The Handicap Principle

Laasya Samhita

Laasya Samhita is presently pursuing PhD in the Department of Microbiology and Cell Biology at the Indian Institute of Science, Bangalore. Her research interests include evolutionary biology, currently addressing evolutionary questions in protein synthesis

The Handicap Principle is an idea proposed by the husband and wife scientist team of Amotz and Avishag Zahavi from Israel in the 1970's. It is among the most innovative ideas of the 20th century in the field of behavioural biology and attempts to explain several long-standing puzzles that have baffled naturalists since the time of Darwin. Although the theory was initially met with scepticism by the scientific community, with time and with sophisticated mathematical modelling it has now gained wider acceptance. In the book explaining their idea, the authors discuss various observations of animal behaviour in the wild and suggest how these can be explained using the handicap principle. Both experiments and long-time observations of animal behaviour fit in smoothly with the authors' hypotheses for the most part. In this article I discuss the concept of the handicap principle and its application to various biological phenomena.

Why Does the Peacock have a Cumbersome Tail?

Charles Darwin, in his path-breaking book, *On the Origin of Species*, proposed a mechanism known as 'natural selection' to explain how the diverse living creatures on Earth possibly evolved. Being both very meticulous and by nature diffident (it took years to consolidate the book) he also simultaneously put before the public several natural phenomena he had observed that he felt could not be adequately explained by his theory of natural selection. Prominent among such puzzles was the tail of the peacock. Why does the peacock possess an apparently cumbersome and huge tail? To most of us it may even seem a stupid question on the face of it. 'Because it is attractive' would seem to be the obvious answer, exposed as we are to tales of rain dances and maybe the occasional lucky sighting of a peacock displaying its gorgeous tail feathers to the peahen during the mating season. But in the

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animal world as we understand it, it is not enough to be beautiful; for a phenotype to be selected, it must be 'fit' or have a higher ability to transmit the trait to the next generation. But the heavy tail seems to almost impede the movement of the peacock and surely it must make it a disadvantage in the face of predators and when it wants to take flight. Why, then, is the long tail 'selected for' over evolutionary time?

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This question has been tackled extensively by behavioural biologists over the years, with Fisher's 'runaway sexual selection' being perhaps the most innovative idea. Fisher suggested that the reason for males of certain species to carry extravagantly developed secondary sexual characters could indeed have started with a slight female preference when the trait first appeared. Initially the slightly exaggerated feature was perhaps linked with stronger or biologically fitter males. However as selection favoured these slightly more ornamented males, the trait itself got out of hand and extravagantly decorative males evolved, individuals who no longer were the fittest since the trait, so to speak, overwhelmed the organism and became ridiculous and cumbersome. In other words, Fisher proposed that the peacock's tail was indeed once upon a time associated with the strongest males but is not so linked any longer and in fact has apparently become a burden.

A Fresh Idea

After Fisher, the subject of sexual selection received its share of interest but there was no major breakthroughs to offer in understanding this puzzle, not least because experimental evidence was insufficient, if not absent. It was only in the mid 1970's that the husband and wife scientist couple of Amotz and Avishag Zahavi published a book titled *The Handicap Principle*. In the book [1], they put forward a novel idea to explain several previously baffling aspects of animal behaviour, including the famous tail of the peacock. The principle relies on three chief tenets – a) Animals communicate with each other through signals; b) these signals, in order to be effective, must be honest, and c) honest signals are expensive, i.e., the animal producing an honest signal incurs a cost in doing so. The peacock carries its tail as an advertisement of its fitness. They suggested that the elaborate tail is a means of saying that "in spite of carrying the handicap of a cumbersome tail, I am able to carry on my daily activities as well as a peacock which has a lesser tail".

The peacock carries its tail as an advertisement of its fitness.

The Zahavis argue that a signal is liable to be effective when it is honest, that is, when it conveys a true measure of how fit the signaller is. An honest signal, however, must be expensive. Why? Because signals do not come for free. They cost something (e.g., energy) to produce. The stronger you are, the more easily you can bear this cost. A strong individual can afford to incur a larger cost than a weak individual can. The upshot is this; if you convey the impression that you are handicapping yourself, and if the nature of the handicap is such that a weak individual could not afford it, you are signalling that you are strong. Assuming that you are not a fool (and fools do not survive long), if you go out to bat against Shoaib Akhtar without a helmet, you are signalling your genuine ability to deal with short-pitched balls. This is the essence of the Handicap Principle

The Handicap Principle was a startling concept when the Zahavis first applied it to animal behaviour. But in some ways it is an old idea. We have an instinctive appreciation for what success in the face of an impediment. Where a good violinist is applauded, a good violinist who is blind is given a standing ovation. In his book *The theory of the leisure classes*, the 19th century economist Thorstein Veblen attempted to explain the squandering of resources by the wealthy. He called it *conspicuous consumption*. Veblen's explanation anticipated a form of the handicap principle. He claimed that the wealthy indulge in waste in order to advertise their wealth.

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Coming back to the peacock, do females in fact prefer males with 'more beautiful' tails? This was answered by a series of experiments carried out by Marion Petrie and her colleagues at the Whipsnade park in the UK and the brief answer is yes, they do. Marion Petrie *et al* used several parameters to define what 'beauty' might constitute, for example they used the weight of the tail (clearly a handicap), the number of feathers and the length of the tail as some parameters. Interestingly they found that the number of eyespots on the peacock's tail is a measure used by the female in choosing a mate! We do not know yet whether in fact the female has some way of counting these spots or whether having more spots simply makes for a more impressive display, for example.

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The Handicap Principle Implies That Signal Have to be Honest

The handicap principle can be used to account for mating preferences in animals. The key idea here is that no female would choose a truly handicapped male to father her children. A desirable male is one who is fit *in spite* of the handicap he carries. The handicap works like a badge that announces quality. Only a confident individual can afford it. Consider a human parallel. Both popular cinema and common perception proclaim that when in danger, a confident individual adopts a frozen stance, with hands folded across the chest and the chin pointing upwards, in fact the worst kind of posture with which to prepare for a fight.

A handicap cannot be faked. This is what makes it honest, and reliable as a signal. This is because flaunting the handicap requires a genuine investment on the part of the animal. If an individual cannot afford to make that investment, it cannot afford to cheat. The courting peacock's eye-catching but heavy tail, the threatened gazelle's spectacular but attention-drawing jumps, the gullible crow's feeding of baby cuckoos – all find an explanation in terms of the handicap principle. Let us look at two of these situations in more detail.

An Example of the Handicap Principle in Operation

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The hunter and the hunted would normally seem to us to have conflicting interests. After all, one is looking for food and the other does not want to be eaten. However, it is in the interests of both to avoid a conflict that is going to result in the prey getting

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away. If such an encounter is predictable before hand, the predator would save time and effort and look elsewhere for weaker or easier prey, while the potential prey can save the energy used in running away. The authors use the behaviour of 'stotting' as an example here. Stotting refers to the up and down jumps exhibited by gazelles upon spotting a wolf or other predators, prior to their running away. The authors argue that this is illogical behaviour for a gazelle that is keen on escaping, it should just run; and not apparently 'waste time' with such jumps. They suggest that a gazelle that indulges in such a dangerous practice must be signaling its physically fit status to the predator. By doing so, it is communicating to the predator that it has seen it (therefore the advantage of surprise is lost), and it is strong enough to outrun the predator in a chase. Based on many field observations, it is known that very often predators faced with stotting gazelles leave and look for other prey. The authors propose this as an example of an honest signal that has evolved as a means of communication between predator and prey. It involves an investment of energy on the part of the gazelle, and so cannot be faked. It would be suicidal for an unfit gazelle to attempt such jumps; it would only expose its inability sooner and fall an easy prey.

Mating Displays Reveal the Handicap Principle in Operation

Like in the case of the peacock, other mating displays also are an oft-quoted example by the authors. Typically, females invest more in their offspring than males do. Also they are receptive only at certain times in the year, and once they conceive they will be unable to conceive again for the period of the pregnancy and for some time after. So they need to be choosy in picking a mate. Males, however, mate with several females in the short period of time when they are receptive, thereby aiming to maximize the chance that their genes are passed on. In the mating season, therefore, each male must do his best to attract, and mate with, as many females as possible. The peacock, as already discussed, holds his tail upright – in itself a process that would seem to need strength – and shakes it vigorously from time to time. By doing so he appears to prove his physical fitness to the watching female. Also, his tail feathers are developed at a time of year when there is a scarcity of food. A male who has developed a fine tail plumage, therefore, is offering proof of his ability to successfully look for and find food even under conditions of stress, and hence is advertisings his desirability as a mate.

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In the mating season, the spectacularly coloured male bird of paradise hangs upside down on a tree, spreads his feathers and flaps the wings. He is dancing with a handicap. During the mating season white pelicans develop bulges at the base of the beak (just ahead of the eyes). A bulge is a handicap. It makes it hard for the pelican to see and impairs its ability to fish. A successful fisher proves to potential mates that it can fish well in spite of the impairment. These mating display observations however, have been made for several years and as observations are nothing new to naturalists. However, when they discuss single celled fungi, the yeasts, the authors put forth both a novel observation and a new hypothesis to explain it.

Yeast cells reproduce both asexually (by budding or fission) as well as sexually. There are two distinct mating types in yeast, referred to as 'a' and 'α'. Both use a peptide molecule on the cell surface as a mating 'signal' as the authors term it. These peptides are seldom bare, and usually carry oligosaccharide moieties and occasionally even lipids attached to them. The authors suggest that yeast cells advertise their desirability as mating partners by 'decorating' the peptide molecule that is their mating signal. To make the modification, they need to use expensive chemical resources (such as lipids and sugars). The modified signal works like a handicap. Most importantly, the hypothesis is testable, and indeed a 'decorated' peptide appears to be preferred to an 'undecorated' one, suggesting that the handicap principle could be one innovative way of looking at signals even at the single cell level.

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In Darwin's Own Words

"As these examples show, there is what looks like wastefulness behind many sexual displays", and the handicap principle tries to explain why this is so. But this theme has been a subject of discussion among naturalists for many years. Indeed, Darwin himself proposed something reminiscent of the handicap principle when he wrote "The females are most excited by, or prefer pairing with, the more ornamented males, or those which are the best songsters, or play the best antics; but it is obviously probable, as has been actually observed in some cases, that they would at the same time prefer the more vigorous and lively males" (*The Descent of Man and Selection in Relation to Sex*)".

Exciting and plausible the handicap principle may be, the authors appear to be carried away by their enthusiasm when they bring up human analogies using unsubstantiated data. Topics ranging from the colour of cheeks and lips to cave-paintings are discussed as examples of the handicap principle in operation. Even beards are not spared. In many instances, they appear to have picked something that could qualify as a signal and then constructed an explanation around it. Having said that, the idea still remains innovative, unique, and above all, provides ample scope for clever experimental design and hypothesis-verification.

When the handicap principle was first proposed in 1975, it met with wide scepticism. Mathematical models seemed to show that it could not work. It appeared destined to share the fate of other ideas in the history of science that were appealing but incorrect. After 1990, however, scientific opinion turned around. This is because of increasing support from observations and due to sophisticated mathematical modelling by Alan Grafen that showed that this is a workable theory. It has come to be accepted as a novel concept, with wide application in understanding animal behavioural strategies. In speaking of the fifteen-year gap, Zahavi says "Biologists remained unimpressed by the logic of the verbal model, and accepted the handicap principle only when expressed in a complex mathematical model, which I and probably many other ethologists (behavioural biologists) do not understand". Budding biologists might well support this rueful statement.

Suggested Reading

[1] **Amotz and Avishag Zahavi, *The Handicap Principle: A Missing Piece of Darwin's Puzzle*, Oxford University Press, 1997.**

Address for Correspondence
Laasya Samhita
Department of Microbiology and Cell Biology
Indian Institute of Science
Bangalore 560 012, India.
Email:
aysaal_ls@yahoo.co.in