10.1 Introduction

10.1.1 The cynical gene

Because of the way natural selection works, it is reasonable for us to picture an animal as a machine designed to preserve and propagate the genes that ride inside it (Dawkins 1976). As a means to this end it will often manipulate objects in its world, pushing them around to its own advantage. Some of these objects will themselves be living creatures—mates, parents, prey, rivals—each one a machine designed to propagate its own genes in similar ways. When an animal seeks to manipulate an inanimate object, it has only one recourse—physical power. A dung beetle can move a ball of dung only by forcibly pushing it. But when the object it seeks to manipulate is itself another live animal there is an alternative way. It can exploit the senses and muscles of the animal it is trying to control, sense organs and behaviour machinery which are themselves designed to preserve the genes of that other animal. A male cricket does not physically roll a female along the ground and into his burrow. He sits and sings, and the female comes to him under her own power. From his point of view this communication is energetically more efficient than trying to take her by force.

Cullen (1972) uses a human analogy to illustrate the distinction between force and communication. '... to a man the command “Go jump in the lake” is a signal, the push which precipitates him is not'. Making a similar point Wilson (1975) cites J. B. S. Haldane's remark that 'a general property of communication is the pronounced energetic efficiency of signalling: a small effort put into the signal typically elicits an energetically greater response'. This is reminiscent of electronic amplification. A transistor or valve in an amplifier receives a low energy fluctuating signal, and uses it to control a high energy signal so that its fluctuations, with more or less fidelity, follow the original. A man's muscles are too feeble to pull a plough, but by a judicious mixture of direct sensory stimulation, reward and punishment, he can manipulate the behaviour of a horse so that it pulls the plough for him. When the man gently tugs the horse's left rein, the horse pulls massively to the left, a high power low fidelity amplifier of the man's weak leftward movement. A male cricket has the physical strength to walk about looking for females, but he can apparently use his muscles to greater advantage by sitting in one place and singing. Communication, which we use interchangeably with 'signalling', could be characterized as a means by which one animal makes use of another animal's muscle power. This can be developed into a definition, although the definition leads us so far from the spirit of what is conveyed by the ordinary English usage of the word that we are tempted to abandon the word communication altogether.

10.1.2 Definition

Call the two animals actor and reactor. Natural selection in the past has worked on individuals of the class to which the actor belongs, to improve their power to manipulate the behaviour of individuals of the class to which the reactor belongs. Statements of this kind may be shortened for convenience, using the phrase 'is selected to'. In this case our short form is that the actor is selected to manipulate the behaviour of the reactor—male crickets are selected to manipulate the behaviour of female crickets. Communication is said to occur when an animal, the actor, does something which appears to be the result of selection to influence the sense organs of another animal, the reactor, so that the reactor's behaviour changes to the advantage of the actor.

10.1.3 The actor

Of course the actor does not benefit every time it communicates. A cricket may spend its whole life singing out of range of any females. Its song may attract a parasite rather than a female. We believe it is fruitful to interpret the attributes of animals in terms of the selection pressures that may have shaped them, but perfectionism is no part of this belief. When you watch a particular animal doing a particular action, the chances are good that on this occasion the action will turn out to be a mistake. Many an animal dies as a direct result of its own behaviour, even if that behaviour is well adapted to average statistical...
circumstances. On average, male crickets who sing propagate their genes more efficiently than male crickets who do not, even though some crickets fail as a direct result of singing. This is no paradox. Motorists who wear seat belts are less likely to be killed than those who do not, yet some individuals die because they are wearing a seat belt and it traps them. As selectionists we are concerned with average statistical benefits.

10.1.4 The reactor

Our definition stipulates that communication results in a net average benefit to the actor, but it says nothing on whether the reactor benefits. The point is irrelevant to the definition. Female crickets may benefit from their tendency to approach male song. Small fish do not benefit from their tendency to approach angler fish lures. Foster mothers do not benefit from their tendency to push food into the coloured gapes of baby cuckoos. But all are examples of communication. The actor in all three cases, male cricket, angler fish, and cuckoo nestling respectively, ‘is selected to’ manipulate the behaviour of the reactor. Then why do reactors respond, if they only harm themselves by doing so? The answer is that in a sense, even in extreme cases like angler fish prey, they do benefit on average from their tendency to respond.

It is the lesson of the seat belt over again. Small fish benefit from their tendency to approach wriggling worm-like objects, because the majority of such objects are good to eat. It is true that a minority turn out to be anglers’ lures, but this is not sufficient to reverse the net average benefit. All sensory discrimination involves some generalization. To a stickleback the definition of a conspecific male is anything red. This is on average a serviceable definition, even if it occasionally leads to wasteful attacks on harmless mail vans (Tinbergen 1953). To a taxonomist, ‘anything small and wriggling’ is scarcely an adequate definition of a worm, but to a hungry fish it is normally good enough.

The existence of anglers’ lures doubtless leads to selection pressure to change the definition or sharpen up the generalization gradient, and some such evolutionary improvement may well have occurred. But this is only one of many selection pressures bearing on the matter, and in any case selection is also acting on the angler fishes to improve the quality of their deception. Like men who wear seat belts, fish who approach worm-like objects sometimes die as a result, but still are on average more likely to survive than those who do not.

10.1.5 Who benefits?

To summarize the point of view we are adopting: as an inevitable byproduct of the fact that animals are selected to respond to their environment in ways that are on average beneficial to themselves, other animals can be selected to subvert this responsiveness for their own benefit. This is communication. It may happen that both parties benefit by the arrangement, in which case the word subvert will seem inappropriate. But as far as our definition of communication is concerned, whether the reactor benefits or not is incidental.

Many authors, on the other hand, use the term communication only when the reactor, as well as the actor benefits. The following quotations are representative:

‘Central to any definition of communication is the reception by an organism of information conveyed by a stimulus from the external world . . . In stimulus exchanges with the environment, or exchanges between an animal and its prey, the relationship between sender and receiver is one-sided; while one participant tries to maximize the efficiency of the stimulus exchange, the other is at best neutral and often seeks to minimize it. In true communication, however, both participants seek to maximize the efficiency of information transfer.’ (Marler 1968.)

‘One party—the actor—emits a signal, to which the other party—the reactor—responds in such a way that the welfare of the species is promoted.’ (Tinbergen 1964.)

‘One of the basic functions of a display . . . is to make the behavior of the communicator more predictable to a recipient by making available some information about the internal state of the communicator.’ (Smith 1968.)

‘Displays are acts specialized to make information available’. (Smith 1977.)

Tinbergen (1952), Morris (1956), Marler (1959) and other ethologists have built upon the ideas of Darwin on the expression of the emotions (1872) to produce an elegant account of how communication systems might have evolved, assuming mutual benefit to both actor and reactor. We here call this the classical ethological approach.
10.2 The classical ethological approach

10.2.1 Ritualization

Each signal is supposed to have been derived in evolution from another behaviour pattern which earlier was used for something else. The evolutionary process whereby an incidental movement becomes built up into an effective signal is called ritualization, defined by Huxley (1966) as '. . . the adaptive formalization or canalization of emotionally motivated behaviour, under the teleonomic pressure of natural selection so as: (a) to promote better and more unambiguous signal function, both intra- and inter-specifically; (b) to serve as more efficient stimulators or releasers of more efficient patterns of action in other individuals; (c) to reduce intra-specific damage; and (d) to serve as sexual or social bonding mechanisms'.

10.2.2 Information

The emphasis on reduction of ambiguity (see also Cullen 1966) clearly makes sense only in the context of an exchange of information, and is not necessarily compatible with the cynical view given at the beginning of this chapter. The idea of an exchange of information is a carry-over from human language, where the end result of communication is that the receiver learns something which he did not know before, from the sender. In the case of animal signals, what is the 'information' supposed to be 'about'? In some cases, such as the celebrated bee dance, discovered in the classic research of von Frisch and ingeniously confirmed by Gould (1976), we can regard the information as being about the outside world. In the terms of information theory, each receiving bee's prior uncertainty about the location of food is reduced when she reads the dance of a successful returning forager. Here one cannot doubt that the benefit is, in a sense, mutual, but we would still prefer to avoid information terminology and would instead think of the dancing bee as a manipulator, making efficient use of the muscle power of her sisters. Wilson (1975) says: 'The straight run represents, quite simply, a miniaturized version of the flight from the hive to the target'. A similar point was made by Haldane and Spurway (1954) in their famous paper on the information-theoretic analysis of the dance. It follows that the receiving bees can be regarded as amplifiers of the dance in two senses. Firstly, each one of them amplifies the 'miniaturized' dance into a full distance flight. Secondly, one dancer may recruit a large number of new foragers simultaneously, and there is thus an amplification in terms of numbers.

Other examples where animals can be said to be communicating information about the outside world are not numerous. Songbirds have an alarm call that 'means' 'aerial predator'. It is reasonable here to regard information as flowing from actor to reactor, but it is no less reasonable to eschew the ideas of information and of meaning and to think instead of the caller as 'manipulating' the behaviour of its companions. (Charnov & Krebs 1975, Dawkins 1976 pp 181-183.)

Most 'informational' interpretations of animal communication have concentrated on information about the actor's internal state rather than about events in the outside world. This is the significance of the phrase 'emotionally motivated behaviour' in Huxley's definition, and of Darwin's title 'The Expression of the Emotions in Man and Animals'. Even an alarm call can be interpreted as meaning 'I am afraid' rather than 'There is a hawk', though we would, of course, add that there is no need to think of signals 'meaning' anything at all.

10.2.3 Origins

The classical theory that signals evolve from involuntary expressions of the emotions is a powerful one, whether or not informational concepts are invoked. It is compatible with the 'cynical gene' view we are adopting. The basic idea is as follows. The behavioural acts in an animal's repertoire occur non-randomly in time with respect to one another. In some cases the sequential or temporal connectedness is obvious, and in others statistical analysis is required to show it up (Nelson 1964). Either way, what it means is that the animal's future behaviour is, at least statistically, predictable from its past behaviour. Tooth-baring in a dog is a practical preparation for biting, and a dog who has just bared his teeth is statistically more likely to bite than a dog whose teeth are covered. We can, if we wish, see this as an expression of emotion: the dog with bared teeth is 'angry'. What is more important is that if an ethologist, with or without a computer, and whether or not he uses words like angry, is capable of predicting what an animal is likely to do next, then so, probably, is another animal. This other animal does not have a push-button event recorder and a computer, but he has the great inductive technique known as learning, and he inherits the genes of a long line of successful ancestors. Between
them, these two equip him for the same kinds of feats of induction as are achieved by the ethologist with his computer. If an animal can benefit by ‘predicting’ the behaviour of other animals, he will tend to do so. Needless to say, there is no implication of conscious prediction. Predicting means, here, behaving as if in anticipation of another animal’s future behaviour. If it is the case that an animal who has bared his teeth is statistically likely to bite, successful rivals will be those who behave in a way appropriate to a future bite, for instance by running away. So selection favours heightened responsiveness in the reactor.

The fact that other animals are responding to their behaviour induces new selection pressures on actors. If a dog can cause rivals to flee simply by baring his teeth, selection will favour dogs who exploit this power. Tooth-baring will become ritualized, exaggerated for increased power to frighten, and the lips may be pulled back further than is strictly necessary merely to get them out of the way. Over evolutionary time teeth may get larger, even if this makes them less efficient for eating.

Signals are thought to evolve from any incidental movements which happen to be perceptible to other individuals, and which happen to have been ‘informative’ even before they became ritualized. Their name suggests that intention movements’ might be good predictors of future behaviour, and they do indeed appear to have been often ritualized (Tinbergen 1952). It is a little less obvious why conflict movements seem to have been so favoured as primordial signals (Tinbergen 1964) but an ‘information’ enthusiast might suggest that it is because they tend to occur at moments of transition between one motivational state and another, i.e. moments of high ‘surprise value’ or uncertainty, which is another way of saying high information content (Dawkins & Dawkins 1973). Byproducts of autonomic system activity are such effective indicators of internal emotional state that they are the basis of police lie-detector tests. Animals cannot strap electrodes to each other, but their sense organs are in any case sensitive to some external manifestations of sympathetic and parasympathetic activity. Morris (1956) has suggested that a large number of animal signals can be traced back to changes in systems involved in thermoregulation (hair and feather erection, surface blood-vessel dilation, sweating), excretion (e.g. urination marking of territory in dogs, urination over female rabbits by males) and respiration. Darwin himself pointed out that changes in breathing are indicative of strong emotion, and suggested that this was the origin of vocalization. The heart beat seems to have one of the two qualifications necessary in a prime candidate for ritualization—it is a good indicator of emotional state. It does not appear to have been obviously ritualized in fact, perhaps because it lacked the other essential qualification—detectability by another’s sense organs before ritualization began. An imaginative classical ethologist might speculate that a population of animals, experimentally fitted with amplifying stethoscopes over hundreds of generations, might evolve heartbeats so loud that the stethoscopes would eventually become superfluous and the ritualization process would take off on its own.

To summarize what we are calling the classical ethological view of the evolution of animal communication, reactors are supposed to be selected to behave as if predicting the future behaviour of actors. Actors in their turn are selected to ‘inform’ reactors of their internal state, to make it easy for reactors to predict their behaviour. According to this view, it is to the advantage of both parties that signals should be efficient, unambiguous and informative. Communication is seen as a vehicle of inter-individual cooperation, and its evolution is mutual co-evolution.

But a consideration of the fundamentals of how natural selection actually works (Williams 1966) leads to the more cynical view of the interactions between individuals which we gave in the first part of this chapter. Cooperation, if it occurs, should be regarded as something surprising, demanding special explanation, rather than as something automatically to be expected. Even mates (Trivers 1972), and parents and offspring (Trivers 1974, Trivers & Hare 1976) often have divergent genetic interests (see also 1.5), and must be expected to conflict with each other rather than to cooperate. Returning to the question of why the heart-beat has not been ritualized, the real reason may be neither the lack of a stethoscopic bridge over the initial audibility gap, nor the potential danger to the heart’s vital function of pumping blood. It may be that the heart-beat is such a true and un-fakeable informer of internal state that it had to be hushed up! For every case of ritualized exaggeration of an external indicator of internal state, there could be many cases of systematic suppression, of negative ritualization.

10.3 Ritualization and combat

10.3.1 Ritualized fighting as an evolutionarily stable strategy

In the case of signals used in fights, the word ritualization has special connotations which raise particular theoretical problems. When two
animals contest a piece of food, a mate, a nest or some other resource, the winner clearly benefits, yet even animals with dangerous weapons often settle such disputes by conventional displays. The loser gives up without a struggle, and even in the moment of victory the winner does not go all out for the kill (Lorenz 1966). Like many generalizations, this one has exceptions (Geist 1971) but there does seem to be a problem here for the ‘selfish gene’ approach to communication. Ritualized combat is obviously ‘good for the species’ because it saves lives and prevents injury, but the crucial question is whether it is good for the genes that cause individuals to indulge in it. Ethologists have often argued in a qualitative way that individuals benefit from ritualized contests because they themselves avoid injury (Tinbergen 1951), but a more searching analysis has only recently been made (Maynard Smith & Price 1973, Maynard Smith & Parker 1976, Maynard Smith 1976c).

The essence of Maynard Smith and Price’s argument, which they developed from earlier ideas on sex ratios (Fisher 1930, Hamilton 1967), was that the best strategy (e.g. ‘fight dangerously’ or ‘fight conventionally’) for an individual to adopt depends on what all the others are doing. Suppose, for example, that in a hypothetical population everyone uses only ritualized or conventional signals, retreating from a contest at the first sign of escalated, dangerous, fighting. A new mutant, called ‘hawk’, which fights viciously in every contest would prosper because it would always win, and would suffer no risk of injury since its opponents always retreat. Now imagine that after a few generations of this prosperity the hawkish mutant has spread and replaced the ritualized signaler. Most contests now involve two hawks, and on average each hawk has an even chance of losing the fight and getting seriously injured in the process. The average benefit from contests is no longer obviously higher for hawks than for ritualized signalers: if the advantage of winning is less than the cost of serious injury the retiring conventional competitor does better on average than a hawk in a population dominated by hawks. The critical conclusion is that both fighters and signalers do well when they are rare, but can be outdone by the other when common. Table 10.1 shows how this hypothetical example can be formalized as a payoff matrix. The ritualized signaler and escalated fighter are named ‘hawk’ and ‘mouse’ and the formulae in the cells of the matrix are the payoffs from a contest (in fitness units) to the two types of individual when fighting against each type of opponent. When hawk meets mouse, its payoff is V, the value of the resource, since mouse always retreats. Similarly, mouse gets nothing from a contest against hawk, but gets on average \( \frac{1}{2} V - T \) against another mouse: \( \frac{1}{2} V \) because each contestant wins \( \frac{1}{2} \) of the contests and \(-T\) because in every contest, whether it wins or loses, mouse has to waste time displaying, which is represented by the fitness cost T.

The important point to note is that, as implied by our verbal argument, if the cost of injury is bigger than the value of victory \( (W > V) \) then hawk does worse than mouse in a population of hawks [i.e. \( \frac{1}{2} (V - W) < 0 \)], while mouse does worse in a population of mice [i.e. \( \frac{1}{2} (V - W) > 0 \)]. Because of this frequency dependence of benefit, neither strategy when common is resistant to invasion by the other or in other words neither is an evolutionarily stable strategy (ESS). An ESS is a strategy such that if most members of a population adopt it there is no rare strategy that would give higher reproductive fitness. There is, however, an ESS for the matrix in Table 10.1. It consists of the particular mixture of hawks and mice in which the payoffs for the two strategies are equal; if either hawks or mice became commoner, they would start to lose ground. As shown in Table 10.1 this mixed ESS can be expressed as a proportion of hawks \( p \) in terms of \( V, W, \) and \( T \). The mixed ESS could also be realised if each individual played hawk with probability \( p \) and mouse with probability \( (1 - p) \).

We have dwelt on this very simple example at some length to show the technique of analysing an ESS but, to return to our original point,
the simple model shows that, as long as \( W > V \), neither pure conventional display nor pure escalated fighting is an ESS. If the benefit of victory is enormous (\( W < V \)) as for example in the case of two elephant seals fighting over a harem where the winner may obtain a huge number of copulations, hawk can be an ESS, and escalated fighting with injuries should be common.

If we extend the model to include three strategies, hawk, mouse, and retaliator, the latter being an individual who displays conventionally against mouse, but escalates in retaliation against hawk, it turns out that retaliator can be an ESS (Table 10.2), again assuming \( V < W \).

<table>
<thead>
<tr>
<th></th>
<th>Hawk</th>
<th>Mouse</th>
<th>Retaliator</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>In a contest against:</strong></td>
<td>1/2 ( (V-W) )</td>
<td>( V )</td>
<td>1/2 ( (V-W) )</td>
</tr>
<tr>
<td><strong>Payoff to:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hawk</td>
<td>( 1/2 (V-W) )</td>
<td>( V )</td>
<td>1/2 ( V-T )</td>
</tr>
<tr>
<td>Mouse</td>
<td>(-S)</td>
<td>1/2 ( V-T )</td>
<td>( 1/2 V-T )</td>
</tr>
<tr>
<td>Retaliator</td>
<td>1/2 ( (V-W) )</td>
<td>1/2 ( V-T )</td>
<td>( 1/2 V-T )</td>
</tr>
</tbody>
</table>

Table 10.2. A payoff matrix similar to that of Table 10.1, but incorporating the additional strategy 'retaliator'. After Maynard Smith (1976c) except that a mouse, before it flees, incurs a risk of injury \( S \) when it meets a hawk. Retaliator is an ESS if \( S > \frac{1}{2} (V-W) \) and \( V < W \).

general conclusion is that on the basis of payoffs to individual genotypes we would not expect to observe animals using purely escalated fighting, if costs of injury are high relative to benefits from winning. They should use predominantly conventional displays, and escalate only in retaliation.

Some animals, however, possess no weapons with which to escalate. When contests are settled purely by conventional means, it seems likely that the one who persists longer wins, in which case one can ask for how long an individual should persist. If all individuals always choose to persist for \( m \) minutes, a mutant persisting for just a little longer than \( m \) would always win contests, the upper limit to \( m \) being set by the cost of displaying in relation to the value of winning. The ESS cannot therefore consist of a single strategy, and in fact the mixed ESS is a random distribution of persistence times. In other words, each individual displays for an unpredictable length of time so that its opponent cannot anticipate how long the contest will last and decide to hang on just a little longer to be sure of winning. As with the hawk-mouse ESS, the mixture could be realised either by an appropriate proportion of individuals using each alternative, or by every individual sometimes using one strategy, sometimes another, and making a random choice according the appropriate probabilities. One example of a random distribution of persistence times is that of male dung flies waiting on dungpats to mate with incoming females (see Chapter 8.7). Although this does not involve a display it is an analogous problem because the best persistence time for any one male depends on how long the others persist.

### 10.3.2 Asymmetric contests and assessment

An important difference between the models discussed so far and the real world is that in contests between real animals there are usually asymmetries (Parker 1974c). These are of three types (Maynard Smith & Parker 1976): (a) the two contestants differ in strength or fighting potential; (b) they differ in their expected benefit from winning the contest (for example, a hungry animal benefits more than a satiated competitor from winning a fight over food); (c) they differ in some way which is unrelated either to fighting potential or expected benefit, but the difference could be used as an arbitrary one to settle contests, somewhat as humans settle a dispute by tossing a coin.

### Differences in fighting potential and assessment

Suppose the two individuals in a contest differ in fighting ability. The weaker individual should withdraw as soon as it assesses its relative strength, since it could not win the contest by outlasting the opponent in conventional display, or injuring it in an escalated fight. At the same time, if the stronger individual can win a contest by means of a simple signal such as a raised crest or a loud shriek, bluff by weak individuals should evolve. What sort of cues would be good to use in assessment of an opponent's fighting ability? Clearly the cues used should be closely linked to fighting ability and give reliable information. Assessment signals which are easily mimicked by weak individuals will, in the course of evolution, soon come to be ignored in ritualized disputes, while reliable cues will become established as displays to the benefit of both sender and receiver of the signal. Cues such as size, which are obviously linked to fighting ability will tend to be resistant to bluff and should be used to settle contests. For example if two hermit crabs (Clibanarius eisenius) differ appreciably in size, the smaller one retreats from a contest immediately (Hazlett 1968). Similarly, ritualized contests are often literally trials of strength: adult male African buffalo (Syncerus...
caffer) charge at each other and collide head on (Sinclair 1977); vixen foxes (Vulpes vulpes) stand on their hind legs and try to push each other over (Macdonald 1977); male bullfrogs wrestle with one another (Howard 1978b); and cichlid fish may be so exhausted after winning a ritualized contest that they cannot start again until after a rest (Baerends & Baerends von Roon 1950). Ritualized trials of strength may also be more indirect. Siamese fighting fish (Betta splendens) settle contests by a series of display movements involving alternation between head on and sideways postures (Simpson 1968). These ritualized swimming movements probably allow each rival to assess the other's strength and fighting ability. It is especially interesting that the movements of the eventual loser of a contest closely parallel those of the winner until a few moments before giving up, just as one would expect if the contest involves both bluff and assessment. A similar effect was observed in red deer stags (Cervus elephus) by Clutton-Brock (in prep.); the stags compete for hinds to add to their harems, and contests consist of prolonged roaring duels. Escalated contests are rare, and they are costly because of the high risk of injury and because subordinate males, known as sneaky fuckers, may steal matings during a prolonged fight. Contests are settled by roaring: the two males roar at each other with a gradually increasing tempo until one suddenly gives up (Fig. 10.1). Clutton-Brock's interpretation is that roaring is a form of assessment and is hard to bluff because roaring contests are so exhausting. A stag will increase its roaring rate in response to an accelerating tape recording but it gives up if the tape accelerates too fast.

Another much more general link between assessment, threat signals, and vocalisations has been discussed by Morton (1977). He points out that the vocal threat signals of many birds and mammals are low pitched harsh sounds. The pitch of a call depends in part on the tension, length and thickness of the vibrating membrane and on the size of the resonating chamber (this second factor is important in mammals but may not be so crucial in birds (Greenwalt 1968). This means that larger animals are capable of making lower pitched sounds so that pitch is a reliable cue for assessment of body size and hence fighting ability of an opponent. Therefore it is not surprising that low-pitched sounds have become ritualized as threat signals. The harshness of threat sounds is probably a byproduct of their low pitch, since a vibrating membrane under low tension tends to produce harmonically unrelated tones which sound harsh.

It seems, therefore, that displays used in assessment are often hard to bluff because they are direct or indirect trials of strength and hence costly to perform. Can we turn the argument the other way round and say that an animal can signal its dominance by the degree of cost it is willing to incur? Zahavi (1977b) argues along just these lines. He notes, for example, that a dominant bird in a flock of Arabian babblers (Turdoides squamiceps) gives food to others in the group, apparently altruistically, and he suggests that the dominant is in effect saying 'I am strong enough to be able to afford to give up food so don't come and fight against me'. There is a striking parallel between Zahavi's idea and the Potlatch tradition of the Kwakiutl Indians of the Pacific Northwest. The tradition was for local chiefs to invite rivals to their village, and lavish on them gifts or food, and even destroy valuable houses in the village to show how much they could afford to spare. The bigger the destruction of resources, the more effective was the ritual at impressing rival chiefs (Harris 1976). The Potlatch ritual
settles disputes over pieces of food (which are not highly valued) by are valued low by the contestants. The ringtailed lemur be settled without probing and escalation when the payoffs for winning second point about fakeable signals is that contests are more likely to both bib size and escalated contests are used in status assessment. The more contests, even though they fought more. The conclusion is that involves in more escalated disputes in which they were defeated by dominants it might eventually grow sufficiently to be able to beat the dominant in a fight. This could not happen, however, when a contest involves the same cost to the winner and the loser, as in red deer roaring competitions. Our conclusion, then, is that assessment signals usually have a cost, but the incurring of a cost itself cannot be said to have selective value. Rather the cost is a consequence of assessment.

Our contention that ritualized contests are usually settled by displays which indicate fighting ability seems to be contradicted by many aggressive signals that appear to be easy to fake. It is important to distinguish assessment signals such as the roaring of red deer that are used to settle contests by ritualized displays, and aggressive signals such as the red breast of a robin which merely enhance a posture by making the displays more conspicuous; but nevertheless there are many examples of signals used to announce fighting ability which would appear to be easily faked. Two points can be made about these signals First, the limit to cheating is set by probing and escalation. This is well illustrated by the Harris’s sparrow (Zonotrichia querula), in which there is a correlation between dominance status in winter flocks and the size of a black bib of feathers under the chin. This black bib is, in effect, a badge of status. When Rohwer (1977) tried to create cheaters by enlarging the bibs of subordinate birds with black dye, he found that the experimental cheaters did not win more contests, but instead they were involved in more escalated disputes in which they were defeated by true dominants. One interpretation of these results is that contests are not settled by bib size alone, and that assessment also involves escalated fights. This is supported by an experiment of Rohwer and Rohwer (1978). They implanted subordinate birds with testosterone at the same time as painting their bibs. These birds successfully increased their status, while controls implanted but not painted failed to win more contests, even though they fought more. The conclusion is that both bib size and escalated contests are used in status assessment. The second point about fakeable signals is that contests are more likely to be settled without probing and escalation when the payoffs for winning are valued low by the contestants. The ringtailed lemur (Lemur catta) settles disputes over pieces of food (which are not highly valued) by

easily faked signals such as staring, calls, and feinting blows. In the breeding season, however, when the stakes are high, things are different; biting, chasing and tearing out of fur are common during escalated contests between males over the chance to mate with receptive females (Jolly 1966).

Asymmetry in benefit

Even when two contestants are equally matched in fighting ability, one of them might be willing to escalate further because it has more to gain (i.e. \( V - W \) will remain positive for higher levels of escalation). As a general rule, an individual should be willing to put more into a fight, the more it can get out of winning. For example, female iguanas (Iguana iguana) try to steal from each other the burrows which they dig for the purpose of egg laying. Both a resident and an intruder are more likely to escalate a fight if the burrow is deep than if it is shallow. A deeper burrow represents a bigger payoff because it requires less future digging before it is ready for egg laying (Rand & Rand 1976).

In an escalated contest over a deep burrow the iguanas use high cost displays such as biting, lunging and rapid approach, while they settle disputes for shallow burrows by milder displays such as opening the mouth and head swinging. Both intruder and resident may gradually escalate the contest, but the correlation between hole depth and tendency to escalate is better for residents than intruders. This is perhaps because the resident has the more accurate assessment of the depth of the hole and can adjust its investment in displays appropriately. This difference in knowledge about the depth of hole probably also explains why residents are more likely to win contests over deep holes.

In the iguanas, the value of the hole is similar for both resident and intruder, the only asymmetry in benefit resulting from the degree of certainty about the state of the hole. Very often, however, the resident defender of a resource such as a territory stands to gain more than the intruder because, having learned the good feeding and hiding places, it can better exploit the territory in the future. An example of this is referred to in section 2.4.3: territorial Hawaiian honeycreepers (Loxops virens) can gain more than an intruder out of their own territory because the territory holder systematically avoids revisiting flowers from which nectar has been taken while intruders do not. With this clear asymmetry in payoff, it would benefit both the resident and intruder to save time and energy by using a cue correlated with the
asymmetry to settle disputes. If the resident has more to gain, an obvious cue would be prior residency. In fact it is well known that prior residency is used as a cue to settle contests in fish and at least some birds (Phillips 1971, De Boer & Heuts 1973, Zayan 1975, Krebs 1977a). Some fish such as the blenny (Blennius fluviatilis) change colour when they establish a territory, and the colour cue is probably used to settle contests (Wickler 1957): the benefit to the prior resident is obvious, and the intruder benefits because it saves time in a contest which it could not expect to win.

Uncorrelated asymmetries

Even if there is no difference in fighting ability or expected gain, a totally arbitrary asymmetry between contests could theoretically be used to settle disputes (Maynard Smith & Parker 1976). If the resource that is being contested is not in very short supply, it could be advantageous for both contestants to save time by settling the dispute with a totally arbitrary convention, just as two men may toss a coin. Table 10.3 illustrates how the strategy of settling contests between hawks and mice by an arbitrary asymmetry such as 'first come first served' could be resistant to invasion by an alternative strategy of ignoring the asymmetry. This is at first sight a rather startling conclusion but there is at least one well documented example in which an apparently arbitrary asymmetry is used to settle contests (Davies 1978b). Males of the speckled wood butterfly (Pararge aegeria) defend patches of sunlight on the forest floor in which they court females. Intruders invariably retreat in contests for a sunspot, but the outcome of a dispute between two individuals can be reversed by only a few seconds of prior residence (Fig. 10.2). This contrasts with the 'prior residence' effect in birds and fish which we discussed in the previous section, where the effect only works if the resident has been established long enough to gain information about the territory and hence expect a higher gain. In the butterflies, the gain to the two males from winning is equal but the totally arbitrary rule of 'resident wins' is used to settle disputes quickly. Sun patches are not in short enough supply to warrant a prolonged dispute.

Table 10.3. An example to show how the acceptance of an arbitrary asymmetry to settle contests may, by saving time, increase the payoff to both participants. Consider the hawks and mice game in Table 10.1 with the arbitrary values of \( V = 60, W = 100, T = 10 \). The payoffs for Table 10.1 are shown below

<table>
<thead>
<tr>
<th></th>
<th>Hawk</th>
<th>Mouse</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
<td>-20</td>
<td>+60</td>
</tr>
<tr>
<td>Mouse</td>
<td>0</td>
<td>+20</td>
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</tbody>
</table>

Now consider a strategy which adopts the arbitrary rule 'owner wins, intruder loses' to settle a contest. The payoffs to this strategy against others of the same type is \( \frac{1}{2} [60p + 20(1 - p)] + \frac{1}{2} [20p] + 10p = 10 \) which is less than 30 for any value of \( p \) (\( p \) has to lie between 0 and 1). Hence adopting the arbitrary rule is an ESS.
If the rule ‘resident wins’ can be used as an arbitrary way of settling disputes, one might expect the rule ‘intruder wins’ to also crop up from time to time. One apparent example is the Mexican social spider (Oecobius civitas) which lives in aggregations on the underside of rocks. Each spider has a nest and if one is drawn out of its nest it may seek refuge in the hiding place of another spider. ‘If the other spider is in residence when the intruder enters, it does not attack but darts out and seeks a new refuge of its own. Thus once the first spider is disturbed, the process of sequential displacement may continue for several seconds, often causing a majority of the spiders to shift from their home refuge to an alien one’ (Burgess 1976). Another equally striking example is described in the following letter addressed to The Times on December 7th 1977 from a Mr. James Dawson: ‘For some years I have noticed that a gull using a flag pole as a vantage point invariably makes way for another gull wishing to alight on the post and this irrespectively of the size of the two birds.’

10.3.3 Graded signals

Our discussion of ritualized combat has implied that the participants use either formalized displays or escalated fighting. If the contest is settled by displaying, neither contestant should signal until the last possible moment that it is going to give up. Morris (1957) noted that many displays are performed in a rather constant manner (‘typical intensity’) regardless of the strength of motivation of the performer. This is just what one would expect if these displays have evolved as a means of winning contests and not as a way of providing opponents with as much information as possible about the subtle variations in motivation of the signaller (Morton 1977). However, many animals, especially birds and mammals, have a whole series of graded threat displays which indicate (at least to the human observer) the exact balance of aggression and fear in the performer. For example the body posture and degree of flattening of a cat’s ears give a good indication of how likely a cat is to attack or retreat during a contest (Hinde 1970). This seems to present a paradox: following Maynard Smith, we have argued that contestants should be selected to conceal their exact motivational state and display with typical intensity, and yet it seems that many animals do precisely the opposite. We must admit that the solution to the paradox is not clear, and we can only offer some guesses.

Graded signals are, in effect, a form of gradual escalation; instead of an abrupt switch from ritualized to escalated fighting, there is a gradual transition involving closer and closer approach to escalation. If graded signals are used in assessment, an individual that uses a ‘high intensity’ threat display must either value the resource highly (and hence be willing to risk more in a fight) or have a high fighting ability. But what is to stop an individual that does not value the resource highly, or does not have a high fighting ability, from bluffing by means of a high intensity threat? As with other assessment signals we have discussed, the answer may be that high intensity signals are costly. Perhaps graded threat signals reflect a gradation of cost that an individual is willing to incur in order to win a contest. The animal is like a man at an auction sale: the best way to win the resource with as little cost as possible is to start with a low bid and go higher only if necessary. ‘Cost’ to the animal could mean either an energetic cost of performing the display, or, more likely, a risk of retaliation with escalated fighting by a rival. One can see intuitively why high intensity threat should have a higher risk of eliciting attack by the rival. Neither individual knows how far the other is willing to go, but if A plays the highest-cost move below escalated fighting and B is willing to go further, the only option for B is to escalate. If, however, A plays a lower-cost move, B can out-bid A without escalating. Although we suggest this as a possible explanation for graded signals, our general point is that such signals are actually something of a puzzle. It has usually been assumed that a signaller benefits by conveying its exact motivational state to others (Smith 1977), but the nature of the benefit is not obvious.

10.3.4 Courtship and assessment

The ideas of assessment and probing discussed in section 10.3.2 can also be applied to the analysis of courtship signals. The traditional view of courtship displays is that they allow females to select a mate of the right species, and serve to synchronise the sexual arousal of male and female, by overcoming male aggressiveness and female coyness (Bastock 1967). Synchronising sexual arousal is a proximate consequence of courtship, but the ultimate significance of overcoming female and male inhibitions, at least in species with pair bonds and parental care, may involve mutual assessment by both sexes. In long-lived monogamous birds such as the kitiwake Rissa tridactyla (Coulson 1971) and Manx shearwater Puffinus puffinus (Brooke 1978) pairs are normally constant from one year to the next, but they split up if breeding is unsuccessful in one season. Pairs also become more successful
intraspecific deceit are pseudo female behaviour by male sticklebacks and deceit might be profitable strategies. In spite of this, ethologists deceit (Otte 1974). Some possible, but as yet untested, examples of signalling. Whenever there is any form of assessment, for example in deliberate misleading, ought to be commonplace too in examples of successful deception in predator-prey relationships having philandered. The male barbary dove contributes considerably to the care of nestlings, so that assessment of mate fidelity and avoidance of cuckoldry are of great importance to him.

10.4 Inter and intraspecific deceit

Interspecific deceit is so well known as to pass almost without comment. Batesian mimicry, twig-mimicking insects, and angler-fish lures are examples of successful deception in predator-prey relationships (Wickler 1968). Complex social signals are also mimicked in interspecific deception: beetles such as Atemes pubicollis parasite wood ants by faking the host’s interspecific signals, for example they induce ants to regurgitate food and groom (Hölldobler 1971). Deceit, or deliberate misleading, ought to be commonplace too in intraspecific signalling. Whenever there is any form of assessment, for example in combat, courtship or between parents and offspring, bluff, exaggeration and deceit might be profitable strategies. In spite of this, ethologists have failed to find many unequivocal cases of successful intra specific deceit (Otte 1974). Some possible, but as yet untested, examples of intraspecific deceit are pseudo female behaviour by male sticklebacks and salamanders (see 7.10) and vocal mimicry in birds. Morris (1952) and Otte (1974) suggest that male ten-spined sticklebacks (Pygosteus pungitius) adopting cryptic female coloration may try to steal fertilisations or eggs from territorial males, using the female colour pattern to gain access to nests. Rohwer (1978) suggests that egg stealing itself may be a form of deception; he argues that males could use stolen eggs as an advertisement of their previous courtship success to encourage new females to mate with them. The function of vocal mimicry in birds probably varies from species to species (Jellis 1977) but one recent suggestion is that mimicry is used by territorial birds to deter rivals. Rechten (1978) points out that mimics often copy large aggressive, or predatory species. She suggests that this mimicry may dissuade rivals from trying to settle nearby by making the area appear to be inhabited by competitors and predators. A similar argument has also been proposed for intra specific copying of songs by birds (Krebs 1977 b) (see 11.4.1). The large numbers of examples of interspecific deceit and relative lack of instances of intraspecific faking call for an explanation.

Is there something special about deceit in intraspecific communication? We have already suggested that both probing and assessment may limit the extent of interspecific bluff although not eliminate it altogether, but perhaps there is also an additional more general reason for the apparent absence of more widespread intraspecific deceit. Successful deceit, whether between or within a species, depends largely on two factors: the deceit must be relatively rare, so that on average it pays the responder to react the way it does, and the responder must at least sometimes be unable to distinguish between fakes and the real thing. The responder’s discrimination ability is limited by unpredictability: it cannot tune its selective response to a signal beyond a certain level of precision, because the true signal is bound to vary slightly from one time to the next. This variability allows the deceiver to get away with a fake signal. These two limiting factors apply equally to inter and intraspecific deception, but as Wallace (1973) first pointed out, intraspecific deceit is further limited by the fact that the deceiver and responder both belong to the same gene pool. Although Wallace did not put it in these terms, he essentially showed that intraspecific lying is not an ESS because its benefit is frequency dependent. The argument is as follows. Imagine a mutant ‘liar’ (A) in a population of non-liars (a). Assuming the mutant raises its relative fitness by deceiving conspecifies, the A gene will spread. However, as it spreads, the likelihood will increase that liars attempt to deceive others with the gene A. Wallace suggested that the A individuals might recognise one another
Advertisements are among the most familiar communication devices in our world, and we should have learned by now that they have little to do with the conveying of information. Sometimes they tell the truth, more often they tell lies, but these terms are usually not even applicable. Advertisements are not there to inform, or to misinform, they are there to persuade. The advertiser uses his knowledge of human psychology, of the hopes, fears and secret motives of his targets, and he designs an advertisement that is effective in manipulating their behaviour. One of the favourite techniques of advertisers, which seems to work, however astonishing our rational selves may find the fact, is redundancy—'repetition to the point of what seems like inanity'. Many advertisements make no attempt to say anything about the product: they simply display its name over and over again.

Packard's (1957) expose of the deep psychological techniques of commercial advertisers makes fascinating reading for the ethologist. A supermarket manager is quoted as saying 'People like to see a lot of merchandise. When there are only three or four cans of an item on a shelf, they just won't move'. The obvious analogy with lek birds does not lose its value merely because the physiological mechanism of the effect will probably prove to be different in the two cases. Hidden cine cameras recording the eye blinking rate of housewives in a supermarket indicated that in some cases the effect of the multiplicity of brightly coloured packages was to induce a mild hypnoidal trance. Again, there may be a functional, if not a causal, analogy in the field of animal signals, and we will return to hypnosis later.

10.5.2 Social psychology

Social psychologists have interesting findings relevant to the general subject of persuasion and 'attitude change' (Howland et al. 1953, Baron et al. 1974, Berkowitz 1975). There is a problem in the interpretation of these results. Social psychologists are especially interested in the effects of persuasion on verbally expressed 'attitude'. Behaviour, say purchasing or voting behaviour, is measured separately and found to be predictable, to a greater or lesser extent, from the previously measured attitude. The evolutionary biologist is interested in behavioural outcomes, and he finds the two-stage reasoning of the social psychologist superfluous: in this sense he may have more in common with the commercial advertiser who presumably is less interested in what his victims say they think about his product than in whether they go out and buy it.

The social psychological approach to persuasion can be considered under three headings: (1) what makes for an effective persuader? (2)
3°6 CHAPTER 10

what makes for an effectively persuasive message? (3) what makes an individual vulnerable to being persuaded? Many of the answers to these questions turn out to accord with common sense. For instance attractive or admired individuals are especially effective persuaders, which is why footballers and film stars are paid large sums to pronounce on subjects about which they have no special expertise. Other findings are less obvious, and some are intriguing. The technique of inducing sales-resistance by ‘inoculation’ is one such. If an individual is in danger of being persuaded by a set of arguments or beliefs, he can be ‘immunized’ by prior exposure in the laboratory to a ‘weakened dose’ of the same arguments. He is then less likely to be persuaded when he meets the real thing. The technique has been shown to work, the parallel with vaccination extending even to details of timing (McGuire 1969). A variant of it is, perhaps, the political satirist’s art of exposing his audience to a ridiculously parodied version of his opponent’s arguments, often using vocal mimicry, like a mockingbird.

We propose no animal analogies for footballers and idols, nor are we suggesting that bird mimicry is an adaptation for boring females with satirical parodies of rivals’ songs. What is valuable for ethology is not the findings of social psychologists, but their questions (1, 2, and 3 above). Ethologists interested in animal communication have borrowed from human psychology, as we have seen, concepts related to language and information. We are now suggesting that if we look to human psychology at all we would do better to concentrate on the psychology of salesmanship and persuasion.

10.5.3 Monitoring and control

The classical ethological view emphasized the motivational state of the actor, and treated signals as formalized readouts of the actor’s internal state. Following our earlier analogy of the lie-detector machine, the reactor might be thought of as being provided with the equivalent of electrodes implanted in the actor’s skull, by means of which he could monitor changes in the actor’s internal state, and hence predict the actor’s future behaviour. Natural selection is thought to favour actors who cooperate in having their intentions read—the recording electrodes are welcomed, perhaps even provided by the actor. In this chapter, we prefer to concentrate on the motivational state of the reactor, as being manipulated by the actor. We may continue to use the electrode analogy, but ours are stimulating, not recording electrodes, and they are implanted in the reactor’s skull, not the actor’s. What actually are these stimulating electrodes? Whatever they are, they must make use of the reactor’s sense organs. It is reported that a flickering light tuned to the frequency of human EEG rhythms can have dramatic effects on behaviour, inducing epileptic seizures in susceptible people, and in one case a man felt ‘an irresistible impulse to strangle the person next to him’ (Grey Walter 1953). Who needs electrodes when the reactor has eyes?

Flickering lights are worth mentioning because it is easy to imagine them as the external equivalents of stimulating electrodes, pulsing away at the brain’s own sensitive frequencies. But man is vulnerable to much more subtle influences than this. Flickering light is just one of the visual aids sometimes used by hypnotists whose primary weapon is verbal suggestion. A hypnotized subject can be persuaded to perform pointless actions in response to irrelevant stimuli, even long after he comes round from the trance and without his recalling anything about the original instructions. Human hypnotists use verbal suggestion, but there seems no obvious reason why some similar persuasive force should not be used by non-verbal animals. At the 1973 International Ethological Congress in Washington D.C., K. Nelson gave a memorable paper entitled: ‘Is bird song music? Well, then, is it language? Well, then, what is it?’ At least as plausible as either language or music is the possibility that bird song should be regarded as akin to hypnotic persuasion.

But it may be that these are not all that different from each other. There may be a continuum between hypnosis as it is commonly understood and ordinary verbal persuasion, with the ‘spellbinding’ oratory of a Hitler or a Billy Graham falling between. There may be little difference between regarding bird song as music and regarding it as hypnosis. ‘Hypnotic’ rhythm and ‘haunting’ melody are clichés in the description of human music. The drug-like effect of the nightingale’s song on the poet’s nervous system (‘a drowsy numbness pains my sense, as though of hemlock I had drunk’) might be at least as influential on the nervous system of another nightingale.

10.5.4 Aesthetics

Complex bird songs repay critical musical (Hall-Craggs 1969) and Gestalt-theoretic (Thorpe & Hall-Craggs 1976) analysis. The notion that bird song might have some aesthetic content has, oddly, been linked to the idea that this aspect of it is functionless in the Darwinian sense. Proponents of this view have spoken of the biological functions
of song ('informing' others of the species and hormonal state of the singers, etc.), and have then gone on to speak of aesthetic reasons for singing as though these were extravagant luxuries superimposed on mundane, biological functions (e.g. Armstrong 1973). With Darwin, we prefer to think that the complex aesthetic beauty of bird song is there because natural selection has favoured it as such. We agree with those authors who say that the traditional views of the functions of communications—transmission of information as to species, sex, breeding condition, etc.—are pitifully inadequate to account for the musical elaboration of bird song. But these authors, having rightly rejected mundane information-purveying as the sole function of song, leapt too hastily to what they saw as the only alternative—music, performed for the enjoyment of the singer (Hartshorne 1973). They forgot oratory, persuasion, hypnosis. Oratory is unnecessary if the purpose is simply to convey information. Oratory comes into its own when the audience is resistant. In the case of singing to deter territorial rivals, the audience can obviously be regarded as resistant. The same might have been doubted in the case of singing to attract mates, but recent theoretical insights, already referred to, strongly suggest that even courtship should often be regarded as a battle of the sexes. As Williams (1966) has put it '... genic selection will foster a skilled salesmanship among the males and an equally well-developed sales resistance and discrimination among the females'. The fact that the same music is used both to repel (rivals) and to attract (females) need not surprise us. Martial music is 'stirring' even though it stirs one group of people to patriotic courage while simultaneously stirring another group into a panic.

If this Darwinian view of the aesthetics of bird song is accepted, it is still quite possible that individuals do in some sense 'enjoy' their own singing. The singer is, after all, a member of the same species as his audience, and his nervous system is presumably vulnerable to the same kinds of stirring stimuli. That his own singing is reinforcing for a bird is indicated by operant conditioning experiments (Stevenson 1967), although unfortunately the control sounds with which the birds' own songs were compared were limited. More interestingly, the reinforcing properties of bird song are strongly implied by the 'template' theory of song development (Konishi & Nottebohm 1969). Many young birds appear to teach themselves to sing by matching a wide spectrum of babblings against a stored template or mental image of what the song ought to sound like. The template may be a kind of tape recording of a conspecific heard earlier in life, as in the white-crowned sparrow Zonotrichia leucophrys. Alternatively, for example in the song sparrow Melospiza melodia, the template seems to be provided even in individuals who have never heard a conspecific. In either case, during the period when the young bird learns the motor patterns of song, the template functions as a reinforcer, albeit a highly complex and elaborate one. We can rephrase the template theory in the language of aesthetics. Because of the way its nervous system is built, any individual song sparrow, of either sex is emotionally affected by the song of the species. Depending on the context, this influence shows itself either as sexual attraction, or as intimidation, or as self-reinforcement, just as a re-splendent cavalry uniform may intimidate enemies, rouse the courage of self and comrades, and sexually attract female camp followers. The template strategy of development is economical, since it exploits a source of information which is already built into the species nervous system for other reasons.

10.6 Conclusions

We are contrasting two attitudes to the evolution of animal signals. One attitude, which we have here called classical, emphasises cooperation between individuals. Cooperation is facilitated if information is shared. Selection favours those actors who make it easy for reactors to 'read' their internal state, and hence to act as if in anticipation of the actor's behaviour. The other attitude, which we espouse, emphasises the struggle between individuals. If information is shared at all it is likely to be false information, but it is probably better to abandon the concept of information altogether. Natural selection favours individuals who successfully manipulate the behaviour of other individuals, whether or not this is to the advantage of the manipulated individuals. Of course, selection will also work on individuals to make them resist manipulation if this is to their disadvantage, just as natural selection works on prey animals to make them less likely to be caught by predators. In both these cases an evolutionary arms race will develop. Predators evolve adaptations so that they do sometimes catch prey in spite of anti-predator adaptations. In the same way, actors do sometimes succeed in subverting the nervous systems of reactors, and adaptations to do this are the phenomena that we see as animal signals.