



## ANNIVERSARY ESSAY

# Indirect selection and individual selection in sociobiology: my personal views on theories of social behaviour

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This is the story of my involvement in sociobiological studies. I first discuss group selection models, which were common in the 1950s. I then move on to kin selection and reciprocity models, which were developed to replace group selection models and are still being used by many sociobiologists, even though I argue that they contain the same weaknesses that led group selection to be rejected. As an alternative, I present the handicap principle, an essential component in all signalling. The handicap principle is useful in understanding many components of social systems, not the least of which is why individuals invest in the benefit of other members of a social system (altruism).

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I have been watching birds since childhood. As a student of biology in the early 1950s, I was attracted by the great advances in cell biology and in biochemistry that took place at that time. But after spending several months cooped up in a laboratory, I could not resist the temptation to go out again into the field, looking for rare birds and watching birds display. For my master's degree, I decided to study the avifauna of the Huleh swamp, even though I was sure at the time that the intellectual challenges in biology were taking place in the laboratory rather than in finding nests and counting birds. It was [Tinbergen's \(1951\)](#) book, *The Study of Instinct*, that convinced me that animal behaviour was a respectable science, full of intellectual challenges, and that the study of it could fit in with birdwatching and field studies. I spent most of 1955 with Tinbergen's group at Oxford and at Ravenglass watching black-headed gulls.

In the 1950s, studies around the world dealt with many aspects of animal behaviour. Ethologists in Western Europe with whom I was acquainted studied mostly the social interactions of animals in the wild. Ethology, then a new branch of the study of animal behaviour, was at that time mostly a descriptive science, which studied sequences of social interactions. We spent most of our time observing the natural behaviour of wild animals and doing simple experiments. [Tinbergen \(1963\)](#) described

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the kind of questions asked at Oxford at the time: '(1) what is the survival value of the observed behaviour; (2) what is its causation; (3) how does it develop; and (4) how has it evolved?' Theories that were developed at that time to explain the adaptive significance of a particular behaviour did not necessarily seek an ultimate explanation of why that behaviour should function the way it did. We often considered proximate explanations satisfactory. For example, when animals neither threatened nor attacked, but instead did something that seemed irrelevant to the situation, the behaviour was called 'displacement activity' ([Tinbergen 1951](#)), the assumption being that the stimulated animal had to do something. When males attacked visiting females, it was supposedly because the males could not control their aggression. Behaviours that were correlated with the strength of the social bond were considered behaviours that strengthen the bond ([Lorenz 1966](#)).

In the 1950s, ethologists explained the adaptive significance of many social behaviours by the benefit they conferred on other individuals ([Tinbergen 1951](#); [Lorenz 1966](#)). All of us used group selection arguments: for example, that 'communication is reliable because if many cheat the system will collapse'. We believed at the time that signals evolved 'for the benefit of the communicating parties, to make the information clearer to the receiver'. Threat signals were supposed to replace aggression 'because it benefits the conflicting parties', and we believed that individuals utter warning calls 'to save their

fellow group members'. In general we believed that it was adaptive to help members of a group 'because a large, successful group benefits all its members'.

In the 1960s, a debate emerged about the importance of group selection in evolution. Wynne-Edwards (1962) suggested that animals often reduced their reproduction in the interests of the population, while Lack (1966) asserted that individuals reproduce as much as they can. Maynard Smith (1964) and Williams (1966) supported the point of view of individual selection. Most evolutionary biologists eventually became convinced that group selection was rarely effective in the real world. This happened not because group selection models were illogical, but because under ordinary circumstances such models can be exploited by social parasites (Maynard Smith 1964). However, rejecting group selection models created big problems for behavioural scientists. There was no obvious alternative model to explain many social adaptations. It was especially difficult to explain the evolution of signals and of altruism by individual selection. Evolutionary biologists attempted to offer new models to explain the social behaviour of individuals. Hamilton (1964) suggested a genetic reason for the investment of animals in their relatives, a theory that was later named kin selection by Maynard Smith. Trivers (1971) suggested that reciprocal altruistic relationships could form a stable model of altruism among nonrelatives. Maynard Smith (1976a, 1982) suggested the use of evolutionarily stable strategy models (ESS) to explain the evolution of threat signals. Altruism and the evolution of signals became central problems in sociobiology. These new theories had a great effect on students of social behaviour, and many attempted to test in the field models based on kin selection and on reciprocity.

From 1955 until 1970 I had only limited contact with the study of social behaviour and ethology. I was occupied with establishing the conservation movement in Israel. By the time I returned to the academic world and to science, ethology had matured and was interacting with evolutionary biology. I was lucky to be able to spend 1970 with David Lack at the Edward Grey Institute at Oxford. Lack convinced me never to compromise on trying to explain adaptations on the basis of pure individual selection. I also learned from him to use my common sense to interpret behaviours. Meeting with many ornithologists, and especially with Peter Ward, gave me the confidence that field workers can use their observations to suggest theories. One result was our suggestion that gatherings of birds serve as information centres (Ward & Zahavi 1973).

My next involvement with evolutionary theory came out of a remark by a student who pointed out a weakness in Fisher's model (Fisher 1958). To solve the problem I suggested the handicap principle as an alternative to Fisher for explaining the use of waste in mate choice. The handicap principle suggests that if an individual is of high quality and its quality is not known, it may benefit from investing a part of its advantage in advertising that quality, by taking on a handicap, in a way that inferior individuals would not be able to do, because for them the investment would be too high. I am grateful to Maynard

Smith, who agreed to publish my paper on the handicap principle (Zahavi 1975), even though he did not believe in verbal models. I am also grateful to him for publishing his own paper rejecting the principle (Maynard Smith 1976b). By doing so he drew the attention of the scientific community to the controversy.

Right away, I found myself debating the logic of the handicap principle with mathematicians (Davis & O'Donald 1976; Kirkpatrick 1986). They could not prove the handicap principle with genetic models, and therefore rejected it, even though I explicitly discussed its use in phenotypic interactions, especially since 1977 (Zahavi 1977a, b). The simple argument of the handicap principle was considered by theoreticians to be 'intuitive'; they insisted on having mathematical models to show its operation in evolution. For some reason that I cannot understand, logical models expressed verbally are often rejected as being 'intuitive'.

In 1990 Grafen formulated a mathematical model for the handicap principle, and thus made it acceptable to mathematically minded evolutionary biologists and ethologists. However, Grafen also stated that the main biological conclusions of his papers were 'the same as those of Zahavi's original papers on the handicap principle' (Grafen 1990a, page 487) and that 'the handicap principle is a strategic principle, properly elucidated by game theory, but actually simple enough that no formal elucidation is really required' (Grafen 1990b, page 541). Still, for some reason, biologists remained unimpressed by the logic of the verbal model, and accepted the handicap principle only when expressed in a complex mathematical model, which I and probably many other ethologists do not understand.

Since 1990 the handicap principle has been generally accepted as a mechanism that could explain the evolution of the reliability of signals; even so, many still believe that in many cases signals do not require handicaps, either because there is no incentive to cheat when the communicating parties are related to each other (Grafen 1990; Maynard Smith 1991), or because the signal evolved to be reliable without any investment (Hasson 1991). But there is an inherent conflict among all social partners: mates (Williams 1966), parents and offspring (Trivers 1974), and members of any social group. For that reason, an individual can never be sure at a particular moment whether or not there is a conflict of interest between itself and any particular collaborator, related or not. To be on the safe side, all signals demand reliability.

I believe that the conclusive evidence to support my suggestion, that the handicap principle is of use in the evolution of all communication systems, including isogenic individuals, comes from chemical signals within the multicellular body, which are also loaded with handicaps. Many signalling chemicals within the body are complex or noxious (such as Dopa, CO, NO, etc.) or have adverse effects on ordinary cells (Zahavi 1993; Zahavi & Zahavi 1997). Why is it that signalling systems within the body do not use nonharmful chemicals that are easy to produce and handle? I suggested that the adaptive significance of complex or harmful chemicals as signals is to

inhibit signalling by cell phenotypes that are not the types of cells that should emit the signal. Since all cells have the same genetic information, some of them, perhaps a few millions out of the billions of cells, could start signalling at the wrong time or transmit the wrong information. For the receiver cell, and for the whole organism, it is important to be sure that the information it receives is reliable. Hence cells that develop into the types that should signal also develop the ability to cope with the adverse effects caused by the production or use of the chemical signal. In other words, the noxiousness is a handicap. Between organisms, handicaps in signals evolve to prevent cheaters from benefiting from using the signal; in the multicellular body, signals evolve with handicaps to decrease the possibility of their use by the wrong phenotypes.

I would like to correct several common misunderstandings about the handicap principle. First, some still assume that a handicap, by definition, evolves to decrease fitness. This is not the case. The selective process by which individuals develop their handicap increases their fitness, rather than decreases it. If 'cost' is measured by a loss in fitness, then handicaps do not have a cost for honest signallers, since honest signallers increase their fitness by signalling. Only cheaters would decrease their fitness if they were to take on a handicap that does not match their qualities, hence the efficacy of the handicap in discouraging dishonest signalling. For this reason, I now prefer the term 'investment' to the term 'cost'. Second, the investment in a handicap need not be very high or very detrimental, as is often assumed. The investment is proportional to the potential gain to cheaters from giving the signal. If the potential gain is small, the investment is small as well. The investment need not necessarily be in energy, risk, or material. It may be in information or in social prestige. (Zahavi & Zahavi 1997). It is not up to the signaller to decide how much to invest; it is the receiver of the signal who is forcing the signaller to invest in the signal.

My study of the Arabian babbler, *Turdoides squamiceps*, followed my study of flocking and territorial behaviour in wintering wagtails, *Motacilla alba*, in Israel (Zahavi 1971) in which I managed to convert flocking individual wagtails into territorial ones by manipulating their food dispersal. I was interested in the ecological conditions responsible for the formation of the group-territorial way of life among babblers, and intended to study whether it would be possible to manipulate their social behaviour. I never did.

I developed the idea of the handicap principle only a year after I began to observe the babblers. Watching these birds at Hazeva in Israel for over 30 years with the handicap principle in mind has been a very fruitful coincidence. Within a few years, I found that the handicap principle could explain many phenomena other than the use of waste in mate choice; why is it, for example, that the same signals that attract mates also deter rivals and predators? This is something that Fisher's model could not explain. I found the handicap principle useful in interpreting babbler vocalizations (including their so-called alarm calls), their colour patterns, and more. I

found that the social bond between partners could be tested by placing a burden (a handicap) on the collaborator ('the testing of the bond'. Zahavi 1977c). Such testing is constantly evident in babbler's clumping, dancing, allopreening and play, and in many other facets of their social behaviour.

The handicap principle and the complementary idea of testing the social bond provide ultimate explanations for, among other things, the importance of displaying hesitation by displacement activities and the aggressiveness of a male towards its mate (Zahavi 1977c), as well as the reliability of signals (Zahavi 1977a). For me as a bird-watcher, perhaps the most satisfying outcome of the handicap principle was the conclusion that there must be a logical relation between the pattern of a signal and its message (Zahavi 1977a; Zahavi & Zahavi 1997). From that point on, recognizing a species' colour pattern or vocal call brought with it not only the satisfaction of identifying it, but also valuable clues to the message encoded in these signals.

The study of the Arabian babblers at Hazeva suggested that their altruism can be interpreted as a signal displaying their claim to social prestige (Zahavi 1977a, 1995). Observations suggested that the help babblers provide to their group, their altruism, is often not needed, and that babblers often reject help offered to them by their group members, are aggressive to the helpers, and compete over performing altruistic acts. I used the handicap principle to interpret their altruism as a 'showing off' of quality to support individuals' claims to social prestige. Social prestige is the respect accorded an individual by others as a result of their assessment of that individual's strength and ability as shown by its actions and physique. Social prestige can be acquired, for example, by aggression, or by a show of waste, or by investing in the benefit of others. We have used the idea of prestige to explain the success of some social parasites (such as cuckoos), as well as to understand why individuals invest in the social welfare of their mates and of other collaborators; we have also discussed the use of prestige as a means to deter rivals.

The handicap principle thus suggests that, even when the altruistic act benefits others, the altruist gains directly from investing in its altruistic behaviours. There is therefore no need for any indirect-selection model to explain altruism. This idea provided me with an alternative to the other theories that were developed to interpret altruism: group selection, kin selection, reciprocal altruism and the other variations of reciprocity models. Only then did I realize that kin selection and reciprocal altruism share the weakness of group selection and should be rejected for the same reasons (Zahavi 1981, 1995; Zahavi & Zahavi 1997). Both are unstable and may be exploited by social parasites.

In kin selection, for example, let us assume that two or more individuals of the same brood have a chance to gain fitness by investing in their kin. Whichever of them invests in its kin loses some of its own direct fitness. But whether or not they invest in their kin, they all gain equally in their inclusive fitness from the investment of those who invest. The total gain by the ones that did not invest is higher, because they gained in inclusive fitness

without investing anything and thus without losing any of their direct fitness. In other words, kin selection is as open as group selection to social parasitism and is not a stable model.

Reciprocal altruism was suggested by Trivers (1971). He proposed that altruism works by reciprocity, and to ensure reciprocation he suggested a system of punishment, for example a grudge, against social parasites. But one who does not invest in the punishment or does not display a grudge gains as much as individuals that do invest. Social parasites will again gain without investing, that is, they will gain more than honest individuals, making reciprocal altruism as unstable as group selection. Trivers (1971) also stated that an individual that can exploit another and does not do so is an altruist. This statement suggests that in all social systems individuals should try to exploit their partners. However, observations suggest that more often than not partners do help each other.

On the other hand, my suggestion that altruism is an investment in advertisement by the individual altruist (that is, a handicap) shows how altruism can provide a direct benefit to the altruist. The individuals that accord prestige to the altruist do so not to encourage altruism, or because they benefit from the altruistic act. In fact, they may not benefit from it at all. Rather, they accord prestige because of the quality displayed by the altruist, quality that the altruistic acts demonstrate reliably. The recipients and the observers, both collaborators and rivals, benefit directly from the information advertised by the altruistic act in their own decision making. The idea that the altruist acts to demonstrate its quality and to gain prestige explains why beneficiaries are often aggressive towards the altruist, and why individuals often compete to act as altruists, even when that competition runs counter to the interest of the group (Zahavi & Zahavi 1997). It is important to note that none of the other theories can explain the observations that altruists compete to act as altruists and may show aggression towards the altruist, and why altruistic activities deter their competitors within the group.

Because social behaviour is a cooperative act, its interpretation can easily slide into group selection arguments. I have made that mistake with Peter Ward (Ward & Zahavi 1973) when we suggested that advertising flights at a roost were selected to attract more individuals to the roost. After all, flock members that do not participate in the display gain just as much from advertising the roost as those who do the advertising. I corrected my mistake of using a group selection argument later, when I was more experienced at identifying group selection arguments (Zahavi 1983).

I consider myself a sociobiologist; I believe that the evolution of social adaptations throughout the biological world adheres to the same general principles. Even social interactions between unicellular organisms are best explained by direct individual selection. Together with my students, I used the handicap principle to explain some of the details of mate choice in yeast (Nahon et al. 1995) and suggested a model based on individual selection that explains the apparently suicidal traits of the

slime moulds (Atzmoni et al. 1997), traits that until then were assumed to exist for the sake of kin or of the group. I believe that in future years ethologists, sociologists and others trying to find the ultimate reasons for the workings of social systems and for the patterns and reliability of signals will benefit from taking into account the importance of the quest for and the effect of social prestige as a mechanism that explains much of what happens in social systems. I also predict that the handicap principle (or 'costly signalling', as some who do not wish to refer to the handicap principle prefer to call it) will be found to be an inherent component in all signals. It is based strictly on direct individual selection, the only stable selection model in evolution.

I have often wondered whether, if I were living in Oxford or any other centre of sociobiological research, I would have developed the handicap principle and its implications. A major disadvantage of a dominant theory that is accepted by everyone around you is that observers in the field have a strong tendency to overlook findings that do not fit in with the theory. Even if the theory is wrong, as I believe that kin selection and reciprocity are, researchers in the field tend not to believe that the exceptions they observe suggest that the theory is erroneous; these exceptions either go unreported, or, if reported, are not considered important in discussions of the findings. The same goes for new suggestions such as the handicap principle that all around you, all your colleagues, consider them wrong. Being on the periphery has its benefits: if I were dependent on my colleagues for the advancement of my scientific career or my social status, I would not have been able to continue developing the handicap principle over the many years in which it was nearly unanimously rejected. Luckily I was living in a corner of the world, and usually interacted with other sociobiologists only once a year, at conferences. At home, my social status and my scientific career were well secured because of my previous 'altruistic' work in conservation.

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