

## Mate Choice Through Signals

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### Abstract

I suggest that the message encoded in signals that attract mates is information about the phenotypic qualities of the signaller. That explains why such signals often deter rivals. These qualities need not be genetic adaptations. The cost of the signal tests the reliability of the message. Signals are not conventions. The reliability of the message is achieved by the particular cost—e.g., energy and time—imposed by the pattern used for a specific message. This theory of signal selection suggests also that complex behaviour patterns, such as the altruistic activities of the Arabian Babbler (*Turdoides squamiceps*), are in fact selfish adaptations that signal social status. This theory has also led me to suggest that set-specific signals (such as adult plumages), species-specific signals, and sex-specific signals have their function in advertising the advantages an individual has over other members of its set in a reliable way.

### Introduction

In this paper, I shall discuss the following topics: (a) the message in signals that attract mates; (b) similarities between signals that attract mates and signals that deter rivals; (c) the cost of signals as a test for their reliability; (d) altruistic activities as signals displaying social status; and (e) the existence of a competitive element in signals that seem to be equally developed in all potential mates.

### Discussion and Conclusions

#### The Message in Signals that Attract Mates

Darwin (1871) interpreted the value of many bizarre characters such as bird song, brilliant male plumage, the long tail of peacocks (*Pavo* sp.), and ritual dances on leks as signals that attract mates. He did not discuss the details of the messages encoded in these signals, and he did not address himself to the

question of why a female (or a male) should be attracted to a mate signalling in such a fashion. He was satisfied with the explanation that these bizarre characters attract mates. Fisher (1930) tried to explain why females should be attracted to seemingly non-adaptive characters that burden the signallers instead of being attracted to mates that bear better adaptations. He suggested that the attractive male is not better in its adaptations to its environment for survival or breeding; its advantage is in the fact that females consider it attractive.

Fisher's model was investigated by a series of mathematical models (Maynard-Smith 1976; Kirkpatrick 1986). These models suggest that non-attractive males that sometimes co-exist in equilibrium with attractive males are in fact better males. The attractive males equal them in fitness because of their being preferred by the females. In other words, females that prefer attractive males are in fact selecting for males inferior in their adaptations for survival. This seems to be in conflict with observations in the field that suggest that the males with the more-developed attracting signals are also the males that successfully acquire territories and retain them against the pressure of less-attractive males.

I searched for a way to explain the advantage to the selecting female in picking a male that burdens itself with an extravagant signal instead of using a simpler and less-burdening signal. I came up with the model of the handicap principle (Zahavi 1975). The model suggests that the burden serves as a test for the reliability of the message of quality.

I agree with Maynard-Smith (1976) and, more recently, Kirkpatrick (1986) that if we assume that the signal advertises the presence of a particular genetic quality in the signaller, my model is not easy to apply. However, I have never suggested that this is the message in the attractive signal. On the contrary, in 1975 I emphasised that I meant phenotypic quality. Even if it is difficult or impossible to find conditions under which advertising genetic qualities through a handicap would benefit the signaller, a handicap would still be of use to advertise phenotypic qualities to a potential mate. That possibility was admitted by Maynard-Smith (1976) but ignored by him as uninteresting. However, the importance of the phenotypic condition of males sharing in the raising of the brood is obvious; recently, Partridge and Halliday (1984) discussed a series of cases in which the phenotypic state of the males affected the fitness of the females even though the males contributed only their sperm.

#### **Are Signals that Deter Rivals Different from Signals that Attract Mates?**

In his book on sexual selection, Darwin (1871) pointed out that the same bizarre characters that attract females function also to intimidate rivals. Partridge and Halliday (1984) also showed that a number of signals that had been considered earlier to be mate-attracting signals function as signals that deter rivals. It is well known that bird song serves both functions in most cases. Displays of colours and movement as well as bizarre structures such as elongated tails seem also to function in deterring rivals as well as in attracting mates. Fisher's (1930) model cannot explain the evolution of burdening signals for intimidating rivals. It may seem reasonable to suggest that a female would gain by being attracted



to an inferior but attractive male because of the chances that his sons would be attractive to the next generation of females. A contestant, however, is concerned solely with its rival's exact phenotypic state at the moment and is not concerned at all with its genetic background. It would not be to the benefit of any individual to be frightened by a rival burdening itself, unless the burdening signals are correlated with the ability of the signaller to fight.

My alternative model assumes that a signal functions to attract or deter because it reflects the qualities of the signaller as a mate or a rival. I suggested that signals function as a test for the qualities they advertise. The burden of the signal (the handicap, as I have termed it) ensures the reliability of the message. In that sense, signals that function in sexual selection are not different from signals that function in other contexts (Zahavi 1981). For example, males in conflict over feeding territories and males in conflict over females often have the same aggressive displays.

#### The Cost of Signals as a Test for Their Reliability

The theory of signal selection (Zahavi 1981) suggests that the correlation between the quality of the advertiser and the pattern of the signal is kept by the cost of the signal. For example, a bird that is not afraid of disclosing its location to predators may advertise by a colourful plumage. The time invested in singing may inform mates and rivals that the singer has ample food.

The connection between the signal and its cost may lead to speculations concerning morphological features of birds. The European White Pelican (*Pelecanus onocrotalus*) grows a bump on its forehead at the time of courtship. The bump hinders its ability to see the area in front of its beak with both eyes. Such a signal may carry a reliable message to a mate that this individual is an expert fisher because it can fish in spite of its handicap. Towards the time when it has to feed its young, the bump disappears, and the pelican once more becomes an efficient fishing bird. The crest, which in many birds advertises the age and maturity of the individual, may be explained as a handicap as well. If the size of the beak and skull of a bird reflects its phenotypic qualities, then the crest reduces their apparent size. Only large individuals that possess large skulls can afford the handicap of reducing the apparent size of their skull and still appear to be large.

A ring around the eye discloses the direction in which the bird is looking. This is a handicap that a dominant bird may afford to take, but it may involve a prohibitive cost to a younger bird. An adult, which is more likely to be dominant than a young bird, can benefit from disclosing its intentions by looking at the object that interests it. A subordinate may fare better with a quick dash at an item of food before the others realise its intentions or with a surprise attack. That may be the reason why eye rings and other facial markings are not as clearly developed in young birds as in adults.

#### Altruistic Activities as Signals Displaying Social Status

Some of the signals used to attract mates and deter rivals can be very complex. Our studies of the Arabian Babbler (*Turdoides squamiceps*), a group-living bird,

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suggest that complex behaviour patterns that were supposed to function because of their altruistic adaptations (such as helping at the nest) are in fact signals that advertise the social status of the helper (Carlisle and Zahavi 1986).

Babblers invest in other apparently altruistic activities. For example, they perch as sentinels when the rest of the group is feeding. The dominant male acts as a sentinel more often than other males; it is usually the first sentinel in the morning. Babblers are attentive to the sentinel activities of others. Dominants often terminate the sentinel activity of subordinates by starting to act as sentinels before the others have gone down. They sometimes go to the same post and pressure the subordinate to go down by feeding it, allopreening it, or just waiting near it until it goes down; young babblers may even use aggression. Subordinates never behave towards dominants in this way. The alpha male is more likely to replace the beta male than to replace a low-ranking sentinel, especially when the alpha and beta males are competing over copulations.

These findings suggest that sentinel activity functions as a competitive signal to advertise status. We have data to suggest that there is a correlation between the investment of the male in reducing the sentinel activity of its rival males and its share in the copulations. Males that do a great deal of guarding and put down their competitors frequently are also able to guard over the female at egg laying and secure all or most of the copulations (AZ, Larkman, and Faran, unpublished data).

It is important to add that competition among adult males of the same group hardly ever involves direct aggression. It is nearly always done through signals such as allofeeding, sentinel activity, or the acknowledgement by the inferior of the superior rank of a rival by vocal displays or postures. Direct aggression is so rare and drastic that when it occurs among adult-male group members, the loser is always either killed or expelled from the group. I suggest that, in such social circumstances, apparently altruistic activities replace aggression as a means of competition.

#### **Is There a Competitive Element in Signals that Seem to be Equally Developed in All Potential Mates?**

A big challenge to the theory of mate choice by signals is the fact that many of the signals, such as bright plumage, are not variable. When all males wear the same plumage, it is difficult to see how plumage serves as a marker for differences in qualities. How can the golden plumage of an oriole (*Oriolus* sp.) serve as a signal of quality when all male orioles possess similar golden plumage?

I suggested (Zahavi 1980) that these patterns function as standards that help display clearly variations in size, morphology, or behaviour of the individual possessing them. In an oriole, the size of the wing in relation to the size of other body parts is displayed clearly by the black wing against the yellow background of its body. The shape of talons, beaks, or feet can be assessed more easily when they are coloured differently from adjacent body parts. It is clear that individuals that have a body of better shape or size would benefit more from advertising it than would individuals of inferior qualities. Hence, the handicap

of investing in these signals is reasonable for the better-quality individuals. I suggest that such signals, which seem to be the same in all members of a set, function as standards for quantitative information and that they have evolved through simple competitive processes.

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