechanics* in the spirit of compromise, but was compromised: the volume has so many little gems scattered throughout that my eye got caught by the glitter and couldn't escape.

In earlier books, Vogel (a biology professor at Duke University) introduced biomechanics piecemeal. Now he has written an integrated textbook on the subject. To begin, we shape up with size, and scales fall from our eyes. For instance, the ratio of surface area to volume, crudely considered as length squared in relation to length cubed, varies with size as well as shape, and so is not much use as an independent metric of morphology. Rather, we need to eliminate all dimensions—mass, length, and time—which Vogel does by dividing the square root of the surface area by the cube root of the volume. For a sphere, this produces a "flatness index" (FI) of 2.2, and for a cube, FI = 2.45. FI is fairly invariant in FIsh, but squid elongate as they get older: their FI increases from 4 in a juvenile to 7 in a 10-meter-long giant. Values for mammals of all sizes are nearly constant at 3.31. Thus Vogel normalizes for the expected or ordinary (a constant flatness index within a taxonomic group indicates phylogenetic isometry), and in so doing he directs attention to the unexpected or extraordinary. Because Flatness is obviously next to Godliness, the FI has been designated the "Vogel number" (*1*). And quite right, too.



Stirring up food. In shallow, rapid streams, black-fly larvae filter plankton from the main flow with one fan while the other intercepts material resuspended in the vortices rising behind the body.

CREDIT: ANNETTE DEFERRARI/COURTESY STEVEN VOGEL

The book next follows a spiral dance: first exploring a physical phenomenon related to the nature of our world of fluids, then showing how animals and plants interpolate themselves between the flows with small effort but large effect. Vogel does this in opposition to the disdain or disregard of physical science by most biologists, and as I approached the end of the fluids section, I began to see that this opposition is his Crusade. He has vanquished my Infidel at least, as I now appreciate that (of course) the physical world was here first and, no matter what animals and plants do to it, it will be here last. We are no more than a cause of temporary discontinuities in a formless web of time and space. It took me some time to recognize why I was experiencing this shift in perception, and then I realized that less than half of Vogel's fluid story is about organisms—it is more about the diffusion and flow regimes, where they originate and how they work.

Caught in this current, and buoyed up by an excellent account of how aerofoils work, I was thrust into my comfort zone—solids. This encompasses the organically constructed environment where many flows are made. But this section of the book offers far less description of the underlying physics and limiting factors. It is more an exercise in comparative structures and materials. Missing topics include Gibson and Ashby's ideas on cellular materials and work by Lakes and by Evans on auxetic materials (which swell instead of shrink when extended). Although Vogel spends 5 pages on materials selection (how to choose the most effective materials for different structures and purposes), further discussion of Ashby's approach (*2*) would have been warranted. And I would have preferred a much more detailed examination of the mechanisms that animals and plants employ for resisting fracture. (It wasn't until I breathed the air of an engineering department that I realized how much failure and fracture dominate our manufactured world, and how little we notice the importance of strength and toughness when they are elegantly done, as by nature.) Perhaps these mechanisms rely too much on understanding at the molecular level, an area that Vogel has, knowingly, largely omitted. In any case, Jim Gordon's books (*3–5*), enthusiastically endorsed by Vogel, can fill many of these gaps.

After an examination of the hurdles, gaits, and styles of locomotion on land together with a very useful discussion of muscles, Vogel moves on to consider the context and potential contributions of the appliance of his science or, as he puts it, the hope and the hype, the counterfactual mythology. Despite the author's downbeat slant, this approach can test our understanding of the complexity of structures, artifactual and natural. Vogel's models in biomechanics are mostly stolen from physicists, rheologists, and mathematicians. Such models are fine until you come to use them to understand a real complex structure such as an aircraft or a tree. And they are less helpful when you find that it's the complexity of the interactions and our lack of understanding (or control) of the boundary conditions which reduce our ability to design and make safe and efficient structures and mechanisms. Hang in there: engineers look at problems and try to find answers; biologists look at answers and try to find out what the problem was. Although there is a real synergy, just as Vogel doesn't need to employ all the models and theories of engineering to explain biology, so nobody should expect to be able to apply all biology to engineering. But we can all explore the overlap, and *Comparative Biomechanics* offers an excellent place to start.

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