

BEHAVIOURAL ECOLOGY

An Evolutionary Approach

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SECOND EDITION

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Many of the externally visible features of animals, many of their behaviour patterns, many chemical substances and most of the sounds given off by them, are best interpreted as being adapted—'designed by natural selection'—to influence the behaviour of other animals, and are often referred to as 'signals' (some authors reserve 'signals' for morphological features like crests, and use 'displays' for behaviour patterns). Just as a wing performs its normal function by working on the air, so a signal performs its normal function by working on another animal, via its sense organs. With the exception of echolocation sounds, all the sounds produced by special sound-producing organs are signals to other animals. They may attract the other animal, as when a male cricket calls females to his burrow; they may repel the other animal, as in a male robin's territorial song; they may exert some long-term influence on the other animal's physiology, as when the song of a male canary causes his mate's ovaries to ripen over a period of days (Hinde 1970). They may be 'aimed' at the individual's own species, as in the above examples, or at other species, for example the snake-like hiss made by nestlings of hole-nesting birds to scare off predators (Sibley 1955; Krebs 1970). They may, of course, have effects other than those for which natural selection 'designed' them. For example, the song of the cricket *Gryllus integer* is 'designed' to call females, but it also has the (eventually fatal) effect of calling parasitic flies (Cade 1979). The flies are probably 'designed' by natural selection to respond specifically to the cricket song, but most people would not wish to say that the crickets were signalling to the flies. Though definitions vary (Hinde 1972), most authors agree in wanting to exclude such incidental consequences. We have begun with acoustic examples, but signals make use of all sensory modalities.

A dictionary offers two alternative definitions of the word signal. The first is 'any sign, gesture, token etc. that serves to communicate information'; the second is 'anything that acts as an incitement to action' (*Collins English Dictionary*). In the previous edition of this book (Dawkins & Krebs 1978) we gave reasons for, in effect, preferring the second definition over the first (given the proviso that signals are 'designed' for incitement). We went further in the direction that we called 'cynical', and defined a signal as a means by which one

animal (the 'actor') exploits another animal's (the 'reactor's') muscle power. In the first part of this chapter we will try to clarify our previous position and extend our discussion from the actor to the reactor. The counterpart to 'manipulation' by the actor is 'mind-reading' by the reactor. The evolution of many animal signals is best seen as an interplay between mind-reading and manipulation. But first we briefly review current understanding of the evolutionary history of animal signals.

15.1 DERIVED ACTIVITIES AND RITUALIZATION

Konrad Lorenz probably did more than anyone to establish the idea that behaviour patterns can be treated like morphological organs, with an evolutionary history that can be traced like the history of morphological organs. Signalling movements, especially in ducks, were among his favourite examples, and indeed, of all behaviour patterns, those concerned with signalling have been most studied from the point of view of evolutionary origins. Some morphological organs, too, have probably evolved solely as a result of selection for signalling function, for instance crests and voice boxes. Sometimes such signalling devices fossilize—the bony resonating chamber in a howler monkey's throat is presumably a good candidate—but generally they do not and their evolution therefore has to be inferred by more indirect means, for instance by using comparative evidence.

One of the main principles of signal evolution could be guessed from common sense even if there were no supporting evidence. This is that signalling movements usually evolve originally from other movements that formerly had no signalling function—the principle of *derived activities* (Tinbergen 1952). Many signalling movements in birds, for instance, can easily be traced back to preening, feather-settling, and temperature-regulating movements (Morris 1956). Others are clearly derived from movements that normally prepare for flight or for drinking. Although signals are presumably derived ultimately from non-signal movements, there are cases in which the ancestral behaviour pattern from which a signal is more immediately derived is another signal, used in a different context. A classic example is the crouching movement used by females of several species of songbird in courtship, which appears to be derived from the food-begging crouch of juveniles.

The reason the principle of derived activities should be expected by common sense is really one of parsimony. It is a special case of a general rule in evolution. The alternative to it is that genetic mutants produced entirely new movements, unrelated to existing movements, and that these were then favoured by natural selection as signals. This is in principle possible, for instance the 'waltzing' mutant behaviour in mice could theoretically evolve into a signal. But behavioural muta-

tions must act by modifying the existing nervous system, and they are most likely to exert some quantitative effect on existing behaviour patterns. More interestingly, there is no particular reason to expect would-be reactors to respond to 'waltzing' or random twitches by actors, whereas they are quite likely already to be in the habit of responding to existing behaviour patterns like preening movements. As we shall see, this is important because unless would-be reactors respond initially to a non-signal movement, there is no reason why it should evolve into a signal.

The process of evolution of signals from non-signal movements is called *ritualization*. Before ritualization, the organ or behaviour pattern concerned performs its normal function, cleaning the feathers, regulating the body temperature, or whatever it is, and it is presumably well designed to do so. It is at some kind of 'utilitarian optimum' for its non-signal function. Before ritualization it is, by definition, not a signal. Although, for reasons to be discussed, it probably has effects on other individuals, these are incidental. After ritualization, the signal has been modified from its old 'utilitarian' optimum, presumably towards a new 'signalling optimum' (see section 15.4). It may, for instance, have become highly repetitive, exaggerated in amplitude, stereotyped in pattern.

Although the word ritualization was originally intended to be applied to behaviour patterns, it is easy to generalize it to structures. For instance, the scent glands that play so large a part in the social life of mammals are clearly 'ritualized' sweat glands and sebaceous glands. Their structure exhibits obvious homology with 'unritualized' glands in the same individuals. In some cases, ritualized organs and behaviour patterns completely lose their original function. For example, in the ritual courtship preening movements of some ducks the bill does not come into contact with the feathers but merely points at them, and so cannot have any cleaning efficacy. In other cases the new function is superimposed on the old. It will usually be hard to decide the issue: who can say, for instance, whether the secretions of a scent gland fulfil some cooling function as they evaporate? The concept of function raises difficult questions of decidability, which we shall not go into here (Hinde 1975). We turn, instead, to a consideration of how natural selection acts on both senders and receivers of signals, and to a justification of our own definition of a signal as a means by which one animal makes use of another animal's muscle power. We shall reconsider the phenomenon of derived activities and ritualization, briefly reviewed above, from the cynical point of view of individuals exploiting other individuals as 'tools'.

15.2 EXPLOITING OTHER ANIMALS AS TOOLS

The world is full of animals whose ancestors succeeded in reproducing. This is trivially true, but non-trivial in its consequences.

Given, in addition, the facts of heredity, we can expect existing animals to have inherited the attributes that made their ancestors successful in becoming ancestors. This is why we feel entitled to regard animals as machines that have been well designed to pass on those attributes—'survival machines'.

Such a well designed machine will tend to use objects in its environment to its own best advantage. These objects will include inanimate ones such as the stone used by a song thrush or by a sea otter to smash mollusc shells. But many of the most important objects in an animal's world will themselves be living bodies with their own nerves and muscles, programmed to work for their own genetic advantage. The possibility of exploitation is there for another living being as it is for a stone. A bolas spider propels its prey towards its mouth by lassoing it and then hauling it in, using the spider's own muscle power. An angler fish propels its prey towards its mouth, not by its own direct muscular force but by waving a tempting lure. Finally, it is the prey fish's own muscles that do the work of propulsion. The angler fish causes this to happen in much the same way as an electrophysiologist might by means of stimulating electrodes. The angler fish has no electrodes, but exerts a similar effect on the prey fish's muscles, via the prey fish's own sense organs. The victims of exploitation do not have to be members of another species as in the case of the angler fish. They might be intended mates, or rivals for a territory. They might be parents exploited by offspring or offspring exploited by parents; hosts exploited by parasites or prey exploited by predators. Whether the manipulated organism is of the same or a different species, or whether it is an inanimate object, makes no difference to the principle.

There are two things that an animal may do if it is to exploit another animal as a tool, and in the previous edition we concentrated on only one of them, manipulation. The other may be called 'mind-reading'. Essentially the difference is that mind-reading involves exploiting the victim's behaviour as it spontaneously emerges from the victim, while manipulation involves actively changing the victim's behaviour. The two may go together or in opposition to each other. One may pave the way for the other in evolutionary time. And both are highly relevant to the study of animal communication.

15.2.1 Manipulation

We are arguing that there is no fundamental difference between the way a living organism might exploit a stone and the way it might exploit another living organism, between the way a male sea otter, say, uses a stone to smash a shellfish, and the way he uses a female sea otter to rear his young. Both are examples of what we are calling manipulation. There is a practical difference between them, resulting from the fact that the female otter is herself a complex machine, while

the stone is a simple object. To manipulate the stone an otter need only apply simple muscular forces to it, and the stone will respond according to the ordinary laws of motion. The female otter needs more subtle handling. If pushed, she is apt to depart from the simple laws of motion. She may turn round and bite the male, or she may accelerate away. She may remember the incident, with the result that it changes her behaviour towards the male on subsequent days. Nevertheless, however complex it may be, her behaviour is governed by laws which are ascertainable. This being so, it is in principle possible to exploit those laws in such a way as to manipulate her behaviour. A male sea otter does not have to be consciously aware of these laws, nor does he have to design his techniques to manipulate the female. Natural selection itself will favour male sea otters whose behaviour happens to take advantage of the lawfulness of female behaviour. The effect is that the male manipulates the female in much the same way as he manipulates a stone.

Of course, in any particular relationship between two individuals, it would not be correct to label one the manipulator and the other the victim in any permanent sense. Both individuals will have inherited the manipulating tendencies of their successful ancestors—most of their ancestors may, indeed, be shared—and each will be attempting to manipulate the other. Nevertheless, it is convenient for us to continue to refer to 'the manipulator' and 'the victim', using the words to refer to roles which any individual may assume at different times. It should also be said that animals may sometimes benefit by being manipulated, in which case words like 'victim' will seem inappropriate. We shall return to this topic later.

The theoretical possibility of manipulating a living organism is confirmed by the fact that ethologists can do it. By studying the normal triggers of an animal's behaviour, the ethologist can manipulate the behaviour. A direct and potentially powerful way to manipulate behaviour is to interfere with the nervous system itself, or with other aspects of the victim's physiology, either by injecting chemicals, or by making lesions, or by using stimulating electrodes implanted in nervous tissue or in single nerve cells.

Ethologists can achieve equally powerful control over an animal's behaviour by presenting appropriate external stimuli to the animal's sense organs. The classic dummy-presenting studies of Tinbergen and others are the best known examples of this. One of the main conclusions drawn from these studies is that animals respond in mechanical, robot-like fashion to key stimuli. They can usually be 'tricked' into responding to crude dummies that resemble the true, natural stimulus situation only partially, or in superficial respects. To a human observer, for instance, it is surprising that a black-headed gull will show its normal aggressive response to a stuffed gull's head mounted on a stick, with no body (Stout & Brass 1969). A well-known anecdotal example is the aggressive response of Tinbergen's male sticklebacks to the red mail van passing the window. A similar, less well documented

anecdote is of the red-coloured *Anolis* lizard that leaped aggressively into a camper's bowl of tomato soup!

Humans are apt to feel superior to sticklebacks aroused to anger by mail vans or to sexual activity by pear-shaped dummies. We think them 'stupid' to be 'fooled' by such crude approximations, since we assume that they, in some sense, 'think' that the mail van really is a male stickleback, just because it is red. But a little reflection on our own species helps us to sympathize. A man may be sexually aroused by a picture of a naked woman. A Martian ethologist, observing this, might regard the picture as 'mimicking' the real thing, and assume that the man was 'fooled' into thinking it was a real woman. But nobody who is aroused by such a picture is actually fooled into thinking it is the real thing. He knows very well that it is a pattern of printer's ink on paper; it may even be a rather unrealistic caricature; yet it has enough visual stimuli in common with the real thing to have a similar effect on his physiology. We should not ask whether the stickleback 'thinks' the mail van really is a rival, nor whether he is so 'stupid' as to be incapable of distinguishing a mail van from a stickleback. Very probably he can distinguish them very well, but both make him see red! His nervous system is aroused by them to the same emotion, even though it is perfectly capable of seeing the difference between them.

Just as an ethologist can manipulate the behaviour of an animal by stimulating it appropriately, so can another animal. Direct interference with brain tissue is rare, though not unknown: the 'brain worm' *Dicrocoelium dendriticum*, a trematode parasite of sheep and ants, makes a lesion in the ant's brain. This changes the ant's behaviour in such a way that it, and therefore the worm, is more likely to be eaten by the worm's definitive host, a sheep (Wickler 1968). More usually, animals manipulate the behaviour of their victims by stimulating the victim's sense organs. The very fact that animals are susceptible to being 'tricked' by the crude dummies of ethologists, especially supernormal dummies, makes it likely that natural selection will favour similar exploitation by other animals. The most striking and best studied examples of this involve interspecific communication. Bee orchids, for example, present male bees with a supernormal stimulus of the female, and the male collects or transmits pollen while trying to copulate with the flower. 'They have, so to speak, "discovered" the releasing stimuli normally provided by females.' (Proctor & Yeo 1973). These stimuli probably include scent as well as visual cues. So effective is the flowers' stimulus that bees of the genus *Andrena* presented with a choice of real females and flowers of *Ophrys* *lutea* prefer to copulate with the latter!

In our previous article we argued that the evolutionary ritualisation of derived activities can be better understood in terms of selection for effective manipulation than in terms of selection for effective information transfer, a view which for want of a better term we called the 'classical ethological view'. We suggested that ritualized signals

are analogous to human advertising signals. In advertising, transfer of information (at least semantic information—see section 15.4.2) is less pertinent than persuasion of the 'victim'. The features that are found to lead to effective advertising include redundancy, rhythmic repetition, bright packaging and supernormal stimuli, features which could be used to characterize a great many signals in the animal world.

It is easy to see that manipulation is a good thing from the manipulator's point of view, provided it can get away with it. But how do manipulation techniques evolve? Why are they victims initially susceptible to manipulation? And why, even if they are initially susceptible, do they remain so in evolutionary time? These are questions which can best be answered after we have considered the other main way in which animals may exploit other animals—'mind-reading'.

15.2.2 Mind-reading

Any animal could benefit if it could behave as if predicting the future behaviour of other animals in its world. At any moment an animal is faced with choosing which of its repertoire of behaviour patterns to perform next: feed, mate, drink, attack, flee, approach, withdraw, etc. (McCleery 1978). The optimal choice will depend on the probable consequences that would follow from each choice. For an animal that has any kind of social life, or that is a predator or is preyed upon, these probable consequences will depend crucially on the internal motivational state and probable future behaviour of other animals—rivals, mates, parents, offspring, prey, predators, parasites, hosts. A dog, faced with the choice of approaching or retreating from a rival dog, would do well to take account of any information he can glean as to the mood or motivational state of the rival, and hence, in effect to predict the probable future behaviour of the rival.

Animals can, in principle, forecast the behaviour of other animals, because sequences of animal behaviour follow statistical rules. Ethologists discover the rules systematically by recording long sequences of behaviour and analysing them statistically, for example by transition matrices (e.g. Nelson 1964; Delius 1969), and in the same way an animal can behave as if it is predicting another individual's future behaviour. Without committing ourselves to a view over the philosophical problems of animal mind in the subjective sense (Griffin 1981, 1982), we may use the word 'mind-reading' as a catch-word to describe what we are doing when we use statistical laws to predict what an animal will do next. For an animal, the equivalent of the data-collection and statistical analysis is performed either by natural selection acting on the mind-reader's ancestors over a long period, or by some process of learning during its own lifetime (Lorenz 1966). In both cases, 'experience' of the lawfulness of the behaviour of victims becomes internalized in the brain of the mind-reader. In both cases it

mind-reading ability enables it to exploit its victim's behaviour by being 'one jump ahead' of it. The mind-reader is able to optimize its own behavioural choices in the light of the probable future responses of its victim. A dog with its teeth bared is statistically more likely to bite than a dog with its teeth covered. This being a fact, natural selection or learning will shape the behaviour of other dogs in such a way as to take advantage of future probabilities, for example by fleeing from rivals with bared teeth. As with manipulation, mind-reading refers to a *role* that an individual may assume.

Animals will come to be sensitive, then, to the fine clues by which other animals' behaviour may be predicted. The clues that a mind-reader may employ are varied and numerous, and are much discussed in the ethological literature (e.g. Tinbergen 1964, 1952; Morris 1956; Marler 1959; Cullen 1972), albeit often from a less cynical point of view than is implied by our 'mind-reading'. As we shall see, the whole theory of derived activities, discussed above, can be best interpreted in terms of mind-reading as well as manipulation, and the literature on the evolutionary origins from which signals are derived is full of good examples. Any movement of a limb, twitch of a facial muscle, or involuntary catch of the breath is potentially a give-away. Humans use them all the time, and such give-aways as heart rate, breathing patterns, and galvanic skin response are systematically exploited in 'lie-detector' machines. In principle, recording electrodes implanted in the brain should enable even more insidiously accurate mind-reading.

Animals cannot insert electrodes into each other's brains, and with interesting possible exceptions like electric fish, we know of no evidence that they measure each other's galvanic skin response. But there are plenty of other give-aways. Natural selection will tend to favour animals that become sensitive to available tell-tale clues, however discrete and subtle they may be. A notorious case is Clever Hans, the mathematical horse who 'appeared to be able to do sums in his head and deliver the answer by striking his hoof on the ground the right number of times. It all looked very impressive until it was shown that the horse had learnt a relatively simple trick. He kept on pawing the ground until he received a very small sign from his master that he had got to the right answer whereupon he stopped' (M. Dawkins 1980).

Humphrey (1976) develops the idea of animals as 'Nature's psychologists', and goes so far as to suggest that the whole faculty of subjective consciousness and self-awareness evolved as a device to facilitate reading the minds of others. Whether or not we buy the whole of Humphrey's elegantly argued case on the origins of consciousness, it is entirely reasonable to presume that Clever Hans and all his colleagues among circus animals and household pets are using, in a human context, faculties which their ancestors were selected to use in the wild. Whether it is done consciously or not, 'mind-reading'

15.2.3 Responses to mind-reading

What might an animal whose mind is being read do about it? It is an evolutionary question we are asking, so we should rephrase it. What mechanisms for responding to mind-reading might natural selection build into lineages that are susceptible to being mind-read?

The first thing we need to know is whether the victim suffers or benefits from having its mind accurately read, in other words whether it is really a 'victim' at all, or a willing participant in the process. There may be many occasions on which an animal benefits from having its mood accurately read, and its behaviour accurately predicted. Males of many species are quite likely to attack even females who enter their territory, depending on whether aggression or sexuality dominates their mood. Therefore a female who is willing to mate with a particular male may nevertheless be afraid to approach him (Bastock 1967). The female benefits by reading the male's mind accurately by making it easy for her to do so. If the male is a 'victim' of mind-reading here, he is a willing one.

Even in a relationship of seemingly unmitigated enmity, such as the predator-prey relationship, victims of mind-reading may be willing victims. Many predators rely upon surprising their prey, for they cannot outrun them. Once a cat has been seen or otherwise detected by a particular bird, unless it is very close the cat has little chance of catching the bird, which simply takes to the air. To stalk a bird and get close enough to strike is a time-consuming business for a cat, only worthwhile if there is a reasonable chance of success at the end of the stalk. The interesting point is that the bird, too, benefits from making the mind-reading easy for the cat. If he can make the cat give up and slink off, he can continue to feed uninterrupted on the ground, rather than having to waste time flying off or keeping himself prepared to fly off. It is possible that a number of signals that were once supposed to serve as warnings to conspecifics are in fact aimed at predators (Smythe 1970; Zahavi, quoted in Dawkins 1976; Baker & Parker 1979).

Some of the earlier literature betrays a tacit assumption that cooperation is the norm within species and the exception between species. The theory of natural selection at the genic level gives no obvious grounds for this assumption. In rejecting it in the previous edition of this book, we perhaps gave the misleading impression that cooperation, or an active 'willingness' to be mind-read, was a rarity. We would prefer to say simply that there are no grounds here for distinguishing intraspecific from interspecific relationships. Depending on circumstances, both can be cooperative or the reverse.

What if an animal is an unwilling victim of mind-reading? What countermeasures might it take? Like any victim of spying, it can resort to counter-espionage. Counter-espionage in human warfare or industrial rivalry takes two main forms, concealment and active deception. Concealment consists in making it difficult for the enemy to gain any information at all as to the nation's or the company's true intentions; the equivalent at the individual level is the 'poker face'. Active deception consists in feeding the enemy deliberately misleading information; the equivalent at the individual level is simulating a mood or intention that one does not really have. It is probable that animals do something corresponding to both these forms of counter-espionage (section 15.5.2; Dawkins & Krebs 1978). But there is another way of looking at the countermeasures that a victim of mind-reading might adopt, whether it is a willing or an unwilling victim, and it leads us right back to manipulation and our questions about the origins and evolution of manipulation techniques. The victim of mind-reading might exploit the fact that its mind is being read, in order to manipulate the behaviour of the mind-reader.

We have reached an interim climax in our discussion. Mind-reading and manipulation are not isolated phenomena. They are intimately locked together in evolutionary arms races and feedback loops. Mind-reading is a prerequisite for the evolution of manipulation. Manipulation evolves as an evolutionary response to mind-reading. Mind-reading and manipulation coevolve, and signals are the result of this coevolution. We can use the dog example again, to illustrate how this coevolution might proceed.

A dog, as we have seen, would benefit if he could forecast the probability that a rival will bite him if provoked. It happens to be the case, for fairly obvious practical reasons here, that a dog usually gets its lips out of the way before biting: it bares its teeth. Although initially in evolution this tooth-baring might have been a slight, almost imperceptible movement, it was just detectable by the senses of rivals and so could be used for mind-reading. Now we come to the evolutionary response of 'victims' of the mind-reading. The fact that baring of their teeth has a predictable effect on rivals presents 'victims' of mind-reading with an opportunity to manipulate mind-readers' behaviour. (Again, remember that we are speaking of *roles* not individuals. The same individual may be both mind-reader and manipulator at different times and with different opponents.) Where the mind-reader might be thought to be saying: 'He bares his teeth and, therefore, I prophesy that he will attack', the manipulator can be thought of as saying: 'I bare my teeth and I will make him retreat'. So 'victims' of mind-reading become manipulators.

Mind-reading is not a necessary prerequisite for the evolution of manipulation, but it is probably a common one. When we ask what it is that predisposes an animal to be manipulated, the answer is quite likely to be that its senses are tuned into mind-reading the would-be

ever communication is a matter of mutual exploitation rather than cooperation. In our previous article we concluded by suggesting that all signals are products of coevolution between manipulation and sales-resistance, a view which we modified in section 15.2.2 by pointing out that mind-reading by reactors is the other side of the picture. We are now going on to suggest that arms-race coevolution is only part of the story of the evolution of signals, although it is the part which accounts for most of the familiar signals described by ethologists.

The other component of the story is a different kind of coevolution arising from mutual cooperation. In communication, as in any kind of social behaviour, most interactions between individuals are not cooperative and mutually beneficial. It is generally recognized, however, that under certain conditions cooperation may be favoured by selection, the two most important conditions being kinship and reciprocity (see Chapters 3, 12 and 13). Cooperative communication might be favoured because of kinship in hymenopteran colonies, in cooperative breeding groups of birds and mammals, among siblings in a brood, within family flocks of birds, and so on, while reciprocity might play a role in long-term groups such as monkey troops, between the members of a pair, between established territorial neighbours, and whenever there are repeated interactions between individuals.

Can signals arising from cooperation and mutual exploitation be distinguished? We suggest that the two kinds of evolution will lead to different kinds of signals, for the following reason. If the reactor benefits from receiving the signal and responding in accord with the actor's interests, instead of heightened sales-resistance leading to exaggeration of the signal during evolution we would expect to see heightened sensitivity to the signal leading to a *reduction* in the amplitude and conspicuousness of the signal. This is because every signal has a cost: it may attract predators, use up time and energy, or reduce the actor's efficiency at doing other things. In the absence of any other consideration, selection on actors should favour a reduction in cost. When signals are cooperative, and reactors are selected to strain their senses to pick up the signal, selection is free (but not entirely free, as we explain in the next section) to favour a reduction in the cost of signalling. In short, the evolution of cooperative signalling should lead not to loud, exaggerated, repetitive, conspicuous signals, but to cost-minimizing conspiratorial whispers. The distinction we are making can be illustrated by an analogy with human communication: contrast the Bible-thumping oratory of a revivalist preacher with the subtle signals, undetected by the rest of the company, between a couple at a dinner party indicating to one another that it is time to go home. The former bears the hallmark of signalling designed for persuasion, the latter of a conspiratorial, cooperative whisper. As we commented earlier, the signals well known to ethologists are probably

he can unlock the other's nervous system.

15.2.4 Responses to manipulation

We have seen that victims of mind-reading are unlikely to submit passively but will, over evolutionary time, tend to turn the situation to their advantage. The same is surely true of victims of manipulation. What responses or retaliations are open to victims of manipulation?

As in the case of mind-reading, the answer will depend on whether the 'victim' is unwilling, as the word implies, or whether it is, in some sense, a willing victim. Much of the earlier literature tacitly implied the latter, in assuming that signals mediated mutually beneficial cooperation. In the previous edition of this book we perhaps went too far in attempting to redress the balance. There are, of course, many occasions on which both actor and reactor stand to gain from the same outcome. In such cases, even in an obviously cooperative endeavour as the foraging facilitated by the honeybee dance, it is still technically correct to speak, as we did, of the actor using the muscle power of the reactor. But in such cooperative cases it is equally correct to speak of the reactor using the sense organs of the actor. If the reactor's muscles are being used by the actor, they are benefiting the reactor at the same time, and selection would not favour resistance to 'manipulation'.

In other cases, however, it is undoubtedly true that the reactor would benefit from not performing the behaviour which is being urged upon it by the actor. This is obvious for the victims of cuckoos and angler fish, and it is now widely accepted that similar resistance to manipulation is to be expected in some within-species interactions: '... selection can act in opposition on the two sexes. Commonly, for a given type of encounter, males will be favoured if they do mate and females if they don't' (Parker 1979). Much the same is true of interactions between parents and offspring (Trivers 1974). In all such cases selection will act simultaneously to increase the power of manipulators and to increase resistance to it. '... genic selection will foster a skilled salesmanship among the males and an equally well-developed sales-resistance and discrimination among the females' (Williams 1966). Depending upon whether or not the victim of manipulation is a 'willing' victim we can expect to see two kinds of coevolution (see also Markl, in press).

15.2.5 Two kinds of coevolution

Our argument so far may be summarized as follows: the conspicuous, ritualized signals familiar to ethologists are the product of a coevolutionary race between what we have termed the manipulator and mind-reader roles. This kind of coevolution is to be expected when-

largely the products of arms-race coevolution: many of the conspiratorial whippers of cooperative signalling may even have not yet been detected.

There may, however, be a constraint on the evolution of conspiratorial whippers, namely the problem of signal detectability. Even a cooperative signal may have to be conspicuous in order for the receiver to detect it.

15.3 SIGNAL DESIGN : DETECTABILITY AND ECONOMICS

In this section we consider the signal design features that might evolve irrespective of whether communication is exploitative or cooperative. Even the conspiratorial whippers of cooperation may be loud, repetitive whippers simply to ensure *detection* by the receiver. However, increasing the detectability of a signal is likely to incur additional costs (energy, risk and so on), so that cooperative signals might evolve to an optimal compromise between detectability and economy. Signals that are a product of arms-race coevolution will not evolve to the same 'engineering' optimum and might be expected instead to be much more costly than detectability considerations alone would lead one to predict.

15.3.1 Signal detection

Wiley (1983) points out that many of the characteristics of ritualized signals can be interpreted in terms of signal detection theory (Green & Swets 1966). In particular he points out that *redundancy*, *conspicuousness* or *contrast*, *small signal repertoires*, and *alerting components* are four common features of ritualized signals which might have evolved to enhance detectability. Detailed studies of bird song have been particularly illuminating in illustrating the role of detectability in signal design. Variation between habitats, both within and between species, in frequency and timing structure of songs has been shown to be correlated with habitat variation in attenuation or degradation of sound (Morton 1975; Nottebohm 1975; Bowman 1979; Hunter & Krebs 1979; Shy 1983; Richards & Wiley 1980). Similarly, there is evidence for variation between habitats in redundancy and repertoire size (Richards & Wiley 1980; Kroodsma 1977) associated with variations in noise level. In noisier habitats, songs tend to contain more repeated elements (redundancy) and in one comparison at least had smaller repertoires. Alerting components have also been identified in bird song (Richards 1981).

15.3.2 Signal economics

A ten-page letter and a two-word telegram ('paper rejected') from a journal editor may convey the same information about the fate of

one's latest brainchild, but the telegram is in some sense a more economical way of reducing one's uncertainty. Economy in this case might be measured as actor's time or energy required to generate the signal. The notion of economy seems appropriate for animal signals as well as communications engineers, as it has proved to be in optimization studies of foraging (Chapter 4) and territoriality (Chapter 6).

Pheromonal communication in social insects has already been discussed in economic terms by Wilson (1971). Insect pheromones are usually organic molecules with between 5 and 20 carbon atoms. Wilson suggests that the design reason for this is as follows: with fewer than five atoms, the variety that can be synthesized is too small. Above about 20 the number of distinct molecules increases astronomically to no good purpose yet the energy costs of synthesis go up too. Further, large molecules tend to be less volatile and so travel less far. Thus the observed range 5-20 carbon atoms represents an optimal compromise between variety of distinct signals required and energetic costs of manufacture.

The notion of signal economics may also be put to use in explaining differences in the size of molecule used for different signals. Relatively large molecules tend to be used for sexual attraction and smaller ones as alarm substances. While it is possible that the reason for this is that species specificity (and hence a greater range of possible molecules) is more important for sexual than alarm signals, another interpretation is an economic one, namely that frequently used signals should be the cheapest ones. To understand why, imagine designing a human language with maximal economy for writing. An obvious starting point would be to use the shortest possible codes for the most commonly used words, and then to proceed to longer codes, as the short ones are used up, for less frequently used words. In the same way, if the optimization criterion was to minimize costs of manufacture, frequently used pheromonal signals such as alarm scents should be small molecules, while the less frequently used sexual signals should be allocated the larger, left over, molecules. The relatively simple nature of chemical signals makes them particularly suitable for this kind of analysis, since costs of production can be judged fairly directly from molecule size. Perhaps an example parallel to that of the insect pheromones is the difference in length between the alarm and sexual vocal signals of birds: the former are usually short, the latter often long and complex.

Economy of energetic expenditure is only one form of cost-saving in signal design. Another frequently discussed cost of signalling is the risk of attracting predators (see our Introduction). Among the best known discussions of signal design with respect to predation is Marler's (1955) analysis of the hawk alarm calls of small passerines. The design features of these calls (narrow frequency range, no sharp onset or end) make them hard to locate for human ears and perhaps for avian predators as well (but see Lewis & Coles 1980), although the

15.3.3 Variations in signal design

Signals vary enormously in stereotypy, conspicuousness, and redundancy. The incessant stridulation of a grasshopper is at one end of the spectrum, the subtly variable facial expressions and inter-troop vocal signals of monkeys at the other. Three (mutually compatible) hypotheses can be proposed to account for this variation: (i) There is variation in selection for detectability: signals used over long distances or in noisy channels will have an engineering optimum of greater conspicuousness and redundancy than those used in close encounters or in noise-free environments (Wiley 1983). Variations in repetition frequency and repertoire size of bird sounds referred to earlier are consistent with this line of reasoning. (ii) The benefit of signal transmission varies, and therefore the cost incurred by the actor varies: a male grasshopper calling to attract a female has more at stake than a monkey in a troop squabbling over access to a morsel of food, so the former pays more in signal costs than the latter. (iii) Variations in signal design are related to whether or not signals evolve through a coevolutionary race. As we have already emphasized (section 15.2.5), arms-race signals should evolve greater conspicuousness, repertoire, and redundancy than those used in cooperative communication.

Often the 'coevolution' and 'detectability' accounts of signal design will make similar predictions. Because long-distance (e.g. territorial) signals often are associated with arms-race coevolution while short-distance signals such as those used within an ant colony or a monkey troop will tend to be conspiratorial whispers, both hypotheses predict more extreme development of the four 'signal detection' traits (section 15.3.1) in the former than in the latter. However, it is possible to think of examples where the two accounts differ in their predictions. An example is nestling begging calls. Engineering considerations alone would not predict loud, repetitive nestling begging since the calls are most frequently given when the parent has already arrived at the nest. The problems of detectability are therefore negligible, and, what is more, begging calls are known to attract nest predators (Perrins 1979). Loud, repetitive calls hardly seem to be at an engineering optimum for receiver detection, traded off against the costs of signalling. However, as Trivers (1974) first pointed out, nestling-parent interactions are likely to be characterized by coevolution between persuasion and sales-resistance, involving positive feedback. Loud, incessant begging at the parent's face makes sense within this framework.

As pointed out by Wiley (1983) and Dennet (1983), discussions of whether or not signals transmit information often confuse two uses of the term. Haldane and Spurway (1954), and Wilson (1962) pioneered the use of *information theory* (Shannon & Weaver 1949) to describe animal communication. Information in the 'Shannon' sense means *reduction in uncertainty of an observer* about the actor's (broadcast information) or reactor's (transmitted information) behaviour contingent upon a signal. In contrast, discussions such as those of Dawkins and Krebs (1978), Maynard Smith (1982a), Caryl (1979) and Hinde (1981) refer to *semantic information* (Dennet 1983). This is roughly equivalent to the more colloquial meaning of 'information about' something. Animal communication may be about the motivation, age, status, strength and so on of the actor. Measurements of Shannon information do not necessarily reveal anything about semantic information, although they often do. Suppose, for example, that an *observer's* certainty in predicting the reactor's behaviour goes up from 20% to 80% after the actor has performed a display: one can be sure that Shannon information has been transmitted but one cannot tell whether or not the reactor acquired any information about the size, age, etc., of the actor. The recent theoretical discussions about whether or not signals convey information and whether or not this is important in their evolution (Dawkins & Krebs 1978; Hinde 1981) concern only semantic information: by definition signals must transmit Shannon information.

15.4.1 Shannon information

If your newspaper headlines consisted of: 'The sun rose this morning'; 'England is in the northern hemisphere'; 'Yesterday lasted 24 hours'; and similar unsurprising facts, you would probably demand your money back. The reason is that you know it all already: it is not news. The facts are all perfectly true but you do not feel informed by them. This idea that a message, in order to be informative, must be at least somewhat surprising to the receiver, has been used by mathematicians to define information as a precisely measurable commodity (Shannon & Weaver 1949). Although this technical usage of the word information was originally coined for telephone and other engineers, it has been applied on a number of occasions to animal communication.

Mathematically, the information content of a message is measured in terms of the reduction in prior uncertainty caused by the message. Prior uncertainty is measured in terms of probabilities. If the message allows the receiver to decide between two alternatives which had previously been equiprobable, say 'heads' rather than 'tails', or 'boy' rather than 'girl', then one 'bit' of information has been conveyed.

(THINK ABOUT) ANIMALS BIOLOGISTS OF THE 1950S AND 1960S WE REFERRED to it in our earlier article as the 'classical ethological approach', and contrasted it with the viewpoint that was consolidated in the 1970s. Game theoretic (Maynard Smith 1972, 1979; Caryl 1979) and gene selection (Dawkins & Krebs 1978; see Chapter 2) analyses lead to the question of whether actors would ever be selected to increase the efficiency of information transfer in their signals, and we suggested that it might be better to abandon the concept of semantic information altogether in discussions of the ritualization of signals.

In trying to assess whether or not signals do or do not transmit information, and whether or not they ought to on theoretical grounds, it is important to distinguish between three kinds of semantic information: information about *intentions* (what the actor will do next), about *strength, status, size, or age* of the actors (*strife* for short), and about the *environment* (see also section 2.5.3). It is also useful to maintain a distinction between whether or not signals in present day populations actually transmit information and whether it is plausible to suppose that they have become ritualized to increase their effectiveness in transmitting information. It will be apparent that most of the evidence discussed below refers primarily to the former problem and only indirectly to the latter.

Intention

It is information about what the actor will do next that poses theoretical problems, for two reasons which refer especially to ritualized contests over resources. First, there is nothing to prevent animals 'lying' about what they will do next, and secondly, for an animal to declare its intention early on in a contest is equivalent to a card player showing his hand to an opponent at the start of the game. It is hard to imagine how selection could favour such behaviour; instead one would expect animals to conceal their eventual intentions until the last possible moment.

The literature on displays performed during contests shows that there are correlations between particular displays and the future behaviour of both actor and reactor, in other words that Shannon information is broadcast and transmitted. This does not necessarily mean, however, that information about intentions is transmitted. When Caryl (1979) re-analysed that data of Stokes (1962) on blue tits Dunham (1966) on grosbeaks, and Andersson (1976) on skuas, he found that displays in these species were in fact rather poor predictors of attack. In blue tits (*Parus caeruleus*), for example, the highest probability of attack following a particular display was only 0.48. Furthermore, the display giving the highest probability at one time of year did not do so at another time, and reactors did not tend to retreat after 'aggressive' displays. In contrast, some displays were good predictors of *retreat*. These do not pose a problem for selection theorists

of the card, say 'clubs', the message contains two bits of information. At first sight this is surprising. Since there were four equiprobable alternatives, and the message narrowed uncertainty from four to one why were not four bits of information conveyed? The answer is that it is crucial to the definition of information that it refers to messages which have been recoded in the most economical way possible. The most parsimonious encoding in the card example is first to specify colour (black not red), requiring one bit of information, and then to specify suit (clubs not spades), the second bit of information. The information content is $\log_2 4 = 2$. If the prior probabilities of different behaviours are not equal, a weighted sum of the alternatives is calculated according to the formula:

$$H = \sum p_i \log \left(\frac{1}{p_i} \right)$$

where p_i is the probability of the i th category and H is uncertainty in bits.

Returning to animal communication, we can formally define *transmitted information* as the observer's estimate of H for the receiver before the signal minus H after the signal. Similarly, *broadcast information* is H for the actor before minus H after the signal (Wiley 1983).

In the field of animal communication, information theory was first applied to the bee dance (Haldane & Spurway 1954), and has subsequently been used to describe communication in a range of species and contexts (e.g. Hazlett & Bossert 1965; Wilson 1962). Although it is relatively easy to calculate transmitted information from transition matrices, its quantitative value depends on how the actor's and reactor's behaviours are classified: if, for example, the animals themselves divide up behaviour into more categories than does the observer, H may be underestimated. For this sort of reason it is not straightforward to make interspecific comparisons of Shannon information. In fact, we suggest that the 'economics' side of information theory (section 15.3.2) may be a more useful application to animal signals than its use to quantify the number of 'bits' of information transmitted.

15.4.2 Semantic information

Signals originate because reactors gain some information about the reactor from the signal (p. 386). Some authors have taken the view that the subsequent evolution of signal design is primarily directed by selection pressure on the actor to increase semantic information available to the reactor (Smith 1977; Marler 1959) or to reduce ambiguity of the information (Cullen 1966). In other words, the effectiveness of ritualized signals should be judged by the extent to which they transmit information. Because this view was influential (but not universal

TABLE 1. THE ASSESSMENT OF RHP

Species	Display/Cue	Reference
Hermit crab (<i>Clibbarius vittatus</i>)	Size	Hazlett (1968)
African buffalo (<i>Syncerus caffer</i>)	Head-on charge	Sinclair (1977)
Red deer (<i>Cervus elaphus</i>)	Roaring tempo	Clutton-Brock & Albon (1979)
Toad (<i>Bufo bufo</i>)	Pitch of croak	Davies & Halliday (1978)
Cichlid fish (<i>Nannacara anomala</i>)	Mouth wrestling	Jakobsson <i>et al.</i> (1979)

of RHP. It seems inevitable that assessment should be based on reliable indicators of RHP, since others could easily be faked (Zahavi 1977b, 1979). Reliable cues are those which are too costly to fake, or which are direct and indirect measures of the factors influencing RHP (size and strength and so on). Some examples are listed in Table 15.1.

Davies & Halliday (1978), for instance, showed that the size of a toad (*Bufo bufo*) is well predicted by the pitch of its croak. They suggest that this is an unfakeable cue—only big toads are physically capable of giving deep croaks—and they showed experimentally that deep croaks are, indeed, more intimidating to toads than high-pitched croaks. It is certainly plausible that selection would favour toads that are intimidated only by genuinely unfakeable advertisements of large size, and that selection would favour the use of such unfakeable advertisements by genuinely large toads. But why do small toads croak at all, since they are, in effect, advertising their small size? Would they not do better to keep silent?

Our answer to this question makes use of the logic, though not the precise mathematics, of ESS theory (Chapter 2). Suppose, in accordance with the last sentence of the previous paragraph, that all toads followed the conditional strategy: 'If larger than a criterion size *s*, croak; if smaller than *s*, keep silent' (the exact value of *s* will, itself, be subject to natural selection). Would this strategy be evolutionarily stable? No, it would not, for the following reason. If a toad croaks, he advertises his exact size; if he keeps silent, he in effect announces that he is smaller than *s*, leaving other toads uncertain exactly how much smaller than *s* he is: in the absence of other good information, they will probably assume that he is close to the average of the set of toads smaller than *s*. It follows that a toad who is only just smaller than *s* can improve others' estimate of his size by croaking. Selection will therefore favour a slight reduction in the criterion size *s*. Recursive application of this argument leads to the conclusion that *s* will rapidly decrease under selection until it reaches the size of the

acquired to surrender. There are two studies of fish displays which also showed that differences between individuals in their displays early in a contest are not good predictors of the eventual outcome (Simpson 1968; Jakobsson *et al.* 1979): in short, the evidence from these studies of birds and fish is largely consistent with the theoretical prediction that signals should not convey the long-term intentions of animals in contests.

Hinde (1981) has criticized Caryl's analysis, arguing that the crucial feature of threat displays is their reflection of motivation conflict and therefore moments of indecision in the actor. 'Threat displays were useful only in moments of indecision: if what an individual would do depended in part on the probable behaviour of the other, threatening by the former might elicit a response from the latter which would precipitate a decision by the initial actor' (Hinde 1981). In other words, displays would not be expected to predict just one activity, say attack, but either attack or something else, say staying put. Hinde goes on to show that Stokes' blue tits do indeed perform 'either a or b' following particular displays, although one has to bear in mind that the greater the number of outcomes included in the analysis, the better the outcomes will correlate with the display, just by chance (Caryl 1982).

While there is no doubt that the 'interactional' view advocated by Hinde is essential for understanding the dynamics of contests (for example, the use of graded threat displays—Dawkins & Krebs 1978), it does not, in Caryl's view, face up to the question of ritualization; he points out that if signals are simply used in moments of indecision to elicit a response from the opponent, there is no reason for them to become ritualized in evolution.

As we have already mentioned, a problem for signals indicating high attack probability is that they are subject to bluff. Andersson (1980) has used this as an evolutionary argument to explain why many species have a variety of different threat signals. He assumes that for each display there is a certain fixed frequency of occasions on which it is followed by attack. If the display is used more often than this, its value as a predictor of attack starts to diminish, so reactors pay less attention to it. Because of this, its frequency of use drops again, and its reliability as a predictor of attack increases. Thus there is a frequency-dependent oscillation of the effectiveness of threat signals, and several different signals could be maintained in equilibrium.

Strige and assessment

Contests often involve assessment. Parker (1974b) coined the term *resource holding potential* (RHP) for the constellation of factors that influence fighting ability; much assessment in contests is assessment

WHILE ROHWER'S observations pose a still unsolved problem for the evolutionary explanation of signals, most badges, such as those identifying sex, age or species, do not present a comparable difficulty.

Information about the environment

The classical example of communication about the environment is the dance language of bees mentioned already (von Frisch 1967; Gould 1976). A more recently discussed example is that described by Seyfarth *et al.* (1980b) in vervet monkeys (*Cercopithecus aethiops*). Like many birds (Marler 1955) and mammals (Sherman 1977) these animals give alarm calls at the approach or sighting of a predator. What is intriguing about the vervet monkey, however, is that there are three different calls for different predators, leopards, eagles and snakes. Playback of the three calls elicits an appropriate response from other monkeys in the group: leaping into a tree, scanning the skies and looking on the ground, in response to the leopard, eagle and snake calls respectively. The calls apparently transmit information about particular kinds of predator (see also Dennet 1983).

15.5 SUMMARY

The main points of our argument may be summarized as follows:

- (1) The evolution of ritualized signal movements or structures from their precursors is the product of coevolution between the roles. We have termed these roles 'manipulator' and 'mind-reader'. The manipulator role is selected to alter the behaviour of others to its advantage, the mind-reader role to anticipate the future behaviour of others.
- (2) The consequences of this coevolution depend on whether or not the signals in question are mutually beneficial. Cooperative communication, in which manipulator and mind-reader roles share a common interest, should lead to cost-minimizing, muted signals, while non-cooperative signalling should give rise to conspicuous, repetitive (in other words 'typical ritualized') signals.
- (3) For both types of coevolution, the form of signals is also influenced by environmental constraints on detectability and discriminability. These may set a lower limit to the degree of muting of cooperative signals, but in general cooperative signals should evolve towards an optimal compromise between economy and detectability while non-cooperative signals should not.
- (4) Signals, by definition, transfer information in the technical sense, reducing the observer's uncertainty about the actor's or reactor's future behaviour. The extent to which they transmit semantic information about the actor or the environment is less clear cut. Game theoretic evolutionary arguments suggest that information about long-term intentions should rarely be transmitted, and that information

be the evolutionarily stable strategy.

The argument of the previous paragraph was expressed in terms of the particular example of toads, but it is, of course, general. Something like it may be implicit in Zahavi's (1979) argument that all signals must be 'honest'. He goes further and suggests that the repetitive stereotypy of many displays arises from selection by reactors for a standard performance on the part of actors. The standardization, he argues, allows the reactors better to judge small variations in RHP, in much the same way that a judge of differences in athletic performance depends on all the athletes doing the same task under the same conditions. A prediction of this idea is that the most variable components of displays (those with the largest coefficient of variation) should be the best predictors of RHP.

Zahavi's view may at first sight seem to be quite incompatible with our earlier article in which we emphasized actor manipulation. But as we have already stressed, in actor-reactor coevolution both sides may gain the upper hand. Whether signals are manipulative or reliable, cues may vary from one case to another.

Badges of status

A striking example of an apparently fakeable signal of RHP, for which we coined the term 'badge of status' in our previous article, was described by Rohwer (1977) (see also Chapter 2). He observed that in winter flocks of Harris's sparrow (*Zonotrichia querula*) dominance status at feeding stations is correlated with size of the black bib of feathers below the beak. Although some of the variation in bib size is related to age and sex, even within an age class there is apparently continuous variation related to status. When Rohwer dyed the chins of subordinate birds to enlarge their bibs he observed that they were attacked more often than before by dominant individuals and did not rise in status. However, painting the bib and injecting with testosterone caused subordinates to rise in rank, while hormone treatment alone did not, showing that both a large bib and aggressive behaviour are necessary for a bird to be dominant. The badge alone is not sufficient. These observations still leave open the question of why subordinates do not increase their status by altering both bib size and behaviour, since neither would appear to be very costly. One possibility is that there is simply phenotypic or genotypic variation in ability, but the view favoured by Rohwer and Ewald (1981; see also Rohwer 1982) is that being subordinate in a flock may not after all be a disadvantage. They point out that subordinates are more readily tolerated at feeding sites by dominants and that there may be a frequency-dependent advantage for dominant and subordinate behaviour. It is not yet clear, however, whether this would produce continuous variation in plumage as observed in the Harris's sparrow.

Chapter 13
signals. The literature on these subjects has primarily discussed the dynamics of interactions, for example between two contestants, rather than the evolutionary ritualization of signals.

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