

Book review of:

The handicap principle: A missing piece of Darwin's puzzle

By Amotz and Avishag Zahavi, New York, Oxford University Press, 1997.

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Evolution maximizes efficiency, right? Adaptations, while promoting survival or reproduction in one domain of life, are supposed to minimize their fitness costs in all other domains. This Darwinian efficiency principle seems obvious, universal, and irrefutable. However, this important, quirky, fascinating book identifies one situation, seemingly very particular but actually quite common, where the efficiency principle breaks down, and a 'handicap principle' takes over. The handicap principle suggests that when individuals are under selection to reveal their quality (e.g. mate value, strength, size, intelligence, or general fitness) to other individuals, they can only signal that quality reliably using adaptations that impose large fitness costs in other domains. That is, "efficient" signals could not function as signals of quality at all. Only profligate wastes of fitness by oneself can signal high fitness to others. Efficiency rules under ordinary "utilitarian selection", but waste can rule under "signal selection".

For example, the peacock's tail is large, heavy, cumbersome, and costly to grow. Fisher's runaway sexual selection model proposed that these costs are side-effects of the tail evolving to excite peahen eyes and brains. The handicap principle offers a radically different account, observing that only highly fit (healthy, strong, mature, well-fed) peacocks can afford to grow such large tails. The tails are handicaps, and their adaptive function is to advertise each male's fitness to potential female mates. The heritable variance in peacock tail length does not reflect a lack of sexual selection on tails, but rather an intense directional selection on tails as fitness-indicators, with biased mutation continually eroding fitness and tail length (see Rowe & Houle, 1996).

This insight seems bizarre and counter-intuitive, but I think it is right, and has far-reaching implications for evolutionary psychology and human behavior. "The handicap principle" lives up to its subtitle -- "A missing piece of Darwin's puzzle". The principle itself is arguably as important a contribution to evolutionary theory as Darwin's mate choice theory, Hamilton's kin selection theory, or Trivers' reciprocal altruism theory. Indeed, it provides a much-needed foundation for mate choice research, offers a radical alternative to the kin selection theory of social insects, and may better explain a lot of 'altruistic' behavior that has been interpreted as a side-effect of adaptations for reciprocity. This book may be speculative, maddening, and possibly wrong in many details, but it is still essential reading for evolutionary biologists and psychologists.

The book

The Handicap Principle is a family affair, written by biology professors Amotz Zahavi and his wife Avishag Zahavi, and very clearly translated from the Hebrew by their daughter Naama Zahavi-Ely and their son-in-law Melvin Patrick Ely. It is beautifully produced, with a striking

peacock's tail cover, and excellent illustrations on almost every page by Amir Balaban. The four-page introduction offers an especially lucid overview of their argument, explaining why gazelles waste time and energy 'stotting' (jumping up and down conspicuously) when threatened by a predator, instead of running away immediately. Since predator and prey have a shared interest in avoiding a pointless chase, reliable signals of prey fitness can evolve, and stotting is just such a signal. This example nicely indicates that almost no biological game is truly zero-sum: even predators and prey have some shared interests that can provide a foundation for communication.

Readable by undergraduates, the book offers a hundreds of behavioral and morphological examples of handicap-type indicators. The authors apply the handicap principle to an astounding range of behaviors, including warning coloration and other fitness-signals to predators by prey, ritualizing fighting and dominance contests between same-sex conspecifics, mate choice based on fitness-signals, reliable signals of offspring need in parent-offspring conflict, pheromone systems in social insects, and communal bird roosts and flocking behavior. They even analyze signalling conflict within cellular slime molds, concerning which cells get to become spore-producers (which reproduce) versus stalk-growers (which 'altruistically' don't reproduce).

Some chapters are compelling and others are quite unconvincing, but the authors' willingness to challenge biological orthodoxy is always refreshing. Indeed, reading it forces one to recognize how much of social behavior is still explained by covert group selection arguments, which the Zahavis demolish with a combination of furious impatience and wry wit. The book's theoretical clarity and revolutionary aura would make it an excellent case study for an advanced undergraduate seminar.

The trouble with handicaps

The handicap principle was first proposed by Amotz Zahavi (1975) over twenty years ago. It set off a firestorm of controversy in theoretical biology, especially in sexual selection theory, and has only recently showed signs of general acceptance (e.g. Grafen, 1990; Hauser, 1996; Miller & Todd, in press). Yet for many evolutionists, the principle continues to oscillate, Necker-cube-ishly, between an obvious principle of how to show off on a school playground, and a deep, maddening paradox of mathematical biology. The showing-off perspective is this: if you want to show that you're better than everyone else, you have to do something that they can't do. It's like Thorsten Veblen's theory of conspicuous consumption: the only reliable, unfakeable way to show that you're rich is to acquire goods and services that only the rich can afford.

On the other hand, the seemingly paradoxical bit is this: signals require inefficient wastes of time, matter, and energy in order to be efficient as signalling adaptations. This seems to overturn the most fundamental criteria for recognizing adaptations in the first place: efficiency, reliability, species-typicality, and even complexity. Handicaps can only work if they're inefficient (imposing large fitness costs on other domains of survival and reproduction), if they are extremely unreliable (breaking down readily if an individual is sick, starving, injured, or depressed), and if they are species-typical only in design but not in magnitude (otherwise they could not signal individual differences). Also, handicaps don't have to be very complex to work, they just have to be expensive. For example, a private jet and a 100-carat diamond are equally good wealth-indicators, though the jet's exquisitely tooled machinery is incalculably more complex than a lump of carbon atoms squished together in the bowels of Namibia and marketed by the international cartel of tiny-carbon-lump dealers.

Anyway, the existence of handicaps demands new criteria for identifying adaptations. Insofar as human behavioral adaptations function as handicaps, the criteria that evolutionary psychologists have traditionally used for identifying adaptations will also need revising. For example, many have argued that human music is not a legitimate adaptation because individuals vary so widely in their musical abilities and musical behavior is so costly and seemingly functionless (e.g. Pinker, 1997). But according to the handicap principle, those are exactly the features we would expect of an adaptation for signalling quality. This raises serious problems of scientific method.

In fact, the book is a methodological nightmare, and will be taken by many as an excellent example of how not to do evolutionary theorizing about animal or human behavior. The Zahavis often make assertions about the likely outcomes of strategic co-evolution, without presenting any formal game theory models, much less any demonstration of Nash equilibria in such models, and still less any demonstration that their verbally outlined signalling equilibria are unique. They routinely present counter-intuitive functional hypotheses about traits without any experimental tests of how variation in the trait's design features affect measures of efficiency with respect to that putative function, or measures of reproductive success. They never draw phylogenies or use the comparative method to distinguish new adaptations from ancestral traits. They alternate between field observation anecdotes concerning strange behaviors and armchair speculation about their significance. Depending on your viewpoint, they act like (1) dangerous hyper-adaptationists even more extreme than Steven Jay Gould's worst caricatures of Richard Dawkins and Dan Dennett, weaving just-so stories out of thin air, (2) harmlessly entertaining, pseudo-scientific fabulists in the tradition of Sigmund Freud and Margaret Mead, (3) classical Victorian natural historians (somehow displaced to contemporary Tel-Aviv University) using the same hypothetico-deductive methods as Darwin himself, or (4) ardent, creative biologists who, whatever one's qualms about their methods and examples, deliver a revitalizing shock to animal communication theory, sexual selection theory, kinship theory, reciprocal altruism theory, and evolutionary psychology. I favor this last judgment.

However, biologists who remain skeptical of adaptationism applied to human behavior may point out the following Panglossian temptation: (1) if a human mental trait works cheaply, reliably, and equally in everyone, we can call it a standard Darwinian adaptation; (2) if it works expensively, breaks down at the slightest provocation, and highlights individual differences, we can call it a Zahavian handicap. The perfect complementarity of standard adaptationism and handicap theory means that their combination seems to explain everything, and thus perhaps nothing. Absorbing handicap theory into evolutionary psychology without really understanding it would open evolutionary psychology to devastating criticism. At least with the standard view of psychological adaptations from Tooby and Cosmides (1990) and Pinker (1997), evolutionary psychologists could start to develop some methodological principles for recognizing adaptations. The handicap principle undermines much of that effort.

For example, the handicap principle suggests that individual differences in general fitness are large, ubiquitous, and highly heritable, and that much of human social, economic, cultural, and courtship behavior consists of people advertising their fitness to each other, to reap sexual, social, and status rewards. This is directly contrary to the standard view (Tooby & Cosmides, 1990), which argues for uniformity of adaptive design through our species and lack of heritability for fitness-related traits. Recognizing the pervasiveness of handicaps and fitness-signals should force a major re-think of evolutionary psychology's attitude towards individual differences, their heritability, and their relationship to species-typical adaptations. Perhaps handicap theory will serve as a sort of binding arbitration arena where evolutionary psychology and behavior genetics will be forced to improve their bizarre love-hate relationship.

Altruism: reciprocity or handicap?

A highlight of the book is the Zahavis' powerful critique of reciprocal altruism theory in chapter 12, wielding a three-ounce group-living songbird called the Arabian babbler (*Turdoides squamiceps*). The Zahavis have been studying these confounding creatures for almost three decades, and have discovered that they do a number of behaviors that look altruistic. They act as sentinels for the group, they share food with non-relatives, they do communal nest care, and they mob predators. Reciprocal altruism theory predicts they should try to cheat, to reap the benefits without paying the costs. Instead, they do the reverse: they compete to perform the apparently altruistic behaviors. Dominant animals, upon seeing a subordinate trying to act as sentinel, will attack and drive off the subordinate, taking over the sentinel role. The birds try forcibly to stuff food down the throats of reluctant non-relatives. The Zahavis propose they are using these 'altruistic' acts as handicaps to display their fitness, thereby attaining higher social status and better reproductive prospects within the group.

Most intriguingly, they extend the handicap principle to offer the only group selection argument for altruism I have ever read that stands up to game-theoretic scrutiny. Consider two hypothetical groups of birds. In one group, the birds compete for prestige by conspicuously throwing food into the sea, showing their fitness through their ability to squander their foraging effort. In the other group, birds compete for prestige by conspicuously throwing food down the gullets of non-relatives. In each group, all individuals are behaving selfishly and rationally, playing the local Nash equilibrium of their subspecies' prestige game. However the feeding-each-other equilibrium is Pareto-superior to the feeding-the-sea equilibrium, so can be favored by group selection between equilibria. Groups that evolve 'altruistic' signals that confer benefits on others while advertising one's own quality will do better than groups that evolve purely wasteful signals that confer no benefits except to increase one's own prestige. This type of group selection between signalling equilibria is not group selection as traditionally defined, and does not entail any conflict whatsoever between individual self-interest and group-interest (Boyd & Richerson, 1990). However, it may be the form of group selection that may best account for the trickle of genuine altruism that we do see in human behavior: altruism as a (sexually-selected) handicap (Tessman, 1995).

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