# A reply to John

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In his commentary John (1997) has the feeling 'that in maintaining a distinction between natural selection and signal selection Zahavi (1991) is also making a mistake'. He also concludes that 'it is neither enlightening nor correct to refer to signal selection as selection for inefficiency'. John also states that: 'The sexual and natural selection dichotomy has been useful, and remains so' and 'That there is something special about elaborate ornamental signals is undeniable'. Our differences are therefore concerned with the importance of this dichotomy and the importance of the term inefficiency to the phenomena created by signal selection. I am well aware that signals, like all other characters, evolve under the constraints of their cost. I quote from my (1987) paper: 'The cost of a character hinders the evolution of every character INCLUDING SIGNALS, but cost is essential for the evolution of signals while it is a necessary evil to the evolution of all other characters. Hence, the selection of signals is different from the selection of all other characters.' I also pointed out in that paper that this relation to the cost constitutes the main difference between the two selection processes: 'The importance of the cost to the evolution of signals is such that signals may not function if their cost is eliminated or markedly reduced. . . . The process by which a signal may be lost is analogous to the inflation process . . . which can be a test for the theory of signal selection.' The importance of the dichotomy between signals and characters that are not signals is strengthened by this unique prediction of the theory of signal selection, which points to a different selection mechanism for signals. John objects to my description of the two selection processes as opposing one another. I attend to these differences in detail in a forthcoming

book on the handicap principle (Zahavi & Zahavi, in press):

'What, then, is the fundamental difference between signals and other traits? It is the relationship between the signal and its cost. Every trait, whether signal or not, demands an investment of some sort, and every trait is constrained by other traits whose requirements conflict with it. In this signals are similar to all other traits. Changes in the environment may change the constraints on the evolution of traits and lessen or increase the cost involved. For example, the size of an animal may be limited by its need to stay small and agile to avoid predators, but if its predators are removed it can afford to increase in size and thus increase its ability to store energy, withstand cold, or deter rivals of its own species. The species then becomes larger because the cost of being big has gone down significantly. If, on the other hand, the cost of a signal is reduced to the extent that every individual can use it equally well, then the signal can no longer reveal differences in the quality or motivation of individuals. In such cases, the signal loses its value and will cease to be effective as a signal. This process may be compared to the inflation process in human currency which often results in the elimination of the inflated currency and its replacement by another. The evolution of signals—signal selection—is thus fundamentally different from the evolution of all other adaptations.'

I understand and agree with John's view that from the perspective of the gene there is no difference between the two selection processes. All genes exist because their benefits exceeded their cost. For some modern evolutionary biologists, who model the evolution of genes, this may be the only interesting topic. However, this is not the only subject of interest for many others who wish to understand why particular characters, including

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signals, have an advantage. Recognizing the dichotomy between the two processes 'enlightened' my understanding of a whole plethora of characters that earlier did not make sense, such as the evolution of altruism, or that of novel characters, such as antlers and feathers (Zahavi 1987; Zahavi & Zahavi, in press).

John objects to the term 'inefficiency'. Peacocks carry long and heavy tails that curb their movements and flight; deer antlers are very inefficient as weapons (Darling 1937 pointed out that although some deer have straight, sharp antlers (pronghorns), which are very efficient weapons, these mutants disappear from all natural populations); and the stotting of a gazelle does not increase the distance between it and its predator. All these are signals and there is no way to describe these characters as efficient, except for their effects on the behaviour of other individuals. None the less it is obvious that their benefits outweigh their cost, otherwise they would not exist. But the interesting challenge for the biologist is to explain the advantages of these costly and inefficient characters. The vast literature, mathematical models and scientific effort investigated in this research testify to the scope of the challenge.

Darwin used the term natural selection to distinguish it from sexual selection. Hence, when I considered the advantage of the term sexual selection I compared it with natural selection as defined by Darwin. But in these same articles I have also defined what I meant in using that term. To eliminate confusion in the future I suggest here the term signal selection for the selection of signals, utilitarian selection for the selection of all other characters, and I reserve the term natural selection for the entire selection process. John agrees with me that the line separating sexual selection from the selection of all other characters was not well defined by Darwin. In his words:

'Would it be more appropriate in defining sexual selection to allow for a form of it that does not involve signalling between competitors or potential mates, or would it be sensible, permitting, perhaps, a clearer definition, to equate sexual selection with sexual signal selection?' He also agrees that 'Zahavi is certainly right that a strong case can be made for emphasizing signal selection as a more encompassing concept than sexual selection'. Following his suggestion, there is not much left of sexual selection to merit its retention; while there is a reason to consider signalling as a special set. This is exactly what I have suggested. Darwin's contribution to evolutionary theory was so great that it can afford the handicap of admitting that his definition of sexual selection was not clear; however, he most certainly indicated a real problem for evolutionary biology; a problem which I believe is resolved by the suggestion of the theory of signal selection.

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