Zahavi's contribution to the understanding of the signal evolution is vital to our understanding of animal communication. Equally important is his impact on the field of sociobiology with respect to the evolution of altruistic behaviour. The classic reproduced here was originally written two decades ago as a chapter in the book 'Evolutionary Ecology'. In this book chapter Zahavi makes a strong case for the Handicap Principle that he had proposed in 1975. He reasons that a signalling system can only evolve if the signals are reliable and receivers respond to the signals. Receivers will continue to respond to signals if doing so benefits them. If, however, in responding to certain signals the receivers are harmed, then over evolutionary course of time it is expected that they will cease to respond to such signals. So far so good, but it is not hard to understand that the real difficulty lies in evaluating whether a signal is reliable or not in the first place. Zahavi's Handicap principle posits that the fool-proof test of reliability of a signal lies in the cost of signal production. Only costly signals are likely to be reliable and receivers must respond only to such signals. In this classic, Zahavi argues that the evolution of communication systems must be driven by mutual benefit conferred to the parties involved (the sender and the receiver) in a signalling system and that this holds true not only when the interests of the parties converge (as in the case of signalling between kin) but even when interests diverge or even oppose each other (as in the case of signalling between prey and predator)..

Manjari Jain

Assistant Professor

Department of Biological Sciences

IISER, Mohali

Email: manjari@iisermohali.ac.in

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21 Reliability in communication systems and the evolution of altruism

Dr A. Zahavi*

The evolution of a communication system depends on the existence of individuals which gain from it, that is the senders of the signals and their receivers. These two share a common interest about which they communicate. Common interests of this kind form the basis of the communication between such individuals as a sexual pair, parents and their offspring, and members of a flock or group which feed, roost or breed together. It is less often realised that individuals which are usually regarded as conflicting in their interests – for example, prey and predator, sexual rivals, a parasite and its host – may also share a common interest which may form the basis for the evolution of a communication system between them. Warning coloration, warning calls and other signals which are given by a prey species towards a predator (Smythe, 1970; Alcock, 1975) and also threat display among rivals, are some examples of signals exchanged between individuals which mainly conflict in their interest.

When two rivals communicate, for example by threatening, there exists the possibility that one of them may gain an advantage by cheating. Thus one may give a signal to show that it is a very powerful and able warrior while it is really a weakling and a coward. If that were possible, there is no reason why all individuals should not resort to cheating. If all cheat, the particular communication system concerned with threat will be worthless. Since from observations it is clear that the communication of threat is effective, there must be a reliability component in the system which guards against cheating. Although the problem of cheating seems to be peculiar to communication between rivals, which mostly conflict in their interests, there is no reason why a smaller conflict between otherwise collaborating individuals may not give some advantage to cheating. A male may try to cheat a potential female mate so as to increase its chances to get more or better females (Williams, 1966; Zahavi, 1975). An offspring may demand of his parents more than his share of care, food and so on (Trivers, 1974) to the extent that a conflict may arise between parents and their offspring. A group of territorial birds may likewise share a mixture of common and conflicting interests (Zahavi, in press). It is not easy to imagine two individuals with a common

*Born in Israel in 1928, Dr Amotz Zahavi is a bird watcher who studied the biology of birds with H. Mendelssohn, animal behaviour with N. Tinbergen and evolution with David Lack. From 1956 to 1969 he was General Secretary of the Society for the Protection of Nature. He is now Director of the Institute of Nature Conservation Research, and teaches eco-sociology, evolution and behaviour at Tel-Aviv University.

interest, that may not conflict in their interests at some time or in certain conditions. Thus keeping as free as possible from false information (cheating) is a basic problem in the evolution of communication systems. This problem has been discussed in an indirect way (Zahavi, 1975) in relation to the evolution of characters selected by sexual selection.

The Theory of the Handicap Principle in Sexual Selection

Certain aspects of sexual display, like the song of birds, their nuptial plumage or various behaviour patterns, may be considered as signals aimed to inform a potential mate about the quality of the sender. Since the sender of the signal may gain by advertising false information, (that is, exaggerating its quality) and a potential mate may lose if it believes a false signal, the receiver of a signal will act in its own interests only if it considers signals that are not easily open to cheating. The theory of the handicap principle (Zahavi, 1975) suggests that a signal is reliable when the difficulty of its performance is related to its meaning in quantity and quality.

A signal which means "I am very strong" should be more difficult to send than the signal "I am strong". Furthermore, a stronger individual should find it less costly to signal its strength than a weaker one, cost being measured in terms of reproductive potential.

An individual that advertises its sexual quality with bright colours may suffer a higher risk of predation than a dull-coloured one. In surviving, however, it advertises a superior ability to avoid predators, demonstrating its quality in a way which the dull-plumaged bird cannot match. Should the brightly-coloured individual lack the inherent ability to avoid predators which its colours advertise, then it is particularly at hazard and likely to suffer predation; thus the reliability of the signal is maintained by direct and rigorous selection.

Parent – Offspring Conflict – the Evolution of Signals which Threaten by Self Destruction

A fledgling which begs for food attracts its parents by sound, by movements of its wings, and by the bright colours of its bill and gape. The signals also attract the attention of the observer and most probably may attract the attention of a predator. Why is this apparently high cost of the communication between parents and offspring necessary? I suggest that when parent – offspring relationships are understood to contain an element of conflict (Trivers, 1974) the cost is a necessary component of the system which makes the signals reliable. The conflict which Trivers identifies is that, although parents must consider their overall breeding potential while caring for young, offspring must care only for themselves (his statement was qualified by reference to the further effects of kin selection). Thus, in their own interests, parents cannot always act according to the demands of the group of offspring which they are tending at the moment. When offspring try to induce their parents to feed them more, by calling louder, they may reveal their whereabouts to predators and consequently stand a higher risk of predation. The cost to the offspring of their begging call maintains the reliability of the message to the parent. A signal for food which does not lower the chances of

survival of the fledgling (for example, in circumstances where predation is low) should not be as effective in inducing feeding behaviour as one made where predation risks are high. The strategem of threat by self-destruction, open to subordinate individuals which are of value to those whom they threaten, is probably widespread in its application. In human terms it appears among children who threaten to run away or damage themselves if their parents do not meet their wishes.

The white colour of the shell of a dove's egg may similarly be interpreted as a signal (a threat) to the parent to incubate more than its own selfish interests demand. Likewise the sparse down of a grebe chick may be an adaptation to make the chick helpless in water, so that the parent will be obliged to take it sooner on its back. The chick signals its body temperature to the parent by a bare patch on the forehead which is blue when the chick is cold and red when the chick is warm (personal observation). The signal of helplessness is an effective blackmail and functions as such only when the individual is really helpless. Consequently some individuals which threaten by evolving helplessness may do worse than they would have done otherwise. But on the average they do better, since parents respond to the threat more readily than they would have responded without it. They respond quicker because, although they sacrifice to the offspring more than they otherwise would, they stand to lose more if their offspring die. They choose the better of the undesirable alternatives which they face.

Warning Calls – as Communication between Prey and Predators

Warning calls are usually considered as a signal by which one prey individual warns other prey individuals of the approach of a predator. Warning behaviour is also considered (Maynard Smith, 1965) as an altruistic behaviour, since the warning individual may expose itself to danger when giving the warning. Perrins (1968) suggested that in certain circumstances the warning call may confuse the predator rather than help it to locate the prey. Charnov and Krebs (1975) suggested that in some cases the warning individual may gain by diverting the attention of the predator to other individuals that are easier to catch. But in many cases, for example with the Arabian babbler *Turdoides squamiceps* (personal observation), the warning individual often leaves cover to warn. The first indication that a group of babblers is present is often their warning call sounds.

Recently Smythe (1970) and Alcock (1975) suggested that warning signals may act as a communication system between predator and prey. Smythe's view is that the signals of the prey inform the predator that it has been seen. In a system in which a predator whose presence is known cannot easily catch prey, it is to the benefit of both prey and predator for the latter to move away to new ground once it has been sighted. I feel that this may explain the willingness of many prey species to give warning calls, even to leave cover and approach or mob the predator, effectively displaying confidence in the message which they deliver. Unless the prey endangered itself in displaying its confidence, the predator need not believe the message to be true. The confidence is shown by the warning call, which gives away the whereabouts of the prey to the predator, but even more by mobbing.

Similarly, it is generally accepted that a non-palatable prey may benefit by communicating, through colour and behaviour, its non-palatability to the predator. I suggest that the reliability of warning coloration depends on the danger to the prey inherent in bright coloration. Since only animals which have the protection of their poison may advertise themselves with impunity, warning coloration is generally a reliable communication system between prey and predator.

Threat Displays

Rivals often use threat display to resolve their conflicts. Threat may be considered as a signal to a rival with the aim of resolving a conflict without a clash (Alcock, 1975). Each of the rivals attempts, with threat signals, to impress its opponent with its potential as a fighter and its readiness to fight. Threat signals are effective since both rivals may profit by resolving the conflict without a fight. But if the threat signals were easily open to bluff, that is, if there were no mechanism to keep the correlation between the signal and the readiness and ability of the individual to fight, threat would lose its value as a means of settling a conflict without a fight. The use of a threat signal which endangers the threatening individual, in correlation to the magnitude of the threat signal, deters fighters of poor quality from threatening too much. Only the high quality fighters may threaten without great harm to their potential as fighters. A survey of threat displays reveals the handicap involved in all of them. The warning which the threat gives to the threatened individual decreases the efficiency of the attack, since it reduces the advantage of surprise. The side display used by many species as threat exposes a vulnerable part of the threatening individual and endangers it more than if it were facing its opponent head on. That is the reason why the 'underdog' in an encounter between dogs usually faces the opponent head on, since it cannot afford the handicap involved in a side display. Likewise a dominant Big horn sheep gives the advantage of the first strike to the subordinate (Geist, 1971). The magnitude of the horns and antlers of dominant ungulates is effective as a threat, since only very vigorous individuals may fight and survive with such a burden carried on their head.

Altruism among Babblers as a Communication System about Dominance Hierarchism

Arabian babblers live in groups of 3 – 15 birds. Each group defends its territory against its neighbours and nomadic birds. Data from population dynamics studies of babblers (unpublished observations) suggest that territory is essential for their survival and breeding. It is therefore reasonable to assume that group members have much common interest in defending their territory against all other babblers. On the other hand, since usually only one pair breeds in the territory, there is also much competition over breeding. There is very little overt fighting among adult group members; on the contrary there is much activity among them, such as allofeeding and sentry duties, which is commonly interpreted as 'altruistic'.

In a system where the survival of an individual depends on the well-being of other individuals, there is much for all – even the strongest and most dominant individuals – to gain by avoiding fights. Strong animals gain by avoiding possible

damage to themselves, and also by preventing damage to rivals which, in other circumstances, become helpers. Thus there should be considerable advantage in the evolution of a system of communication which enables conflicting group members to predict, communicate and agree about the outcome of a potential fight, and consequently avoid the need for it.

I suggest that the 'altruistic' activity of babblers may fit such a demand. Details and data of many of these activities will be published elsewhere; here I am concerned only with a reinterpretation of altruism illustrated by allofeeding among adult male babblers. A few hundred observations of the passage of food among known individuals show that the donor of the food is, with fewer than 1 per cent exceptions, practically always dominant to the recipient. It is possible indeed to draw up a dominance hierarchy from observations of allofeeding. Do babblers use allofeeding as a communication system?

If presenting food is a display of status, accepting it indicates a lowering of status. Hence it is not surprising to see babblers, especially those high in the hierarchy, which refrain from accepting food from their superiors. The very few cases where food is passed from a subordinate to a dominant become displays of rebellion against the established dominance hierarchy: it happened, in the cases observed, that fights (which are normally exceptionally rare among adult group members) immediately followed such rebellion, presumably to re-settle the changed social order. If allofeeding were simply a passage of food from one individual which has surplus to another in need of it, it would be difficult to explain situations in which an individual acts at one moment as a donor to its social inferior, and a minute later as a recipient from its superior.

My interpretation of allofeeding in this species is further supported by the proclamation of the feeding act by the donor. When allofeeding occurs in other species it is usually the receiver which makes a call – generally referred to as a begging call. In babblers the donor calls just before delivering the food, often delaying the passage as if to enable other members of the group to see the act. Furthermore, allofeeding usually occurs on top of a tree or in open spaces, where it can readily be seen by the group.

Much altruistic activity, if not all, may have originated in this way through simple individual selection among animals that cooperate with each other. It may thus be unnecessary to invoke more complicated selective mechanisms, such as group selection and kin selection, to explain its evolution.

Some General Considerations of the Handicap Principle

In the preceding paragraphs a number of characters have been reinterpreted on the basis of simple individual selection. The handicap principle suggests that every communication system has its reliability component which takes the form of a handicap. Since communication systems occur commonly, and many may not yet have been recognised as such, it is possible that several characters besides altruism may be reinterpreted as reliability components of hitherto unsuspected communication systems. In this context it is interesting to re-examine the controversy between Lack and Wynne-Edwards about the role of territorial behaviour in the regulation of animal populations to the level of their food supply.

It was Wynne-Edwards's view (1962) that territorial behaviour regulates size of

population through a mechanism involving group selection. Lack (1966) did not support the concept of group selection, but took an opposing view which, in its extreme, questioned whether territorial behaviour had any role at all in regulating population numbers through the partitioning and conservation of food supplies. My own interpretation of territorial behaviour, in terms of the handicap principle, is based on an assumption that an animal advertising ownership of territory is, at the same time, advertising its own quality as a territory holder. The handicap (that is, the cost in terms of extra work) involved in defending a territory that is larger than the animal needs for feeding, is repaid by its value as an advertisement of the superior quality of the individual. Thus the phenomenon which Wynne-Edwards explained in terms of group selection, and Lack had difficulty in accounting for at all, can be resolved as a simple case of individual sexual selection. This interpretation is based on an earlier suggestion by O'Donald (1963) which involved, however, a different understanding of sexual selection.

When handicaps are considered as no more than the costs of social signals, it is not necessary to postulate a causal relationship between the cost of the signal and its meaning. This present reinterpretation, which regards handicaps as essential reliability components in communications systems, suggests that the cost is a necessary component of the signal; the more significant the signal, the higher the costs to the performer. Since it is reasonable that individuals should attempt to advertise (that is, signal) differences in their qualities, the characters important in determining quality should be affected adversely by the signal.

With this hypothesis it should be possible to predict from a study of the signal (for example its colours, sounds, movements) the nature of the selecting factors that are acting on the population. Theoretically a long-term experiment may decide between the two approaches. If it is true that a communication system simply has its costs, lowering the costs should result in increased use of the system. On the other hand the handicap principle elaborated here suggests that lowering the costs may at first increase the use of the system, but further decrease in cost should destroy it altogether. Since the lowering of cost has probably occurred often in nature, it should not be surprising to find adaptations in communications systems which maintain the value of the systems despite cost reductions. Such an adaptation should imply the understanding of a signal in relation to the circumstances – that is, whether the cost in a particular situation is high or low, whether a consequent evaluation of the particular situation is high or low, and what the signal accordingly means. This we understand intuitively; the man who dares to stand up when the bullets are *not* flying around is not considered particularly courageous.

Although I have discussed the value of the handicap principle in a restricted range of contexts, I believe it to be applicable to all communications systems. Other examples to which it may apply are relationships between host and parasite, and host and symbiont, and that between two interacting unicellular organisms which communicate by chemical means. With adaptations which will be discussed elsewhere, relationships among true social insects and even among cells of a multicellular organism may also be explained in this way.

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