ANIMAL SIGNALS AND THE OVERLOOKED COSTS OF EFFICACY[1]

Michael J. Ryan[2] and Molly E. Cummings

Section of Integrative Biology C0930, University of Texas, Austin, Texas 78712
[2]*E-mail: mryan@mail.utexas.edu*

The most striking aspects of many animals are signals. Thus one might expect *Animal Signals* by John Maynard Smith and David Harper to discuss the detailed biology of this half of the communication dyad. Not so. Instead, they concentrate on a single question, why signals are reliable, and emphasize one methodology to its solution: game theory. Although not embracing the entire biology of signaling, the book grapples with a continuing problem.

Signals evolved to communicate information and manipulate receivers to the signaler's benefit. Similarly, the receiver's response to signals is under selection to promote its fitness. The issue at hand is the conflict between signal and receiver: what keeps the signaler from providing false information to the receiver?

Zahavi (1975) explained signal reliability with the handicap principle: males evolve costly signals to indicate their underlying genetic quality for survivorship. The authors detail how this theory was rejected enthusiastically by modelers, including Maynard Smith (1976; see also Kirkpatrick 1986), and resurrected as enthusiastically a decade later (Pomiankowski 1987; Grafen 1990).

Maynard Smith and Harper, however, argue convincingly that although sufficient, the handicap principle is hardly necessary to explain reliable signals because not all signals are costly, and not all costs are handicaps. Several situations enforce signal reliability without handicaps: signalers and receivers share common interests, both parties have conflicting interests yet agree on preferences for outcomes, cheaters are punished, or signals cannot be faked. In this last and most interesting case, signals are constrained to be reliable by morphology and physiology—this type of signal is an *index* (p. 60; see also Enquist 1985). The authors offer as an example the frequency of a red deer's call being constrained by larynx size. Males can evolve larger larynges and behaviors to expand its size, but once such innovations are fixed in the population, call frequency again becomes a reliable index (p. 46).

Many signals that are not indices are costly to the signaler. Is this cost prima facie evidence for a handicap, as Zahavi might suggest? No. ''Demonstrating that a signal is costly, therefore, is not evidence that it is a handicap.'' (p. 16; see also Ryan 1998a) Why? The authors point out that there is more to signaling than reliability, and they identify a dichotomy of signal costs. Efficacy costs are those required to ensure that signals can be transmitted efficiently to the receiver (p. 73). Strategic costs are additional costs that ensure signal reliability—Zahavi's handicaps. Effective signaling is

costly; handicaps can make it more costly, but lack of handicap does not make it cost free. This book concentrates on strategic costs, but offers some tantalizing discussions of efficacy costs, which the authors suggest are underappreciated. We second that notion but feel it is not strong enough.

The most basic efficacy costs of signaling are incurred in creating its morphology, behavior, and neural circuitry. In addition, some animals scour the environment to obtain their signals; bowerbirds steal decorations for their bowers (Borgia and Mueller 1992), and some moths sequester plant alkaloids for the flocculent showers they bestow upon females (Conner et al. 2000). There are also costs imposed by the environment. Once the signal is built, it then needs to be presented against an acoustically noisy and visually cluttered world. When background noise is loud, finches increase their songs' amplitude to be heard above the ambient din (p. 16). More generally, the evolution of signals for environmental contrast is well known (e.g., Morton 1975). In his sensory drive model, Endler (1992) argues that factors such as ambient light, background pattern, and the sensory capabilities of predators can all be important factors in signal evolution. Signal amplifiers or exaggerators, we are told (p. 47), might be viewed similarly. Substantial features of signals result from selection for environmental contrast, and thus are driven by efficacy costs.

Efficacy costs are incurred in achieving two other types of contrast, which we call social and neural contrast. To transmit a signal reliably, it must also contrast against the social environment. One who can produce a different syllable or color, or present a signal out of phase with the cacophony of one's competitors, might gain social contrast, making its signal more noticeable and thus salient to the receiver. At the level of the individual, receivers can habituate to signals. Complex bird song, for example, might have evolved for ''neural contrast,'' to release receivers from habituation at the behavioral, neural, and gene expression levels (reviewed in Ryan 1998b). These varied efficacy costs of contrast could initiate an arms race that culminates in the extreme elaboration of signals associated with, though indistinguishable from, Fisher's runaway sexual selection.

The most intriguing example of an efficacy cost given by the authors is the behavior involved in presenting the signal. A nightingale spends most of the night calling and can lose 5–10% of its body weight while doing so (p. 16). This seems the perfect candidate for a handicap: males courting vigorously to display their overall genetic health to females. But suppose males need to attract females flying overhead and unseen; then continuous display is the only option. Thus, when females are unpredictable in space or time, vigorous and constant display is an efficacy cost and not an index. We expect this to be so for most long-distance signaling. Many animals invest considerably in time, energy, and predation

risk to casting sounds, odors, and reflected light upon the environment with no assurance that anyone is listening, smelling, or watching. Although often viewed as handicaps, perhaps these investments are efficacy and not strategic costs. The discrimination will not always be clear. For instance, the authors suggest that courtship vigor in fruit flies (Maynard Smith 1956) is an index of overall male health and thus a reliable indicator of male genetic quality to females (pp. 51–52). Although possible, vigorous signaling might only indicate that the male is a good signaler. A frog's metabolic rate increases manifold when he calls, thus the notion that the male is advertising his physical fitness does not seem farfetched (see e.g. Welch et al. 1998). But Taigen and Wells (1984) found no relationship between calling effort and total aerobic capacity in American toads. Are female toads being fooled by cheating males, or are we the ones being fooled by assigning the wrong function to signaling?

Of the many lasting contributions of John Maynard Smith, the use of game theory to model animal behavior is most prominent (e.g., Bradbury and Vehrencamp 2000). The authors have used these models like a surgeon's tool to dissect the assumptions and consequences of the handicap principle in general, and reliable signals in particular. The conclusion, as we note above, is that the handicap principle is one, but only one, of several scenarios that can achieve reliable signals. But the authors also note that game theory is not an ideal approach for analyzing communication systems involved in sexual selection in which there cannot be a single optimum (p. 12). Where simple economic models fall short in addressing the important factors in sexual signaling evolution, Maynard Smith previously (1982) offered quantitative genetic models such as Lande's (1981) as a more appropriate alternative, and here the authors suggest that Enquist et al.'s (2002) artificial neural network model demonstrating the influence of sensory exploitation on signal evolution may be a more informative alternative.

That segue into alternative models highlights a more general weakness in the use of economic models to analyze animal communication. For us, it is hard to imagine a deep understanding of how and why animals use and respond to signals as they do without detailed attention to the contingencies of the animal's external environment, internal physiology, and evolutionary history. The authors address these issues in their chapter on signal form. Several phenomena such as peak shift displacement and supernormal responses can result in the evolution of signals and responses that can never be predicted by economic models. Add to that other phenomena such as stimulus categorization, generalization, and historical contingencies of the brain, and we see that the economics approach by itself is left somewhat wanting (Enquist and Arak 1998; Ryan et al. 2001). The costs and benefits of signaling are critical to understanding signal evolution, but so are the other factors. Game theory by itself will never tell us why birds sing, frogs croak, crickets chirp, and fish flash, although on a finer scale it might reveal which song, croak, chirp, or flash works better. Game theory results in explicit statements about underlying assumptions, a refreshing contrast to some arguments for the handicap principle in which the elegance of the metaphor substitutes for the sig-

nificance of the data. It has made critical contributions to signal evolution, but, as the authors themselves insinuate, it is time to move on to a more integrative biology of animal communication.

This book is typical of several previous books by Maynard Smith, such as those on sex (1978) and game theory (1982): it is engaging, short, to the point, and emphasizes arguments from first principles rather than exhaustive documentation. Anything that Maynard Smith says is worthy of our undivided attention, and this volume co-authored with Harper is no exception. Sadly, this is our last opportunity to have our attention engaged by a new work from this incredible intellect, as John, a dear friend, passed away as we finished chapter 2.

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