

On the definition of sexual selection, Fisher's model, and the evolution of waste and of signals in general

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In this note a signal is defined as a character the adaptive significance of which, to the signaller, is to provide information which may change the behaviour of other individuals. Characters other than signals (i.e. size, shape, etc.) may provide information to individuals that observe them, but this is not different from information gathered by observation of the inanimate world. A character is a signal only if the response of other individuals to the character has been a factor in the selection of that character.

Darwin (1874) suggested that two selection processes operate in evolution: 'natural selection' which is a consequence of the struggle to survive among all the members of the species; and 'sexual selection' which is a consequence of the competition to reproduce among members of the same sex. He defined the process of sexual selection to explain the evolution of secondary sexual characters which are expressed in a different way in males than in females: 'The males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone. Sexual selection must here have come into action.' Darwin's definition of sexual selection as the 'competition of individuals with members of their own sex' included mate choice, male deterrence, and other properties which are of help in reproduction and combat, such as body size and weaponry.

Lack (1968) did not find anything special in the process of sexual selection to justify its designation as a unique selection process. Mayr (1972) was convinced of its importance, but was unable to define it as a distinct process. He only pointed to its importance in attracting our attention to an interesting set of problems which stimulated the collection of important data.

Fisher (1930) was not interested in characters that are of help in reproduction or physical fighting, since such characters do not seem to require a special evolutionary mechanism. He also narrowed the interest in sexual selection to mate choice as a factor that produces extravagance. He suggested that a female that prefers an attractive male benefits through the advantage of her sons, which are likely to inherit the attractive character their father possessed. He further suggested that this female preference may co-evolve with the investment of the male through a runaway process, which may cause the evolution of the extravagant characters.

Although Fisher's model may explain the high cost involved in the evolution of extravagant characters that attract mates, it cannot explain why extravagance should function to intimidate rivals. Fisher was aware of the shortcomings of his model in explaining the evolution of extravagance in signals used in male–male conflicts: 'As a propagandist the cock behaves as though he knew that it was as advantageous to impress the males as the females of his species, and a sprightly bearing with fine feathers and triumphant song are quite as well adapted for war-propaganda as for courtship'. Fisher stated 'that the evolutionary reaction of war paint upon those whom it is intended to impress should be to make them less and less receptive to all impressions save those arising from genuine prowess'. But as he did not know of any way by which 'war paints' could be correlated with prowess, Fisher believed that it is mate choice rather than conflict between males that is responsible for most of the extravagant displays in nature. Since Fisher, modern interest in the mechanism of sexual selection has centred around the problem of mate choice, ignoring the problem of the evolution of extravagance in threat signals.

The same signal, however, often functions both to attract a mate and to deter a rival, e.g. song of song birds, their song flight, their nuptial plumage, etc. Darwin's book (1874) is full of such examples. In many other cases extravagance functions only to deter rivals (Partridge & Halliday 1984). There is therefore no reason to suppose that the adaptive significance of extravagance in deterring rivals evolved in a different way to that in mate choice, and it is not reasonable to accept Fisher's model as a mechanism that explains the functioning of a signal to attract mates while that mechanism may not explain the functioning of the same signal to deter rivals.

The special and difficult evolutionary problem in sexual selection is not the mechanism of mate choice, but rather the adaptive significance of extravagance. But sexually selected signals are not the only signals that evolve extravagance. Signals that deter predators by brilliant coloration e.g. aposematic coloration of poisonous organisms (Hingston 1933; Cott 1940) or exaggerated movements, e.g. stotting in ungulates, often equal in extravagance those that deter sex rivals. Signals that induce parents to feed their young, such as the movements, coloration and vocalizations of nestlings and fledglings are often very conspicuous and exaggerated (Trivers 1974; Zahavi 1977). There is no reason to assume that signals that function in sexual contexts will be selected by a different selection process. Indeed the same signals that are used against sex rivals are often used in the defence of winter feeding territories, e.g. the song of robins, *Erithacus rubecula*, and the movement displays of white wagtails, *Motacilla a. alba* (Zahavi 1971). During pairing on winter territories wagtails use similar displays to those used on their breeding grounds, even though these pairs bond for the winter territory only, and break before the wagtails migrate to their breeding grounds. (A young female that first met and joined a male in mid-winter would not be able to migrate alone, after the male has gone, and still resume her bond with him on the breeding territories.) Extravagant group displays, such as the morning group dance of babblers, *Turdoides squamiceps* spp. which has a function in social circumstances unrelated to sex (Zahavi 1990), are not less extravagant than displays used between sexual partners.

Sexual selection as defined by Darwin does not encompass a set of characters that pose a common

problem to modern evolutionary biology. The only reason to continue using this term seems to be respect for Darwin's historical definition. But this respect blurs the main interesting problem within sexual selection. The central problem that sexual selection presents for evolutionary biology today is the selection for extravagance and waste; however, as already stated, these are not unique to sexual selection. The common denominator of all those characters that display extravagance and waste is that they are all signals, whether they are included within the definition of sexual selection or not. According to the theory of signal selection (Zahavi 1981, 1987), signals must have a cost in order to be reliable. The higher the investment in it the more reliable is the signal. In this respect the evolution of signals differs fundamentally from the logic by which all other characters are selected. All other characters are selected for efficiency; the smaller the investment required to achieve a particular result the better. In signals the investment in reliability may increase markedly the total investment, much beyond that needed to transmit a clear message. In some important interactions, the need for reliability justifies extra high investment that takes the form of extravagance and waste (Zahavi 1987).

The theory of ritualization (Huxley 1914; Lorenz 1966) seems to contradict the idea that all signals must have a cost. According to that theory the value of the ritualized signal is due to its clear and standard performance. Morris (1957) has already emphasized that ritualized signals retain a certain degree of variance and apparent redundancy. He suggested that the variance functions to display the degree of motivation of the signaller. As a consequence of the theory of signal selection I suggested that the ritualized pattern has evolved as the best standard that enables individuals to assess in a reliable way the variation by which the motivation is displayed i.e. cheaters will not be able to use the signal in the same way as honest signallers, owing to the cost involved in performing it exactly as honest signallers do. The problem is dealt with in more detail elsewhere (Zahavi 1980).

The great potential of the theory of signal selection to interpret the evolution of signals has recently gained more theoretical support (Grafen 1990a), and some field observers have used its logic to interpret their data (Carlisle & Zahavi 1986; FitzGibbon & Fanshaw 1988; Hasson et al. 1989).

Thus I agree with Darwin that two distinct selection processes exist in nature, but I suggest that these are 'natural selection' and 'signal selection'. The sooner we abandon Darwin's definition of sexual selection and concentrate on understanding the special mechanism of signal selection, the better we shall understand the patterns of signalling systems and the evolution of extravagance.

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