



## Principle with a Handicap

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*The Quarterly Review of Biology*, Vol. 73, No. 4 (Dec., 1998), 477-479.

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## PRINCIPLE WITH A HANDICAP

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A review of  
THE HANDICAP PRINCIPLE: A MISSING PIECE OF  
DARWIN'S PUZZLE.*By Amotz Zahavi and Avishag Zahavi; with Naama  
Zahavi-Ely and Melvin Patrick Eby; illustrated by Amir  
Balaban. New York: Oxford University Press. \$25.00.  
xvi + 286 p; ill.; index. ISBN: 0-19-510035-2.  
1997.*

Amotz Zahavi has been one of the most enduring and controversial figures in behavioral ecology since its inception. His idea of the Handicap Principle has been both the foundation of many arguments for the adaptive significance of female mate choice, and the target of criticism for what many consider an overzealous Panglossian view of nature. This book presents the Handicap Principle in its most inclusive form, explaining its role in Partners in Communication (Part I), Methods of Communication (Part II), The Handicap Principle in Social Systems (Part III), and Humans (Part IV). Readers who expect this volume to be restricted to a discussion of how females choose mates with "good genes" are in for both a rude and wonderful awakening.

In its original minimalist form, the Handicap Principle addresses the fundamental question that led Darwin to develop his theory of sexual selection as an addendum to natural selection: Why do males often develop courtship traits that reduce male survivorship? Darwin's answer was simple but incomplete: If females prefer to mate with males bearing elaborate traits (such as the peacock's tail), then the cost of decreased survivorship could be offset by the male's increased mating success. But Darwin did not resolve why females would deem such males more attractive.

Zahavi asserts that it is precisely the cost of the male trait that makes it so valuable to the female in assessing male quality. The Handicap Principle is simple in its basic premise: "To gauge the reliability of a signal, then, one has to consider the investment it entails. The cost—the handicap that the signaler takes on—guarantees the signal is reliable" (p xv). In its application to female assessment of mate quality, reliable is defined as indicating heritable vigor, an assurance that offspring fathered by the male will have an advantage in nonreproductive components of fitness. Handicapped males should sire offspring who live longer.

At an International Congress for the Society of Behavioral Ecology in Uppsala, Sweden in 1990, I was seated beside Amotz Zahavi when John Maynard Smith delivered a plenary lecture in which he generously offered a public apology to Zahavi for initially rejecting the Handicap Principle. Maynard Smith, one of the foremost critics of the Handicap Principle, reversed himself and offered an enthusiastic endorsement of support for this hypothesis, although he offered some emendations of his own, which were enthusiastically rejected by Zahavi in the ensuing discussion period.

What was responsible for the controversy surrounding the Handicap Principle? Here we have an interesting view of science in action. The Handicap Principle had always been intuitively appealing to some field biologists confronted with the complex and seemingly adaptive features of organisms that are exquisitely designed to promote survival and reproduction. This theory was less tenable, though, for those taken with the mathematical elegance of population genetics models. After its introduction and development in the mid-1970s and early 1980s, the Handicap Principle was quickly assaulted with a series of mathematical models from some of the most prominent practitioners in the field; they concluded that the Handicap Principle could not work. For a decade or more there was a tension between (mainly) theoreticians, who supported Fisher's theory of runaway sexual selection as the explanation for the evolution of female mating preferences, and (mainly) field biologists, who were staunch advocates of the Handicap Principle and various other forms of "good genes" hypotheses. There seemed to be very little meaningful discussion between these two groups.

With the same speed with which they had initially rejected Zahavi's theory, many population geneticists reversed their views in the early 1990s. The Handicap Principle does work, we were told. Interestingly, the way it works is strikingly similar to the models used to support Fisher's hypothesis of runaway sexual selection—there is a genetic correlation between the female's preference for the male's handicap and the male's "good genes" that are responsible for the enhanced physical vigor advertised by the handicap. The female preference evolves under indirect selection as a correlated re-

sponse to the evolution of the male's genes for better survival, which are under direct selection. Runaway sexual selection differs in that the genetic correlation is between the female preference for the display trait and the male display trait itself. Female preference directly selects for certain traits and, because of the genetic correlation, indirectly reinforces itself.

The birth, near-death, and resurrection of the Handicap Principle could have provided a segue into a discussion of the relationship between verbal models and mathematical models, between models and data, and between the somewhat different cultures of theoreticians and field biologists. For example, in that same plenary lecture I mentioned above, Maynard Smith suggested that the field of sexual selection is somewhat unusual in that empirical studies drive theory, as opposed to theory driving the types of empirical studies that are conducted. Is there a lesson here? And for whom? Should field biologists be more confident in their intuition, and less concerned about mathematical models that suggest a shaky foundation for some of their most cherished ideas? Unfortunately, the authors are quite nonchalant about all of this. They treat this change of heart by some theoreticians with the dismissive self-confidence of those who have never doubted their premise.

The redemption of the Handicap Principle by the population geneticists was based on their changing view of the theory's underlying logic, that female preferences for traits that indicate heritable vigor could evolve even if such traits are costly in terms of survivorship. But "could have, would have, should have" does not equal "did." Neither in the rejection of the Handicap Principle nor in its rejuvenation did data play much of a role; there are a few studies (but only a few) that offer unqualified support. Many studies are consistent with the theory, but they do not demonstrate heritability for survivorship with a controlled breeding design. Admittedly, these data are difficult to acquire. The lack of data does not seem to dampen the Zahavis's enthusiasm—Who needs data when metaphors abound?

The bulk of this book consists of a large number of descriptions of social interactions that are then interpreted in light of the Handicap Principle. The interpretations are based upon one major premise: the cost of signals makes them reliable; therefore if signals are costly, then they must have evolved to be used as handicaps. This is a shaky proposition at best. Signals, by definition, transmit information. Information must contrast with noise sufficiently to be perceived, and signals compete to gain the attention of receivers. Increasing the signal-to-noise ratio is costly. It takes energy, behavior, and morphology to send a signal, and most channels

of communication are not private, but can be eavesdropped upon by predators. Are animals able to achieve these feats because they are merely good signalers or also because they are good survivors?

Although the data resulting from some studies are discussed in detail, analogy and metaphor are the primary tools of persuasion, especially in examples of human behavior. The authors make the argument that "anthropomorphic models, if anything, are closer to the reality of animal behavior than mathematical ones" (p 9). Many would take exception to this. Most evolutionary psychologists seem to acknowledge the interaction of epigenetic rules and culture in forming human behavior. There is likely to be less interaction of this type in the animal systems discussed in this book. But most of the arguments marshaled in support of the Handicap Principle are based on intuitive logic rather than on a critical testing of hypotheses. We are told some quite plausible as well as quite fantastic stories. Here are a few samples. Only frogs capable of evading frog-eating bats while they vocalize for mates can successfully breed (p 29); this is obviously true, but there is no evidence that survivors are distinguished by their good genes rather than by their good luck. Crows feed nest parasites in order to gain prestige (p 189). White pelicans (male and female) grow bumps between their eyes during the breeding season in order to interfere with their ability to catch prey and thus demonstrate their hunting prowess (p 28). Men grow beards, which are easily pulled in combat, to demonstrate their superior fighting ability (p 213). Waiters, classical musicians, and European males at formal social occasions wear bow ties to de-emphasize their masculinity (p 217).

There is no question that the Handicap Principle can generate testable hypotheses. The incredible range of unbridled speculation, however, might damage the credibility of this book for some. I was intrigued by the discussion of how honest signaling might regulate the interactions of the social amoebae in slime molds (Chapter 15). But one cannot as seriously accept the more rampant speculation as to, for example, why men drink alcohol (another form of demonstrating superiority, we are told). The danger is that some readers might dismiss all of the book's speculation as too fanciful. That would be a serious mistake, but I believe the authors have made a similarly serious mistake by not injecting a bit of caution.

Another frustration with this book is that other analyses that do not deal with the Handicap Principle are either not acknowledged or are dismissed out of hand. For example, the authors state that animals did not evolve verbal communication because nonverbal communication serves them better (p 221). This assertion totally ignores the volu-

minous literature on morphological and neural constraints on speech articulation and grammar acquisition. Studies of the historical evolution of behavior, which suggest that sensory biases might influence the phenotypes best used to convey information, are acknowledged in a footnote but dismissed out of hand as nonadaptive with a straw-man argument (p 235).

The Zahavis have presented us with an analysis

of their world view of social communication that is far reaching, and it is predictably both stimulating and frustrating. It is an important work because it summarizes Amotz Zahavi's contributions to animal behavior, it is frustrating because the elegance of the metaphor seems to replace the significance of data, and it is charming because it will remind many who know Amotz Zahavi of why we appreciate his sometimes outrageous discourse, whether we agree with him or not.