

## SHORT COMMUNICATIONS

### Assessment of expected performance and Zahavi's notion of signal

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Zahavi (1991) has recently proposed that the two main selection processes that exist in nature are not natural selection and sexual selection, but natural selection and signal selection. In his view, the term sexual selection would be justified only as a historical term rendering homage to Darwin. Zahavi's objection to Darwin's (1871) definition is that 'it blurs the main interesting problem within sexual selection, that of selection of extravagance and waste'. Extravagance and waste can be understood as signals and can be selected by both the processes of 'classical' sexual selection and natural selection. *Sensu* Zahavi, '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. 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'. Zahavi further suggests that ritualized signals '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 do, owing to the cost involved in performing it exactly as honest signallers do'. While I agree with Zahavi that the processes selecting for signals are not restricted to sexual selection (i.e. intraspecific processes) and that the interspecific processes (e.g. aposematism) may essentially follow similar rules, I would like to question (1) Zahavi's classification of signals and in particular his view that body size or shape etc. cannot be signals, and (2) his interpretation of ritualized patterns as reliable indicators of variation of motivation.

Zahavi's definition of the term 'signal' depends on whether a receiver contributed to the evolution of the signal or not. This criterion allows one to view interspecifically selected signals (e.g. aposematic colouring) and intraspecifically selected signals (intra- and inter-sexual selection) under a common

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denominator. Taking examples of non-sexually selected characters, under Zahavi's definition the yellow belly of the firebellied toad, *Bombina variegata*, is a signal if it can be shown that it evolved because the predators (i.e. the receiver of the signal) responded by ignoring the more yellow-bellied individuals and thus contributed to the evolution of the trait. Or, under Zahavi's definition, the lure of the angler fish, *Lophius piscatorius*, is a signal if it can be shown that it evolved because the prey animals (i.e. the receivers of the signal) responded to it by trying to eat it and were then eaten themselves, thus contributing to the evolution of the lure by giving a selective advantage to angler fishes having prey-like lures. An example of an intersexually selected signal is the red belly of sticklebacks, *Gasterosteus aculeatus*, which is selected through the females' preference for intensely coloured males (Milinski & Bakker 1990). By analogy, why is body size not a signal if it could be shown that smaller individuals (i.e. the receivers of the signal) respond to a larger individual by leaving him prior access to resources, and thereby giving him an advantage which contributes to the evolution of larger bodies (i.e. the signal)? Or if females can take male size as a signal indicative of resource-holding potential (i.e. a constellation of factors that influence competitive ability; Parker 1974), then the females (the receivers of the signal) will by their positive reaction to the signal contribute to the evolution of larger bodies (i.e. the signal). By extension, if females can take a male's territory size as a 'signal' indicative of resource-holding potential, then the females (the receivers of the signal) will by their positive reaction to the signal contribute to the evolution of mechanisms for acquiring larger territories (i.e. the signal). In fact an individual's territory size is not an item of information similar to information from the inanimate world, but an expression of the individual's interaction with the inanimate world, which could be used as a signal indicating its resource-holding potential as accurately as a deer's antlers may indicate resource-

holding potential. A deer's antlers may as well partly be an expression of the animal's interaction with the inanimate world in the sense that they may indicate its access to resources, for example, food.

Thus, Zahavi's classification of signals and non-signals cannot be maintained. Body size can be a direct signal indicative of an individual's resource-holding potential, and similarly, territory size can be an indirect signal indicating an individual's resource-holding potential. Zahavi (1975, 1977) proposed the ingenious idea that the reliability of a signal is positively correlated with the cost of the signal. This has recently been supported by a theoretical analysis (Grafen 1990a, b). In that sense, body size (or territory size) could be a very reliable character for signalling resource-holding potential. First, it is more expensive to build up a larger body than a smaller one, and second a larger body has larger costs of maintenance than a smaller one, and the same is true of territory size. Selection for even higher reliability of the information contained in body or territory size may even select for extravagance in body size or territory size, that is selection for bigger bodies or larger territories than would be predicted for the pure satisfaction of requirements. Note that this argument may provide a new view of the 'superterritory' question. Verner (1977) has proposed that superterritories may evolve through the negative effects of a superterritory holder on its neighbours' fitness, a view that has been rejected on theoretical grounds (Rothstein 1979; Parker & Knowlton 1980), whereas I propose that superterritories may evolve through selection for reliable information about territory quality and/or resource-holding potential. For species where the female chooses the male on the territory, we would then predict territories to be largest during mate choice and, for economic reasons, become smaller thereafter. Decreasing territory size with progress of the reproductive cycle has been found in several species (e.g. Schoener 1968; Yarrow 1970).

In conclusion, Zahavi's classification of signals is not consistent with his criterion for the definition of signals. His present classification or his proposed criterion need justification in biologically meaningful terms.

In this section I analyse the view that ritualized signals may display motivation (Morris 1957; Zahavi 1980, 1991). Let us consider the intra- and inter-sexual processes separately. In intra-sexual contests between two individuals the dispute most commonly concerns a limited resource. The main

task of an individual is then to assess two factors which will determine an opponent's expected performance (OEP): its resource-holding potential (RHP; Parker 1974) and its willingness or motivation (M) to contest the resource. In the simplest form we can write the opponent's expected performance (OEP) as

$$\text{OEP} = f_1(\text{RHP}) + f_2(\text{M}) + f_3(\text{RHP} \times \text{M})$$

where the last term indicates that there may be an interaction between the factors, for example, motivation may vary as a function of resource-holding potential (see Archer 1988 for discussion and examples of such interactions).

Zahavi holds that the variation in motivation of individuals can be reliably assessed from the display of a ritualized behavioural pattern. This may be true if resource-holding potential can be assessed independently, but not if resource-holding potential cannot be assessed. For example, if an individual meets an opponent on neutral ground, a ritualized behaviour may be indicative of all three terms in the above equation. If it meets the opponent with its resource (e.g. its territory) it may evaluate its resource-holding potential from the quality of the resource, and evaluate its motivation to defend the resource by other signals, for example, a ritualized behaviour. If no behavioural pattern has been ritualized, then the information regarding the motivation may be acquired during the course of a conflict, which can be seen as a series of rounds between two unequal opponents, where at the end of each round the individual has acquired more precise information concerning the opponent's motivation. The conclusion concerning the evolution of ritualization is that it simply allows the assessment of the opponent's expected performance in a safe manner. It is adaptive since damaging escalation is costly to both opponents (Parker 1974). In Zahavi's view 'ritualized behaviour is the best standard that enables individuals to assess reliably the variation by which the motivation is displayed', whereas I am suggesting that a ritualized pattern is indicative of the opponent's expected performance, i.e. of both resource-holding potential and motivation. Only if the resource-holding potential can be assessed independently, will the ritualized pattern reliably indicate the variation in motivation only.

In inter-sexual contexts, the problem is the choice of a mate, and the difficult task of an individual is to assess a potential mate's expected performance

(MEP, e.g. expected investment, care, etc.). Important factors influencing the mate's expected performance will be a potential mate's resource-holding potential, its motivation (M) or willingness to invest in the individual's offspring, and additionally its parasite resistance (PR). In its simplest notation a mate's expected performance can be expressed as

$$\text{MEP} = f_1(\text{RHP}) + f_2(\text{M}) + f_3(\text{PR}) + f_4(\text{I})$$

where (I) denotes all possible interactions between the three factors, for example, a potential mate's resource-holding potential may vary as a function of parasite resistance. The same arguments as in the intra-sexual example above apply here. Only if the resource-holding potential and the parasite resistance can be assessed independently will a ritualized behaviour reliably indicate the variation in motivation. The stickleback could present such an example: a female could assess a male's resource-holding potential from the quality of the nest and territory, its motivation from the ritualized zig-zag dance, and its parasite resistance from the intensity of the colouring of its belly.

If the factors in the above equation cannot be independently assessed, the theory of signal selection would still predict that a ritualized behaviour should contain reliable information, not about motivation alone, but about the mate's expected performance. It may be that the possibility of an independent evaluation of the three factors may give a more accurate estimation of a mate's expected performance. However, as far as I can see, signal selection theory would not predict this because the indication of the mate's expected performance should be reliable by itself. Is it useful to be able to assess how much each of the three factors contributes to a mate's expected performance? Since the successful production of offspring depends on both individuals of a pair, one could imagine that an individual has information about the three components which determine its own performance, and could therefore maximize its fitness by selecting a mate with complementary qualities regarding the three factors. For example, a pair where both individuals have low parasite resistance (or low resource-holding potential, or low motivation to reproduce) may be less successful than a pair where at least one individual has high resistance (or resource-holding potential, or motivation). Thus it would present an advantage if the three factors could be assessed separately, and hence there could be selection for signals permitting an independent assessment.

In summary, I suggest here (1) that Zahavi's view of which characters can be interpreted as signals is too narrow because it excludes features of an individual that can be used as signals indicative of its expected performance, although these features comply with Zahavi's signal definition and are used by animals as a source of information; (2) that as a consequence the criterion of what defines a signal has to be clarified; (3) that ritualized behaviour may in many cases not reliably indicate motivation alone but be an expression of other features or a combination of features that determine an individual's expected performance (in a contest, or as a mate); and (4) that there may be selection for separate features which contain reliable information about each component of a potential mate's expected performance because this may allow a complementary matching of the components of an individual with the ones of its mate and thereby increase the individual's fitness.

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