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The Handicap Principle

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Synonyms

Costly Signaling; Honest Signaling

Definition

The Handicap Principle suggests that many aspects of animal morphology, behavior, and communication are best understood as *handicaps*. A handicap reliably advertises an animal's quality because it signals that the organism is of sufficient quality to tolerate the burden the handicap places on it. Central to this principle is the idea that the costliness of the handicap ensures the reliability of the message being conveyed.

Introduction

Upon spotting African wild dogs (*Lycaon pictus*), Thomson's gazelles (*Gazella thomsoni*) will sometimes start *stotting* – repeatedly leaping up and down using all four legs. Instead of fleeing to safety, these gazelles call attention to themselves, squandering valuable time and energy. Why do they engage in such an ostensibly dangerous behavior, and how could it possibly be favored by natural selection? The answer lies in the handicap principle – one of the oddest and most counterintuitive theories in evolutionary biology.

The Logic of the Handicap Principle

The Handicap Principle suggests that a stotting gazelle is sending a message to its predator - and that this message is effective precisely *because* it is wasteful (Zahavi, 1975; Zahavi & Zahavi, 1997). The gazelle is advertising its physical fitness to persuade the predator to pursue a less physically fit gazelle instead. In essence, the gazelle is saying "look at how physically fit I am – I see you coming, but I'm so confident in my ability to outrun you that I can afford to waste time and energy in this otherwise pointless behavior. You would be better off chasing one of my less physically fit peers instead". The key idea is that only physically fit gazelles can afford to engage in this wasteful display. Consequently, stotting is a reliable indicator of the gazelle's fitness. It is precisely the costliness of the display that guarantees the veracity of the message, rendering it an

T.K. Shackelford, V.A. Weekes-Shackelford (eds.), *Encyclopedia of Evolutionary Psychological Science*,
https://doi.org/10.1007/978-3-319-16999-6_2100-1

"honest signal". And because the message is reliable, it behooves the predator to attend to the information it is receiving. Indeed, studies confirm that predators prefer to chase gazelles who stot weakly or do not stot at all – and they are more likely to succeed in the hunt when they go after a nonstotting gazelle than when they go after a gazelle that stots (FitzGibbon and Fanshawe 1988).

The key claim of the handicap principle, then, is this: many features of animals – ranging from bodily markings to behavior and communication – are handicaps. These handicaps exist because they convey honest, reliable information about the animal bearing the handicap. It is the costliness of the trait that ensures the truthfulness of the message conveyed.

The peacock's tail provides a canonical example. It requires physiological resources to build and maintain, attracts the attention of predators, and hinders the peacock's ability to escape. From the point of view of natural selection, it seems costly and wasteful – a metabolically expensive burden that decreases the peacock's chances of escaping predation. So why do peacocks build such extravagant tails?

Many readers will know an initial answer: because peahens find it attractive. But *why* do peahens find such a wasteful burden attractive? The handicap principle's counterintuitive answer is that they like it *precisely because* it is a wasteful burden. Because it is so costly, only males of high quality can *afford* such a burden. As such, the size, color, and patterns on a peacock's plumage serve as reliable indicators of the male's underlying genetic quality. The peacock's tail thus provides reliable information about his physical fitness and genetic quality – key information for a peahen's mating decisions. This captures the central logic of the handicap principle: the costliness of the handicap ensures the honesty of the message.

Before we evaluate the theory on its scientific merits, considering other examples of the handicap principle may help bring the logic of the theory into relief and simultaneously offer a sense of its scope.

The Handicap Principle in Nonhuman Animals

Skylarks escaping from falcons sometimes sing in mid-flight (Cresswell 1994). Because singing requires oxygen and energy, only skylarks in the best physical condition can afford to sing while fleeing – it is a reliable signal to the falcon that this particular skylark is healthy and fit, and that the predator would do better to pursue one of the skylark's weaker peers. And indeed, studies show that if a skylark sings during escape, the falcon often aborts the chase. But if the skylark does not sing, the falcon continues to pursue it, and often succeeds (Cresswell 1994). The handicap principle thus explains a behavior that would otherwise appear inexplicable.

Siamese fighting fish offer another illustration. When two such fish get into an altercation, they may flare their gill covers, holding them erect. This is a wasteful display – it needlessly surrenders partial use of the gills and thereby impairs respiration. Gill flaring is a signal to one's competitor that one is so formidable that victory is assured despite the handicap of partial respiration. Weaker, less formidable fish cannot afford to do this. Sure enough, when such a fight takes place, the fish that holds its gill covers erect for the longest period of time toward the end of the fight is most likely to be the victor (Simpson 1968).

The Handicap Principle in Humans

The logic of the handicap principle is not limited to any particular species and should theoretically apply with equal force to our own. Are there features of human morphology, psychology, or behavior that are best understood as handicaps?

One candidate is female preference for testosterone-dependent traits in men. Testosterone is a known immunosuppressant (e.g., Folstad and Karter 1992) and is one of the reasons why men are more susceptible than women to a range of diseases (Bouman et al. 2005) and die several years earlier than women, on average (Buss 2015). Like the peacock's tail, high levels of testosterone can be a heavy burden in terms of health and survival. As such, only high-quality males can afford to produce high levels of this immunosuppressant. The handicap principle suggests that one reason why women are attracted to

testosterone-dependent features such as a deep voice, strong jawline, and high shoulder-to-hip ratio is that these traits are evidence that the male in question is of sufficient quality to be able to tolerate high levels of a harmful immunosuppressant. Just like the peacock, his ability to afford a heavy handicap is a reliable indicator of his underlying genetic quality (Hamilton and Zuk 1982; Smith 1985).

Is the Theory Likely to Be Correct?

When Zahavi first proposed the handicap principle (1975), many scientists ridiculed the idea. Ethologist Richard Dawkins evaluated the idea unfavorably in his landmark work *The Selfish Gene*, and evolutionary biologist, geneticist, and game theorist John Maynard Smith published a mathematical model showing that the principle was unworkable (Smith 1976). The handicap principle met with much resistance in the scientific community.

With time, attitudes changed. Ethologist and evolutionary biologist Alan Grafen published a mathematical model demonstrating that, under more realistic assumptions than those of the previous model, the handicap principle could indeed work in natural populations (Grafen 1990). This turning point, in conjunction with the continued flow of empirical evidence emanating from the Zahavi research team, gradually changed the opinions of many scientists. The handicap principle now enjoys both a mathematical proof of concept and a wealth of empirical evidence. Some questions remains about the principle's scope – some thinkers regard it as an extremely wide-ranging theory, while others are more circumspect. But the remaining debates no longer center on the conceptual tenability or mathematical feasibility of the concept, and the theory is now well-regarded among evolutionists. Richard Dawkins went so far as to reverse his initial view, saying this in the 30th anniversary edition of *The Selfish Gene*: "If Grafen is correct – and I think he is – it is a result of considerable importance for the whole study of animal signals. It might even necessitate a radical change in our entire outlook on the evolution of behaviour, a radical change in our view of many of the issues discussed in [The Selfish Gene]" (Dawkins 2006, p. 313)

Evaluating the Theory on Its Scientific Merits

The handicap principle has several scientific strengths. First, the hypotheses that fall under its umbrella are eminently testable. Second, the theory is broad in scope, dealing with topics as diverse as mate selection, predator-prey interactions, parent-offspring relationships, chemical communication, animal coloration, ritualized fighting, parasite-host coevolution, altruism, humans, social insects, and even social amoebas. Third, the theory unifies diverse, seemingly unrelated phenomena by pointing to a deeper logic that underlies their surface variability. Fourth, the theory is parsimonious, and while the biological processes involved can be complex, the underlying logic of the principle is clear and simple. And fifth, the theory has heuristic and predictive power, suggesting new avenues of exploration and making new predictions. For example, because the principle maintains that there must be a logical, nonarbitrary connection between the nature of a signal and the message it conveys, the theory enables one to deduce from the nature of a signal what message it conveys and vice versa.

Novel Hypotheses

We would like to end by advancing a few novel handicap hypotheses in humans. It has been argued that, since immune function may be inversely related to disgust, people may downregulate their disgust in front of potential mates in order to convey a robust immune system (e.g., Al-Shawaf et al. 2015). Although it has not been framed as such, this is essentially a handicap hypothesis: individuals' decreased disgust exposes them to heightened risk of pathogens, thereby conveying reliable information about their health and immunity.

Second, we suggest that the pride display, which involves a raised chin, lifted arms, protruding chest, and exposed torso (Tracy and Matsumoto 2008), is also a handicap. The person showing pride in this manner is exposing himself to attack and making himself vulnerable. This cost

is tolerable for formidable individuals but constitutes a heavier burden on weaker or less capable individuals. We suggest that pride displays therefore convey reliable information about the quality of the individual engaging in them.

Third, we suggest that the practice of fighting for the right to pay the bill in a restaurant (common in the Mediterranean, for example) is a manifestation of the handicap principle. Despite the surface-level variability between this cultural practice, potlatch dinners in tribal environments, and conspicuous consumption in urban environments, they are all underlain by the same logic: people are attempting to publicly handicap themselves with a financial burden in order to reliably convey their socioeconomic standing to their peers.

These examples represent only a small subset of the many manifestations of the handicap principle detectable in modern cultures, ranging from golf handicaps through chess handicaps to blindfolded skateboarding. The idea is not that humans have evolved adaptations tailored to modern innovations like golf or skateboarding, of course, but rather that selection favored the evolution of psychological mechanisms designed to flexibly use local cultural cues as handicaps, thereby honestly advertising an individual's ability or quality.

Conclusion

The handicap principle suggests that most animal communication is honest and reliable. This honesty is guaranteed by the cost of the communication – the message is too costly to fake. In other words, the cost is prohibitive for liars but not for those who are telling the truth. For example, the investment required to build the peacock's brilliant plumage is manageable for a male of genuinely high quality, but prohibitively costly for a male lacking the relevant physiological and genetic resources. The costliness of the peacock's tail guarantees the reliability of the information it conveys.

Scientists initially rejected this idea but have generally come to accept it. Though strikingly counterintuitive at first, its underlying logic is sound, and it has the hallmarks of a good scientific theory: testable hypotheses, unifying explanatory ability, parsimony, broad scope, and heuristic and predictive power. It is buttressed by both mathematical and empirical support, and it changes the way we look at much of animal communication.

Cross-References

- ▶ Alan Grafen
- ▶ Amotz Zahavi
- ▶ Animal Signaling
- ▶ Communication, Cues, and Signals
- ▶ Costly Signaling
- ▶ Costly Signaling and Altruism
- ▶ Costly Signaling Theory
- ▶ Disgust
- ▶ Fitness Benefits of Costly Signaling
- ▶ Game Theory
- ▶ John Maynard Smith
- ▶ Richard Dawkins
- ▶ Signal Reliability
- ▶ Testosterone

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