ANIMAL BEHAVIOUR

A SERIES EDITED BY

T.R. HALLIDAY
Department of Biology
The Open University

AND

P.J.B. SLATER
School of Biology
University of Sussex

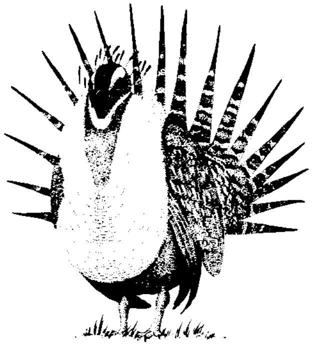
ANIMAL BEHAVIOUR · VOLUME 2

COMMUNICATION

EDITED BY T.R. HALLIDAY
AND P.J.B. SLATER

BLACKWELL SCIENTIFIC PUBLICATIONS
OXFORD LONDON EDINBURGH
BOSTON MELBOURNE

1983



CHAPTER 5

THE EVOLUTION OF COMMUNICATION: INFORMATION AND MANIPULATION

R. HAVEN WILEY

5.1 Introduction

Communication occurs when one individual's actions provide a signal that changes the behaviour of another individual. The evolution of communication thus depends on the changes in fitness of the sender and the receiver of a signal. By change in fitness, we mean a change in the rate at which genes influencing an individual's actions spread in the population. This rate depends in turn on the survival and reproduction of individuals carrying these genes. As a result of natural selection in past generations, an individual should only produce signals that increase its fitness. Likewise, an individual should only respond to signals in ways that increase its fitness. This superficially simple situation, however, leads to some fascinating complexities, which are the main subject matter of this chapter.

In recent years, there have been three approaches to understanding how natural selection affects the evolution of communication. The first focuses on the signaller. The main question here is: what strategies for signalling are most effective in evoking responses from a potential receiver? The second approach focuses on ways that signallers and receivers might take advantage of each other. The issue here is: how can a signaller (or receiver) manipulate the behaviour of the other individual to its own advantage? The third approach has relied on the theory of games to analyse how animals should behave in conflicts. In part, this approach asks: how should animals communicate with each other in the course of conflicts? Although aspects of these three approaches have seemed incompatible (Dawkins & Krebs 1978), we shall see that much concordance exists among them. In fact, they illuminate the evolution of communication in complementary ways. This chapter takes up these three approaches in sequence.

5.2 Adaptations for efficient communication

5.2.1 *Information and noise*

The basic phenomenon of communication involves two individuals with signals passing between them. For an objective analysis of this system, however, we need to introduce a nonparticipant observer, in our case the ethologist, who monitors the behaviour and characteristics of the signaller (also called the source or sender), the receiver and the signal (Fig. 5.1; Shannon & Weaver 1949; Cherry 1966).

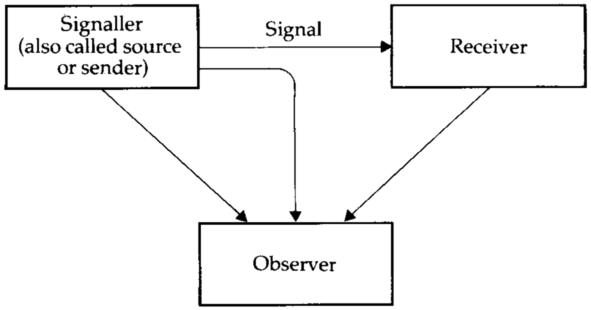


Fig. 5.1. The nonparticipating observer, by recording the behaviour of the signaller and the receiver and the characteristics of the signal, acts like a privileged receiver 'tapping the wires' of communication between nonhuman animals.

Chapter 2 presented a number of measures of the effects of one animal's behaviour on that of another, including Shannon's measure of the information transmitted from a signaller to a receiver (section 2.11). The term 'transmitted information' has a technical meaning defined by changes in the predictability of the receiver's behaviour as viewed by a nonparticipant observer. By this definition, a signal transmits information to a receiver when its occurrence increases the predictability of the receiver's subsequent behaviour. An important consequence for the evolution of communication immediately follows. Whenever the receiver's response to a particular signal increases the sender's fitness, selection favours senders that maximise the efficiency of that signal in transmitting information. In other words, the signal should evolve to maximise the predictability of the response for a given time and effort committed by the signaller.

It is important to distinguish between transmitted information and broadcast information. An observer measures the first by an increase in the predictability of the *receiver's* behaviour after a signal occurs. The latter, in contrast, is an increase in the predictability of the *signaller's* identity or behaviour after a signal. Thus broadcast information is a measure of the information obtained from a signal by the observer. It is loosely analogous to Smith's (1968, 1977) concept of the message of a signal. Note that broadcast information accords more closely with the everyday use of expressions like 'this book contains a lot of information'. Yet transmitted information, not broadcast information, is fundamental in an objective analysis of communication, where the primary concern is the effect of a signal on a receiver.

Broadcast information depends on the process of encoding. The signaller translates its internal state into actions or other external changes that produce signals. The internal state of an animal, for our purposes, is the state of its nervous system, which at any moment has a unique 'value' determined by the activity and condition of every neuron. Particular values of an animal's internal state then result in corresponding actions that can serve as signals to others. This mapping of an animal's internal state on to its actions is called *encoding* (see Green & Marler 1979).

The receiver also performs a translation, in this case from the reception of a signal to a change in the subsequent values of its own internal state. These changes might result in an immediate response, but need not. The receiver's translation depends on concurrent external stimulation other than the signal (the context) as well as the current value of the receiver's internal state, which in turn is influenced by its history. This process of translation by the receiver is called *decoding* of the signal.

Intended receivers do not always detect signals nor, even when they detect them, do they always classify them correctly. Furthermore, receivers on occasion respond when they confuse some irrelevant stimulus with a signal of interest. These errors in reception are noise. Note that we have again adopted a technical definition of an everyday word. We usually think of 'noise' as irrelevant sound that masks our perception of something interesting. Noise in the technical sense can indeed result from irrelevant stimulation, acoustic or otherwise, that masks signals, but there are other causes of errors in reception of signals as well.

The degradation and attenuation of signals between source and receiver can also interfere with correct reception (see Chapter 3). After transmission over long distances, two signals can become indistinguishable, or a signal can become indistinguishable from irrelevant stimulation. A bird's song in a forest, at a distance from the singer, is often difficult to distinguish from that of other individuals or even other species and might barely stand out against the noise of wind and rustling leaves.

Furthermore, the receiver's threshold for detecting a signal has a fundamental effect on the errors it makes and consequently on the nature of noise in communication. As mentioned above, there are two kinds of mistakes in detecting a particular signal: missing some occurrences of the signal (missed detections); and reacting to some stimuli that are not the signal (false alarms). A receiver cannot minimise missed detections and false alarms simultaneously (see review by Wiley and Richards (1983)). Instead, it must make a trade-off. A receiver that sets its detectors at a lower threshold for response misses fewer signals but risks making more false alarms. The opposite happens when a receiver sets its threshold higher.

5.2.2 *Improving the detection of signals*

To improve the efficiency of communication, a signaller cannot directly influence the processing of the signal by the receiver's nervous system, but it can employ signals that are easy for the receiver to detect. The theory of signal detection predicts that receivers become more reliable, in other words, miss fewer detection for a given number of false alarms, provided signals have certain features. Four features that increase the reliability of detection are redundancy, conspicuousness, possession of small signal repertoires, and use of alerting components (Wiley & Richards 1983).

Redundancy

Redundancy results from predictable relationships among different parts of a signal. Consequently, a receiver knowing these relationships can identify the kind of signal even if it correctly recognises only a part of that signal. Simple repetition of a signal, or elements of a signal, is the clearest sort of redundancy. However, redundancy can apply to spatial, as well as to sequential, arrangements of the parts of a signal.

The displays of animals have widely varying degrees of redundancy. The more complex and stereotyped the composition of a signal, the more redundant it is. At one extreme are displays that involve movements of many parts of the body in stereotyped coordinations. The elaborate strut display of male sage grouse (*Centrocercus urophasianus*) provides an extreme example (Fig. 5.2; Wiley 1973). In comparison, the 'push-up' displays of male *Anolis* lizards lack such extreme temporal stereotypy, and some components of the display have low correlations with each other (Jenssen 1971; Stamps & Barlow 1973). In another such case, the song-spread display of Carib grackles (*Quiscalus lugubris*), the elevations of the beak and the wings vary independently (Wiley 1975).

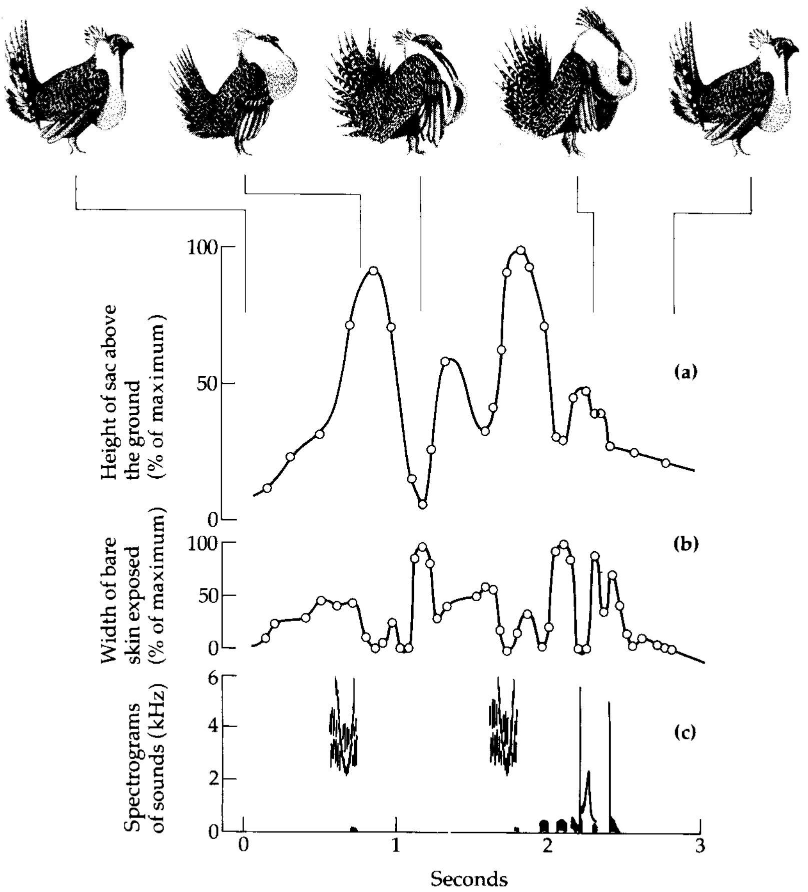


Fig. 5.2. The strut display of the sage grouse lasts nearly three seconds and provides both visual and acoustic signals. **(a)** The strutting male inflates his large oesophageal sac by heaving it upwards and letting it fall twice. **(b)** This manoeuvre exposes bare patches of olive-coloured skin on his chest. **(c)** At the climax of the display, he compresses the inflated sac and then releases the air explosively to produce a ringing pop and low-pitched coos. Since the timing of this display varies only slightly among performances of any one male or among different males, it is one of the most elaborate and stereotyped displays of any bird.

Redundancy in signals has some obvious disadvantages. First, redundancy takes time or requires additional components that could otherwise be used to send more refined messages. Secondly, redundant displays take more time and energy to encode any given message. Even if the response to the signal benefits the sender, why take extra effort or time to produce a redundant signal?

The answer is that redundancy can reduce errors in the detection and recognition of signals. It thus has advantages for a signaller faced with high levels of noise in communicating with a recipient. Noise, leading to errors by the receiver, can reach high levels for several different reasons. First, accurate detection of signals is likely to be difficult during interactions at long range, when signals are often attenuated to near the level of background stimulation or become distorted by degradation in transmission (see Chapter 3). In fact, many long-range signals of animals, such as the advertising songs of male birds or the loud calls of forest primates, are notably complex and stereotyped in comparison with other displays in the same species' repertoire (Marler 1973). In contrast, the signals employed in close-range communication among members of stable social units, like primate troops or mated pairs, have great variability. In the latter case, where redundancy is not so necessary to facilitate accurate detection of signals by recipients, the additional variability can be used to encode further variants of the sender's state.

High levels of noise can also result from the communication signals of other species. Many species of duck that nest in the northern temperate regions form pair bonds on wintering grounds or during migration, when many related species frequent the same locations. In identifying conspecific males, females cannot rely on segregation of related species in different habitats or geographical ranges. Males of these species have conspicuous plumage in elaborate species-specific patterns: this complexity provides redundant visual cues for recognition of species. Males of related nonmigratory species of duck have much drabber plumages.

Other conspecifics can create high levels of noise for mates communicating with each other in dense colonies. Many colonial birds have complex, individually distinctive vocalisations that mates use for individual recognition (White & White 1970; Wiley 1976; Moseley 1979), often in the presence of phenomenal levels of background stimulation from conspecifics using very similar calls.

Another situation likely to result in noisy communication is when a brief but biologically crucial interaction occurs between unacquainted individuals, such as when an animal chooses a mate. In some species, females may have to choose mates rapidly and with little or no prior experience of potential partners, for example when arriving at breeding grounds after migration. When opportunities for heterosexual association are limited, avoidance of errors is vitally important. In such cases, a female should raise her threshold of response to males so as to minimise her chance of making false alarms. As a result, a female would also fail to detect more signals from potential mates. To counteract this problem, males should evolve inherently more detectable signals, ones with greater conspicuousness and more redundancy. It is in birds with brief association of the sexes that plumage and displays of males reach their most extravagant development (Darwin 1871; Sibley 1957). The strut display of sage grouse provides a good example. Such extravagant signals are, from this point of view, adaptations for efficient communication with cautious receivers.

Conspicuousness

The inherent detectability of a signal depends on its conspicuousness, its contrast with spurious stimulation reaching the receiver. Even other types of signal constitute part of the background from which a receiver must distinguish a particular signal. Darwin (1872) recognised this point when he proposed his 'principle of antithesis' in behaviour: actions accompanying contrasting 'emotions' (values of internal state, in our present terminology) often have contrasting form (section 1.2.2). The examples in the preceding section reveal that conspicuousness of signals often accompanies complexity and stereotypy, aspects of redundancy.

Small repertoires and typical intensity

The theory of signal detection predicts that receivers do better, in the sense that they miss fewer detections for a given rate of false alarms, when they must classify signals into fewer categories. This theoretical prediction has been confirmed in psychophysical experiments on human subjects (reviewed in Wiley & Richards 1983). The smaller the repertoire of signals that a receiver must identify, the better is its performance. The results apply with great generality to signal detection, regardless of specific mechanisms, to animals as well as to electronic devices.

Small repertoires for communication in potentially noisy circumstances could explain variation in repertoire size among North American species of wren. In those species with dense populations in habitats occupied by few other passerines, such as marshes or desert, individuals have large repertoires of song patterns, sometimes over 100 (Kroodsma 1977). In comparison, individuals of those species with sparser populations in habitats with diverse avifaunas, such as forest or broken woodland, have relatively small repertoires. In this case, the greater average distance between territorial neighbours and the presence of additional species tend to make communication noisier.

The advantages of a small repertoire can also explain a striking feature of many displays—'typical intensity'. Displays with a typical intensity maintain a standard form over a range of a signaller's internal state, instead of varying with it (Morris 1957); typical intensity thus reduces information broadcast in a display. Fewer and more-distinct signals as a result of typical intensity in displays reduces ambiguity (Cullen 1966), but a clearer way to understand the effects on a receiver is to focus on the reliability of signal detection.

Rather than producing signals which vary in a complex way, in an effort to evoke varying responses from a receiver, it would pay when noise is a problem to produce one or a few standardised signals that would have a greater chance of reliable detection. Consider a situation in which a signaller would benefit from a prompt response by the receiver, perhaps recognition by its mate; promptness of correct recognition might be more important than the exact form of the response. The signaller would have to strike a balance between uttering a standard signal that would have greater chance of quick, correct recognition and uttering one of a number of possible signals that could evoke a more specific response but which might need repeating before correct recognition occurred. Typical intensity thus serves to improve the accuracy of detection and recognition of signals by a receiver.

Alerting signals

An alerting component at the start of a signal assists a receiver by specifying the interval of time during which it can expect to receive the remainder of the signal. The alerting component must have high inherent detectability, in other words little degradation during transmission and maximum contrast with the background. On the other hand, it need not encode much information about the signaller. For instance, it need not permit recognition of the individual or even of the species producing the signal. The subsequent message component, on the other hand, might well encode information about the identity and internal state of the sender. The receiver can thus set a relatively high threshold for response and still have a satisfactory level of correct detections in relation to false alarms. Once the alerting signal is detected, the receiver can then lower its threshold for the precise interval of time that the message component occupies. By knowing the time of onset of the message component, the receiver can detect and recognise it more reliably. Alerting signals thus permit a receiver to devote less time to being attentive to signals and more to other activities, such as foraging, without any significant reduction in its vigilance. From the sender's point of view, an alerting component increases the chances that a receiver will detect and recognise the message component of a signal (Raisbeck 1963; Wiley & Richards 1983).

Vocalisations used in territorial behaviour are signals that are produced intermittently but to which animals need to be constantly attentive. The territorial songs of many birds and the loud calls of some forest primates begin with a single tonal component and then become more complex in their acoustic structure. The introductory note seems ideally suited as an alerting component. Field experiments with rufous-sided towhees (*Pipilo erythrophthalmus*) have shown that the initial tonal component of the song (Fig. 5.3) evokes little response but does permit more reliable responses to subsequent, more complex components (Richards 1981b).

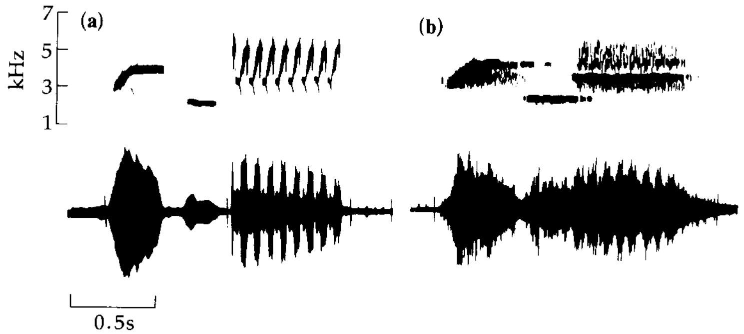


Fig. 5.3. Spectrograms (displays of sound frequency versus time) and oscillograms (displays of sound amplitude versus time) of a typical song by a male rufous-sided towhee illustrate the degradation of acoustic structure by reverberations which occurs during transmission of the song through woodland. The distinct notes of the song at the source (**a**, left) become run together by reverberation (**b**, right). The two clear tones that introduce the song are less severely degraded, however, than the trill of rapid glissandos at the end. These introductory tones serve as an alerting compoment, which serves to call a listening towhee's attention to the message component that follows. (From Richards 1981b.)

5.2.3 *Conclusion: Ritualisation as an adaptation for efficient communication*

A single display often incorporates several adaptations for improving a receiver's detection and recognition of signals. Redundancy by repetition and stereotypy, contrast with the background, and typical intensity often go together. Ethologists describe a display that shows these features as 'ritualised' (see section 2.2). These adaptations benefit a signaller by counteracting noise in communication. Noise, in the technical sense, can result from cautious receivers as well as from high levels of irrelevant stimulation or from degradation of signals in the external environment.

5.3 Communication as manipulation

5.3.1 *Selfishness of signallers and receivers*

So far we have concentrated on the ways in which a signaller can improve the effectiveness of a signal in evoking a response. The consequences of the response for the receiver's fitness must also be considered in an analysis of the evolution of communication. In general, it is clear that selection should favour responses to signals that raise the receiver's fitness, just as it favours production of signals that raise the signaller's fitness. Individuals, both when signalling and when responding, should tend to act in ways that increase their fitness.

Dawkins and Krebs (1978) developed a case for 'manipulation' of receivers in ways that increase the fitness of the signaller but not that of the receiver. Signals should not evolve, they argue, to 'provide information' to receivers but to induce them by any means possible to behave in a way that benefits the signaller.

Clearly, receivers should also evolve such 'selfish' tactics. They should not necessarily respond as 'directed', but should use information derived from the signaller's acts, in any way possible, to increase their own fitnesses. We can classify the four possibilities according to whether an association of signal and response increases or decreases the signaller's and receiver's fitnesses, (Table 5.1).

Signallers can manipulate receivers by employing deceit: signals conveying something incorrect about the signaller. If a male competing for mates could indicate that he was larger than his actual size, he might gain an advantage over his rivals; of course, his rivals would have to be fooled. The deceitful signaller in effect exploits the receiver's rules for decoding signals. If the existing rule relates a particular size of horns, for instance, to males of a certain level of fighting ability, then a male might gain by growing larger-than-normal horns and bluffing a rival. Alternatively, if the existing rule relates a certain plumage to females or young that do not compete for territories, a male might benefit by adopting this plumage and entering rivals' territories unchallenged for surreptitious feeding or even copulating. The possibilities for deceiving receivers thus depend on the receivers' current rules for translating signals into their responses. These rules need not, of course, be consciously recognised; they could result from any decoding mechanism that associates external stimulation from communication signals with particular responses.

Table 5.1. A 2 × 2 classification of communication based on Hamilton's (1964) classification of social interactions in general.

		Change in receiver's fitness	
		Increase	Decrease
Change in signaller's fitness	Increase	Mutuality	Deceit (manipulation by signaller)
	Decrease	Eavesdropping (manipulation by receiver)	Spite

Receivers can manipulate signallers by obtaining information about the signaller against its own best interests. Eavesdropping is a clear case: signals intended for one receiver are intercepted by another. For instance, a male's displays in courting a prospective mate might well attract rivals as well. In addition, it is reasonable to suppose that receivers might take advantage of any imperfection in deceit. After all, deception succeeds only when the signaller does not, in some other way, reveal its true nature. If such perfect control fails, then receivers have some chance of 'reading' the signaller's true state in spite of its attempts to mislead the receiver.

Thus manipulation in communication cuts both ways. Signallers might, in some circumstances, manipulate receivers as a result of constraints on the latter's responses to signals. On the other hand, receivers might also manipulate signallers as a result of constraints on the latter's production of signals.

In thinking about opportunities for manipulation in animal communication, analogies drawn from human interactions tend to dominate. For this reason, it is important to pay special attention to terminology. As in our previous discussions of information and noise, we have provided technical definitions for everyday terms, like 'deceit' and 'selfishness'. These familiar words make visualisation of technical discussions easier, but we must always guard against misleading inferences that can result from loose usage of technical terms.

Manipulation in communication between members of the same species also has parallels with some well-known interactions between species. Thus, deceit in intraspecific communication is paralleled by various forms of mimicry, bluff and feigning by prey in response to predators. On the other hand, predators and parasites often eavesdrop on signals inadvertently produced by their prey, or 'read' the vulnerability of individual prey from their actions or appearance. These analogies with human interactions and with predator–prey or parasite–host interactions suggest two considerations important for any study of manipulation.

5.3.2 *Relative rarity of deceiving signals*

First, misleading signals must occur only rarely in relation to correct ones. In other words, signals following the prevailing rule for encoding and decoding must predominate. Thus in Batesian mimicry, in which a palatable species of prey gains some protection from predation by resembling a distasteful or poisonous species, the mimics must occur infrequently relative to the models. Otherwise, predators would not reliably learn to avoid the mimicked stimulus. If receivers do not encounter misleading signals sufficiently infrequently in relation to correct ones, they should readjust their rules for decoding signals.

This conclusion needs some refinement, however, since in addition to the probabilities of each kind of event consideration must be given to the consequences for the receiver's fitness of responding to misleading signals on the one hand, or failing to respond to correct ones on the other. Imagine a fox that occasionally encounters a plover fluttering one wing on the ground. The plover might have a broken wing and thus provide a meal if the fox could catch it, or it might have a nest nearby and only feign a broken wing in order to distract the fox from the nest.

Should the fox adopt the rule 'stalk the bird', or the alternative, 'look for a nest', when it encounters an apparently crippled plover? Suppose the value of stalking, provided the plover really is crippled, equals $p_s \times w_s$, the probability of success when stalking times the amount of food obtained if the stalk is successful. Similarly, let the value of searching for a nest, provided the plover is pretending, equal $p_n \times w_n$, with symbols analogous to the first case. Finally, suppose a proportion f of fluttering plovers are really crippled, and the rest, $1-f$, are deceitful. Now, the yield to a fox that adopts the rule to stalk is $f \times p_s \times w_s$; the yield to one that adopts the rule to search for a nest is $(1-f) \times p_n \times w_n$.

Which alternative has the greater yield and thus will tend to confer the greater fitness? Stalking will be superior to nest-searching provided that

$$fp_s w_s > (1-f)p_n w_n$$

If $p_s = p_n$ and $w_s = w_n$, then f must exceed one-half for stalking to pay. In other words, more than half the fluttering plovers encountered must really be crippled. Conversely, sham fluttering only deceives foxes, in the long run, provided it occurs in the presence of foxes less often than the real fluttering of cripples. If $p_s \neq p_n$ or $w_s \neq w_n$, as is likely, other solutions result.

5.3.3 *Manipulation and information*

A second general point that needs emphasis is the distinction between information and manipulation. We have so far provided exact definitions of 'information' and 'manipulation'. In the tripartite system of an ethologist studying animal behaviour, with a signaller, a receiver and a nonparticipant observer, the transmitted information depends on the association between a signal and the receiver's behaviour. There is no distinction here between 'correct' and 'deceitful' signals. The observer can, in addition, determine the broadcast information in a signal about the sender's state or identity and could thus compare the broadcast information and the transmitted information, to determine whether or not the receiver uses the information available in a signal. The observer could also determine whether signals conceal important features of the signaller, by bluffing or mimicry for instance.

Manipulation, in any of its forms, depends entirely on the relative changes in the fitnesses of the signaller and receiver. It is independent of the definitions of transmitted and broadcast information. We have emphasised that selection should act on senders to increase the efficiency of transmitting information whenever the sender's fitness is increased by the response. Selection should act just as well on receivers to minimise this efficiency whenever the receiver's fitness is reduced.

In practice, many difficulties arise, not only in estimating amounts of information but also in estimating changes in fitness. Yet it is important to recognise that transmitted information, broadcast information and manipulation are three distinct features of communication. All three can in principle be estimated for any set of communicatory interactions.

5.4 Evolution of deceit

5.4.1 Deceit by signallers, retaliation by receivers

Mimicry or bluffing by signallers, as we have seen, depends on the receiver's rules for decoding signals into responses. Deceit occurs in effect when signallers can take advantage of the receivers' rules. Thus receivers can retaliate by a change in their rules. Two related possibilities exist:

(1) a devaluation or recalibration of the association of signals with responses; and

(2) use of supplementary signals for finer discrimination of the states or identities of signallers.

Inflation and devaluation of signals

Bluffing, deceit by inflation of a single cue (or a correlated complex of cues) for a response, leads to selection pressure on receivers to devalue the cue. If the size of antlers, for example, is a cue for overall size and fighting ability in rival males, then any bluffing by signallers which evolve larger-than-normal antlers stimulates selection for receivers to readjust their rule for decoding the size of antlers. Such a process tends to accelerate once started (Dawkins 1976b; Dawkins & Krebs 1979). After devaluation of a cue, all signallers that do not bluff are placed at a disadvantage. Furthermore, as the devaluation spreads among receivers, selection favours further bluffing, greater inflation of the cue. The escalation of signals and decoding finally ceases when further inflation of the cue becomes too costly or risky for signallers. In other words, the increased risk of predation or loss of opportunities to feed, for example, just balance any beneficial effects of bluffing on the signaller's fitness.

This sort of escalation of bluffing and devaluation could explain why many territorial birds have large repertoires of song patterns

(Krebs 1977). Suppose intruding males seeking openings for territories do best to avoid areas with high densities of established birds. If they judge the density of established birds in an area by the number of song patterns heard there, then resident males could bluff by each singing more than one song pattern. Escalation of the sizes of males' repertoires would ensue, as intruding males devalue the diversity of song patterns as an index of the density of established territories. More inflated bluffing would lead to more devaluation until the acquisition of larger repertoires became too costly, perhaps in terms of the time required for learning, in comparison with the benefits from fooling intruders.

Some experiments provide initial support for this idea. When male great tits (*Parus major*) are removed from their territories, reoccupation of the resulting vacancies by new males is delayed by tape-recordings broadcast in these areas (see section 1.4.1). Recordings that include many song patterns have a greater effect than those with fewer, suggesting that the number of song patterns heard in an area does indeed influence males deciding where to set up territories (Krebs *et al.* 1978; Yasukawa 1980). It is not clear yet how the sizes of repertoires influence intruders' behaviour. Repertoires might indicate the probable density of established territories or the probable fighting capabilities of individual territorial residents, or particular song patterns might differ in effectiveness (Krebs & Kroodsma 1980). The fact remains that any of these possibilities invites bluffing and consequent escalation of signals.

In the end, such escalated signals would no longer be deceptive once devaluation by receivers completely compensated for inflation of the signal by senders. Such costly, but no longer deceptive, signals might conceivably fall into disuse, since selection might favour substitution of less costly signals. These new signals would then lead to a new round of escalation by inflation and devaluation (Andersson 1982). On the other hand, there are some reasons to expect that selection might maintain costly honest signals, as we shall see below.

Increased discrimination by receivers

Bluffing and mimicry need not lead to escalation in the cost of signalling, however, when receivers can adopt countermeasures other than devaluation. Another way for receivers to counter misrepresentation is by increased discrimination among signals. Rather than devalue an unreliable cue, receivers should instead attend to additional cues or scrutinise signals in more detail. For example, some probing of a signaller's reactions might reveal its true mettle, even when some try to bluff. Of course, each additional cue or detail that a receiver examines is susceptible to the same possibility of escalation by inflation and devaluation. In some cases, this process would lead to exact imitation of a model by its mimic. However, particularly in intra-specific communication, the effects of multiple assessments by receivers presumably stop short of exact mimicry by deceitful signallers. After all, carried to the extreme, exact mimics must become indefinitely similar to the model. We must seek limits to the advantages of mimicry by signallers or, conversely, limits to the advantages of discrimination by receivers.

In some cases, there may be no advantage to signallers in indefinitely exact mimicry. Consider sparrows that compete for food in winter. In some of these species, younger individuals have duller plumage than older birds. An extreme example is Harris' sparrow (*Zonotrichia querula*) in which older males in winter have much more extensive black patches on their throats and breasts than do females and younger males (Fig. 5.4). Since older males tend to dominate other birds in contests over food, the size of a bird's black patch is a cue for its status. Experiments show that dying a pale bird's breast black, in order to increase its resemblance to a dominant male, also increases its success in competition with other subordinate birds (Rohwer 1977; section 1.4.3). Why then do not females and young males bluff by evolving larger black patches? The interactions of the disguised subordinates with dominant males provide an answer. The older, dominant birds persecute the dyed individuals. Evidently, they detect the disguised birds by their behaviour, perhaps by their reactions when challenged. If the disguised birds are also treated with the male hormone testosterone, then they can rise in dominance to equal even the true dominants (Rohwer & Rohwer 1978). Bluffing in this case would require changes in a signal indicating dominance, an extensive black patch, but also adoption of the behavioural reactions typical of a dominant. If the costs of acting like a dominant are too great in relation to the benefits so derived by a young individual, it would do better to avoid bluffing that requires such exact mimicry. In general, if the costs and benefits of achieving a particular social position differ for two individuals, it might not pay the inferior to mimic the other so closely that it must adopt most of its characteristics.

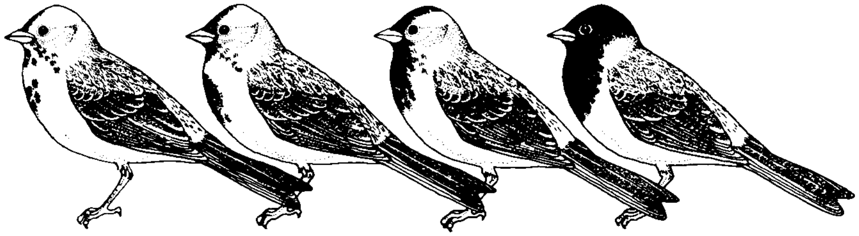


Fig. 5.4. The throat and breast feathers of Harris' sparrows in winter are unusually variable in colouration. The birds with more extensive black patches tend to dominate those with less black. Although the variation is almost continuous, older males tend to have more black than younger males and females. By painting some pale birds' throats black, Rohwer (1977) could create individuals that mimicked more dominant birds.

Increased discrimination by receivers might also incur disadvantages. A limit on discrimination would then permit the evolution of deceit by partial mimicry. Cases of males mimicking females, in order to take advantage of rival males, are good candidates here (see section 2.8.3). For instance, young male elephant seals (*Mirounga angustirostris*), like females, are smaller than the older males that defend harems. By behaving like females and mixing with the harems (Fig. 5.5), these young males can try to sneak copulations (Le Boeuf 1974). Although the harem masters expel them when detected, the level of vigilance and aggression necessary to exclude all sneaking males could well disrupt the harem enough for the master bull to lose many of the females. In these circumstances, a harem master should increase his level of discrimination (both detection and eviction) until any further increase results in more copulations lost as a result of disrupting his harem than gained as a result of evicting males that mimic females. An interesting complication here is provided by the females. By producing loud screams during copulation, especially with smaller males, they ensure that only the most dominant male within hearing normally completes copulations (Cox & Le Boeuf

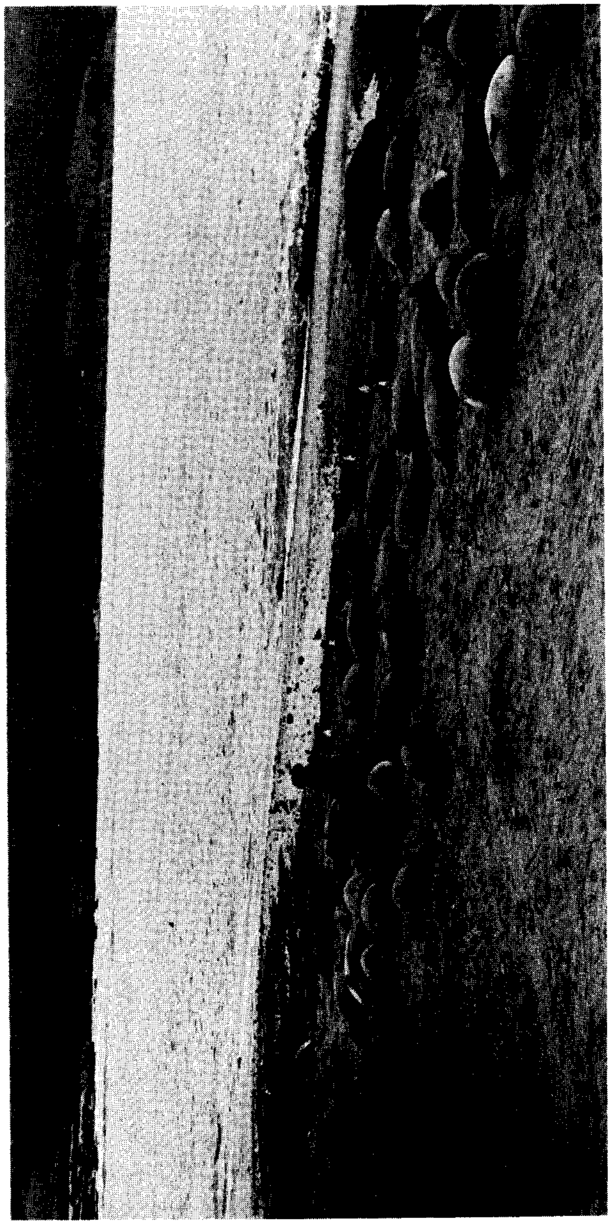


Fig. 5.5. A harem of elephant seals illustrates the predicament faced by the harem master, an old bull (centre, with his head and large proboscis raised). He attempts to guard the numerous females (smaller and lighter in colour) from the attentions of other males, including several younger males that hang around the periphery of the harem (somewhat larger and darker than the females, left edge and right background). Nevertheless, one young male has infiltrated the harem (right foreground). In response to a threatening call from the female next to the interloper, the harem master prepares to roar a warning. (Photograph by B.J. Le Boeuf.)

1977). In effect, they make the harem master's task of detecting and thwarting sneaky males easier.

Another example of males mimicking females is provided by the scorpionfly (*Hylobittacus apicalis*), in which males present females with a nuptial meal of a dead insect before copulation (Thornhill 1979). Sometimes a male hunts for and captures prey itself, but at other times he steals prey from other males. In the latter case, the thief sometimes mimics a sexually receptive female in such a way that the rival male gives up its prey. This ruse does not always work, as the duped male occasionally discovers his mistake and snatches the prey back. Here a male carrying prey must balance the advantages of increased vigilance against thieves against the advantages of responding quickly to receptive females. Too much probing of the credentials of apparent females might lose him prospective mates, a consequence of courting too slowly, while insufficient probing would lose him his nuptial offerings, a consequence of gullibility to female mimics.

In these cases of males mimicking females, receivers (the seal harem masters or the scorpionfly males carrying prey) are caught in a double bind: discrimination of deceivers from females has conflicting advantages and disadvantages. The net benefit of any level of discrimination or probing depends on the relative frequencies of mimics and models encountered. Probing should increase as the frequency of mimics rises and decrease as it falls.

5.4.2 *Unbluffable signals*

Bluffing, as we have seen, confers a disadvantage both on the gullible receiver and also on the honest signaller. We have considered how the receiver might evolve counteracting adaptations. Those honest signallers that serve as models might also evolve measures to avoid their exploitation by bluffers. For example, suppose size has an effect on the outcomes of fights. Then the largest individuals, which are exploited by the bluffing of smaller ones, would gain by evolving 'unbluffable' signals indicating size. For instance, a deep voice might be an unbluffable cue for size in toads (*Bufo bufo*) and other animals (Davies & Halliday 1978; Morton 1977). This is because the pitch of an individual's voice generally correlates with the size of its sound-generating structures in the larynx or syrinx, which in turn correlates with overall size. Phylogenetic or physiological constraints, one must assume, prevent evolution of the larynx or syrinx independently of the rest of the body.

Perhaps the clearest possibility for the evolution of unbluffable signals comes from the escalation of signals, by counteracting inflation and devaluation, to produce a signal that has become too expensive to inflate further. Signals should evolve by this process to become as expensive as the benefits permit. Honesty would accordingly entail a high price. It has even been suggested that signals should evolve to become a net handicap to signallers (Zahavi 1975), although this proposal seems unsound (Davis & O'Donald 1976; Maynard Smith 1976a).

5.4.3 *Conclusion: When can deceit persist?*

This section has compared three consequences of deceit in animal communication: escalation by counteracting inflation and devaluation of signals; mimicry limited by disadvantages of incidental consequences for the signaller; and mimicry limited by disadvantages of increased discrimination by the receiver. Selection on signallers in some cases favours inflation of signals by bluffing, but in other cases favours the use of unbluffable signals. Selection on receivers faced with inflated signals favours devaluation or increased discrimination of signals, although there are sometimes limits to the advantages of increased discrimination.

The outcomes of the three scenarios listed above are not easy to predict exactly. The first, escalation, would often lead to costly but honest signals. Once bluffing became too costly, no further deceit would occur. The second scenario for the evolution of deceit, mimicry limited by disadvantages to the signaller, would also lead to universally honest signals, provided receivers could match any deception with increased discrimination. In contrast, the third scenario, mimicry limited by disadvantages of increased discrimination by the receiver, results in the indefinite persistence of deceitful signals. The advantages of increased discrimination tend to increase as mimics increase in frequency and to decrease as mimics decrease. The level of discrimination by receivers reaches a stable compromise depending on the relative frequency of deceivers encountered by a receiver.

5.5 Communication in contests

5.5.1 *Withholding information*

Withholding information about identity or internal states is sometimes the best course to take. Clearly, signallers attempting to deceive receivers should withhold as much information as possible about their true condition. Likewise, signallers susceptible to eavesdropping by competitors or rivals should direct signals as narrowly as possible to intended receivers.

Theoretical analyses of strategies for fighting also suggest that individuals should often withhold information about themselves. It is important to emphasise that 'information' as used here is broadcast information, which an observing ethologist might receive. In fights, individuals are of course selected to act in ways that influence their opponents' behaviour, in other words to transmit information, as effectively as possible. Broadcast information is another matter, though. Recent analyses of the actions of birds and fish in competitive interactions suggest that displays in contests are in fact generally poor predictors of an individual's following actions or the outcome of a fight (Caryl 1979). In other words, the level of broadcast information for these displays is low.

One possible interpretation of such findings is that ethologists have not yet detected all of the broadcast information, since it is likely to be complex or subtle (Hinde 1981; van Rhijn 1980). It seems clear that competing individuals should never volunteer unconditional information about their next move, except perhaps before surrender or retreat. The element of surprise or the possibility of negotiation preclude any advantage for signals providing unconditional information. The analogy with human combat and diplomacy is persuasive.

Providing more complex information, on the other hand, could well have advantages. Particularly likely here is information about contingent behaviour: a signal that indicates the likelihood of particular responses following a move by the receiver. Possibilities include signals that indicate commitment to retaliate if the receiver attacks or to withdraw if the receiver withdraws. A signal indicating 'I will fight if and only if attacked' would particularly assist an individual defending a territory or mates. Such complex predictions about a signaller's future actions have possibly escaped the attention of ethologists.

5.5.2 *Bluffing as an initial strategy*

Another possible explanation for the apparent lack of broadcast information in contests is bluffing. In human bargaining, in the absence of perfect information about the opponent's intentions and resources, it usually pays to demand more than one expects from an opponent or to threaten more than one can deliver. The same seems reasonable in contests between nonhuman animals (Maynard Smith 1974; Maynard Smith & Parker 1976). Individuals should initiate confrontations with threats of maximum intensity, within the bounds of the receivers' gullibility.

This case nicely fits our third explanation for the persistence of deceit: disadvantages of increased discrimination by the receiver. At least when contestants differ only slightly, time presumably limits possibilities for accurate discrimination of abilities at the outset of contests. Rapid judgments of an opponent carry risks of unnecessary withdrawal or premature attack, the latter with consequent chances of injury. Thus mutual bluffing and cautious response make good initial strategies and would result in little broadcast or transmitted information. Once contestants begin to feel each other out, in other words learn more about each other's capabilities, then a contest can proceed to a resolution. Contests between female Siamese fighting fish (*Betta splendens*) fit this pattern (Simpson 1968).

The problem of assessing opponents' capabilities should be greatest when contestants are most similar; consequently, contests between well-matched individuals should require the longest time for settlement. Observations of fighting animals tend to support this expectation (Riechert 1978; Sigurjónsdóttir & Parker 1981).

Bluffing at the outset of a contest also provides an explanation for typical intensity of displays (Maynard Smith 1974; Maynard Smith & Parker 1976). In fact, this explanation and our earlier one, based on adaptation for efficient signal detection in a noisy environment, do not conflict. As noted, an opponent at the outset of a contest is likely to respond cautiously, introducing noise to the communication channel (section 5.2.1). Signals in this case should evolve redundancy, conspicuousness and typical intensity.

5.5.3 *Uncorrelated asymmetries*

Is there ever an advantage to contestants that respond to signals conveying no information whatever about the sender? In theory, this is a possibility. Imagine encounters between two individuals that are indistinguishable so far as they can themselves detect, except for a clear difference that has no relation to their respective fighting abilities or their rewards for winning or losing. Such a difference is termed an 'uncorrelated asymmetry'. Suppose further that any individual is equally likely to have either of the arbitrarily determined characteristics, A and B. In such encounters any two opponents do best to decide the outcome solely on the basis of this difference, by an arbitrary rule that the animal characterised by either A or B wins (Maynard Smith 1974, 1976b). Thus a signal with no information about the state of the sender would still have a predictable effect on the receiver, in the long run to the mutual advantage of each contestant. The obvious human example of this kind of behaviour is tossing a coin to decide a contentious issue.

It has been suggested that residence on a territory could provide such an arbitrary signal, with 'owner wins' the arbitrary rule for deciding encounters between owners and intruders. It seems doubtful, however, that ownership of a territory is often a completely arbitrary asymmetry. The stronger or older individuals often get territories in the first place, or residence on a territory might increase an individual's size or strength by providing a reliable source of food, or a territory might become more useful with time as a resident learns the terrain. In each case, ownership would correlate with superior fighting abilities or greater rewards for winning. It is likely to be difficult to determine whether or not fights between animals are ever decided solely on the basis of an arbitrary signal, but one species in which they seem to be is the speckled wood butterfly (*Paraage aegeria*), contests over occupation of territories being settled by an 'owner wins' ruling (Fig. 5.6). The territories defended by these butterflies are of very little value; they contain no resources and, being patches of sunlight, they are highly ephemeral. Furthermore, the delicacy of their wings would make any more severe form of fighting very costly (Davies 1978).

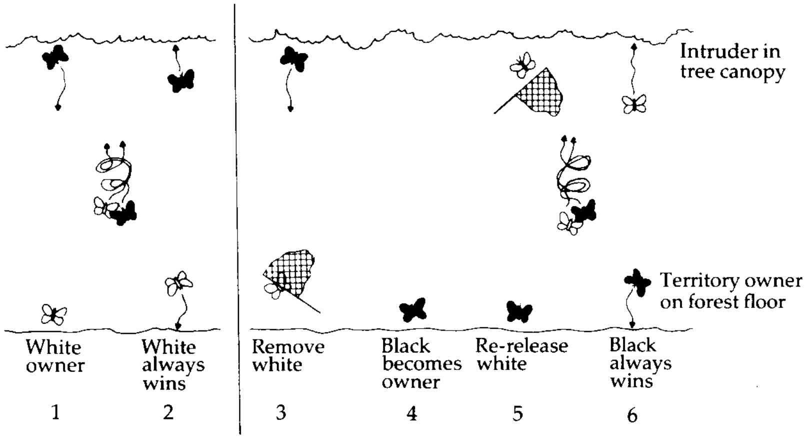


Fig. 5.6. Territorial behaviour in the speckled wood butterfly (*Paraage aegeria*): 1 and 2: when an intruder (black) enters a territory, there is a brief interaction involving a spiral, upward flight, at the end of which the resident (white) always retains his territory. 3–6: if the original resident is experimentally removed, a new butterfly quickly becomes the resident and subsequently wins contests with intruders. (From Davies 1978.)

5.5.4 *Contests with no information*

When opponents lack any information about each other, even about arbitrary differences, some clear hypotheses result. Imagine contests that are settled by which opponent persists longest. The opponents' costs, we can assume, increase in proportion to the duration of the contest. Suppose that opponents, who know nothing of each other's intentions, select their duration of maximum persistence in advance of each contest. Then whoever has selected the longer time wins. This is the 'war of attrition' (Maynard Smith & Parker 1976; Maynard Smith 1974, 1976). Clearly it does not pay for an animal to adopt a strategy of fighting for the same duration in all fights. It would always lose to individuals that fought longer. It turns out that an evolutionarily stable strategy, one that cannot be invaded by mutants with any other strategy, involves selecting a maximum persistence (and a corresponding maximum cost) from a negative exponential distribution. Either each individual can select a new persistence for each fight or individuals with the same genotype can nevertheless differ

consistently in persistence, so long as persistences fit the required distribution.

This argument leads to the prediction that the duration of fights, like the preselected persistences, should fit a negative exponential frequency distribution. In fact, the durations of fights in several species do fit this prediction. One might be tempted to conclude that animals fight wars of attrition on the basis of no information about opponents. However, in a carefully analysed case the evidence does not support this conclusion. In fights between male dung flies (*Scatophaga stercoraria*) over females (Parker & Thompson 1980; Sigurjónsdóttir & Parker 1981), the durations of fights fit the predicted distribution, but this is for some other reason. There is clear evidence that opponents do acquire information about each other. Smaller males usually withdraw, for instance, and prior possession of a female also confers an advantage.

If a complete absence of broadcast information in signals seems improbable, even in fights, signals that completely specify opponents' characteristics are equally unlikely. The problem is that animals fight too much for this possibility to hold up. If opponents have complete and accurate information about each other's fighting abilities and the rewards from winning or losing, then no fight should ever occur; the inferior or less-committed animal should withdraw before any contest escalates to a fight (Parker 1974; Maynard Smith 1979; Parker & Rubenstein 1981). Animals clearly do fight, often frequently and severely.

In view of this discussion, it seems likely that animals often do obtain information about opponents during contests, although initially only incomplete or contingent information. Opportunities for bluff are also clear, but otherwise the role of signals that broadcast no information about the sender remains elusive.

5.6 Evolution of simple honesty

5.6.1 *Mutuality and competition*

Communication, we have seen by now, takes both mutualistic and competitive forms. In some situations, it has advantages for both sender and receiver; in others, one can take advantage of the other. Honesty in signalling can result from competition, as discussed above, either by counteracting escalation and devaluation of signals or by limitations on the advantages of deception for signallers. These forms of honesty require either high costs for escalated signals or special limitations on deception. What about simple honesty? Can signals evolve so that they broadcast information about the signaller without escalation or special limitations on deception? For the evolution of this form of honesty, mutualistic cooperation rather than competition provides the most straightforward explanation. It is thus important to consider the circumstances which favour the evolution of mutuality in communication. In particular, we must ask whether mutuality can evolve even when manipulation has advantages for the signaller or receiver, as so often happens in communication.

Kin selection provides one way in which mutuality in communication can evolve. Kin selection results from the presence of the same genes in related individuals, by virtue of their descent from a common ancestor. An individual that manipulates a close relative to increase its own survival or reproduction also has a certain probability of reducing the survival and reproduction of the same genes in the relative. Manipulation of relatives is thus not always favoured by selection, depending on how close the genealogical relationship is and on the benefits to the signaller and the costs to the recipient.

5.6.2 *The Prisoners' Dilemma*

In the case of unrelated individuals, evolution of mutuality is best analysed by means of game theory. In such analyses, the net benefits to an individual (expected changes in its fitness) depend both on its own strategy and on the strategy played by its partner. Our discussion has emphasised how characteristic this dependence is for communication. The benefits of deceit depend on whether receivers are gullible or discriminating. The benefits of devaluation or discrimination depend on whether or not the sender is deceitful or honest.

When manipulation has advantages for signallers or receivers, it seems at first that mutual cooperation, simple honesty in signalling and trust in receiving, cannot persist. A population comprising only honest signallers and trusting receivers invites invasion by mutant individuals with tendencies for deception, since deceitful signallers gain in interactions with trusting receivers. This deceit in signals creates an advantage for discriminating or devaluing receivers. Unless there are limitations to the advantages of deceit or discrimination, as discussed above, a population would eventually contain only mimics and discriminators or bluffers and devaluers. Such a population could not be invaded by mutant individuals with tendencies for either honesty or trust.

Table 5.2. The pay-offs for two individuals, A and B, who can adopt either of two strategies, cooperating and defecting. In each cell, the first symbol represents the pay-off to A, the second that accruing to B.

		Individual B	
		Cooperating	Defecting
Individual A	Cooperating	P, P	S, R
	Defecting	R, S	T, T

Yet there is a dilemma. The net benefits to individuals in a population of deceivers and sceptics are lower than those in a population of honest and trustful individuals. This situation suggests comparison with the Prisoners' Dilemma of game theory, named after the situation facing hypothetical prisoners who can escape only by cooperating with each other but who can obtain leniency by defecting to report their comrades to the authorities.

The Prisoners' Dilemma permits formal treatment as follows. Imagine two strategies, Cooperating and Defecting. Each individual can select either strategy, either permanently or for each separate interaction. The rewards to an individual then depend on both its own and the partner's strategy. Each cell in Table 5.2 presents the reward (called pay-off in game theory) for two individuals. Note that the players have symmetrical roles: when one defects and the other cooperates, the pay-offs to the defector and cooperator are the same regardless of which individual plays which role.

The Prisoners' Dilemma exists when $R>P>T>S$. When others cooperate, it pays to defect ($R>P$). When others defect, it still pays to defect ($T>S$). Yet the rewards of defecting among other defectors are not so great as those of cooperating with other cooperators ($P>T$).

An evolutionarily stable strategy for this game is to defect. No matter which strategy the partner selects, an individual that defects always does at least as well as its partner. In fact, whether this game is only played once between any two partners, or whether it is played any predetermined number of times, defecting appears to be the only evolutionarily stable strategy (Rapaport 1960; Rapaport & Chammah 1965; Axelrod & Hamilton 1981).

The situation changes, however, when partners play an indeterminate number of times. When there is always a possibility for at least one more interaction between any two partners, the strategy called 'tit-for-tat' can prevail. This strategy is a conditional one: in any particular interaction, an individual cooperates if its partner cooperated in the previous interaction, but defects if its partner defected previously (Axelrod & Hamilton 1981). Thus, particularly if partners occasionally test each other's willingness to cooperate, any two partners tend to lock into cooperative interactions and avoid the pitfall of mutual defection.

This result has two prerequisites: individuals must remember their partners in interactions, and any two partners must interact an indeterminate number of times. Such conditions are probably met by many communicating individuals. Among birds, territorial neighbours and long-term mates are obvious candidates. Individual recognition is well documented for both these cases in birds (Falls & Brooks 1975; Wiley & Wiley 1977; Jouventin *et al.* 1979; Moseley 1979). Communication within stable social groups, such as primate or canid groups or birds that defend group territories, could also clearly meet these criteria.

5.6.3 *Cooperation and defection in communication*

How closely, though, does deceit in communication fit the basic model for the Prisoners' Dilemma? In communication, signaller and receiver do not always have symmetrical roles. It is true that roles can change reciprocally, as often occurs in interactions between territorial neighbours. Other cases of communication, for instance between mates, do not always have even such long-term reciprocity. Is strict symmetry necessary for the preceding analysis to hold?

Imagine a game of communication with interactions between a signaller who can produce either honest or bluffing signals and a receiver who can either trust or devalue these signals. By analogy with the example above, we can tabulate the pay-offs from each of the four possible kinds of interactions as in Table 5.3.

Table 5.3. The pay-offs for two communicating animals, one of whom can be an honest or bluffing signaller, the other a trusting or devaluing receiver. In each cell the first symbol represents the pay-off to the signaller, the second that accruing to the receiver.

		Receiver	
		Trusting	Devaluing
Signaller	Honest	P, P′	S, R′
	Bluffing	R, S′	T, T′

Here we have distinguished between pay-offs that we previously assumed to be equal. In the present game, signaller and receiver do not necessarily have symmetrical roles. Hence the receiver's pay-offs are identified by primes.

How are these pay-offs related for each individual? Take the signaller first. We can easily imagine that $R > P$: deceit pays when your opponent is trusting. Furthermore, $P > S$: an animal is at a disadvantage when opponents devalue its signals, for example by reacting as if the signaller is smaller than it actually is. Also, $P > T$, provided bluffing signals are more costly or risky than honest ones, as discussed above. Finally, $T > S$, since signallers would presumably do best to bluff when receivers devalue signals. In summary, a signaller faces a situation rather like the Prisoners' Dilemma: $R > P > T > S$.

For the receiver, clearly $P' > S'$: a trusting receiver loses when an opponent is deceitful. Also, $P' > R'$, provided there is some advantage in recognising a dangerous opponent for what it is. Reacting to a large opponent as if it were small might well incur some risk. This relation deviates from the Prisoners' Dilemma. Furthermore, $P' = T'$: a receiver does not suffer a disadvantage from escalation of a signal by bluffing and devaluation. Finally, the relationship of S' and R' depends on the balance of different disadvantages. In summary, a receiver faces a situation quite different from the Prisoners' Dilemma: $P' = T' > S'$ and R'.

Nevertheless, the outcome of this game might not differ substantially from that of the Prisoners' Dilemma. In a population of trusting receivers, it clearly pays for signallers to become bluffers (R > P). Yet when bluffers appear, it pays for receivers to become devaluers (T′ > S′). If T > S, the population would reach an evolutionarily stable state with all signallers deceitful and all receivers devaluers. Like the Prisoners' Dilemma model, the defecting strategies are not open to invasion by the alternatives.

When two individuals play this game of communication repeatedly, it is possible that 'tit-for-tat' could prevail, as it does in the Prisoners' Dilemma. Note that the receiver can do no better than P′, the pay-off when honesty and trust prevail. Thus there is no incentive for the receiver to defect. If a signaller tries deceit, the receiver can switch to devaluing for the next interaction, so the signaller does worse than when honesty and trust prevail (P > S and T). Thus tit-for-tat in responding might make simple honesty in signalling an evolutionarily stable strategy.

What purpose can such abstract discussion serve in understanding actual communication among animals? First, it identifies some sufficient conditions for simple honesty in signalling and trust in receiving: there must be repeated interactions over an indeterminate period between acquainted individuals. Secondly, it emphasises that the evolution of signallers' and receivers' behaviour depends on a large number of parameters. There are eight pay-offs (changes in fitness) for the four kinds of interaction. The relationships among the pay-offs in the above example for a game of communication might not apply to other possibilities for deceit, such as mimicry countered by increased discrimination by receivers. In addition, the relative frequency of each strategy in a population influences the evolution of signalling and receiving when each individual interacts with many others. None of the examples that have been suggested as involving deceitful communication has considered all the parameters necessary for a full evolutionary analysis.

5.6.4 *Bluffing and ritualisation*

Simple honesty, as we have just seen, is favoured between acquainted individuals that interact repeatedly. Previously we saw that unritualised signals are likewise favoured between acquainted individuals, particularly at close range. In contrast, ritualisation and escalation by bluffing and devaluation should both evolve more often for interactions between unacquainted individuals.

Thus, the same conditions that favour trust and simple honesty in signalling also favour lack of ritualisation.

When we recall that a cautious receiver creates noise in communication, an association of bluffing and ritualisation in signalling on the one hand, and of simple honesty and lack of ritualisation on the other, makes good sense. Bluffers faced with cautious receivers need to use every trick to elicit a response, including redundancy, conspicuousness, and typical intensity. Ritualised signals are just the sort that bluffers should use.

5.7 **Rules in communication**

A theme that runs through all sections of this chapter is the importance of rules in communication. Rules for encoding and decoding have a central place in communication for the basic reason that signals do not provide the power to produce responses directly. Every signal influences the behaviour of a receiver as a result of neuronal decoding mechanisms in the receiver that associate the stimulus of a signal with responses or changes in internal state. The encoding of a signal similarly results from mechanisms in the sender that associate internal states with actions or external changes that produce signals.

These mechanisms in the sender for encoding signals and in the receiver for decoding them do not evolve independently. Regardless of whether communication is mutualistic or manipulative, the consequences of a communicative interaction are determined by the relationship between encoding and decoding. The consequences for a sender of producing a particular signal in a particular situation depend on the receiver's mechanism for decoding that signal into responses. Likewise, the consequences for a receiver of responding to a signal in a particular way in a particular situation depend on the sender's mechanism for encoding that signal. Deceitful signalling, we have seen, takes advantage of the receiver's decoding mechanisms, and eavesdropping by receivers exploits the sender's encoding mechanisms. This interdependence of encoding and decoding mechanisms in determining the consequences of any communicatory interaction gives the evolution of communication its peculiar complexity.

This interdependence also justifies our recognition of rules in communication. Rules are simply descriptions of the coordination of prevailing mechanisms for encoding and decoding. Philosophers of human language in this century have placed much emphasis on rules of usage. Some, like Ludwig Wittgenstein (see Fann 1969), have emphasised that rules are not a private invention of any one mind. Instead, they result from the coordinated usage of language by a community of people. These rules of usage often cannot be explicitly formulated within the language itself; indeed, it is even difficult to enumerate all rules for the usage of a particular expression.

Coordination of encoding and decoding results in rules of usage for any system of communication. Our analysis of animal communication has shown that rules are just as central here as in human language. Furthermore, rules are as essential for manipulation of receivers by deceit as they are for mutualistic communication, since deception results from infrequent violations of established rules.

Our conclusions about evolution, however, leave open the question of the mechanisms for the development of encoding or decoding in an individual's lifetime. In fact, remarkably little is known about the ontogeny of usage, either encoding or decoding, in animal communication (for an example, see Seyfarth & Cheney 1981). Philosophers of language rightly presume that the usage of language by humans develops predominantly by learning. When they apply the term 'conventional' to rules of usage, they suggest both that rules are arbitrary, in lacking any necessary form, and that they are acquired by learning within a community of users.

For nonhuman animals, the entire question of the interactions of genes and experience in the development of rules of usage has hardly been addressed. Although we have seen how the encoding and decoding of signals evolve in synchrony, as a result of the central importance of rules in any system of communication, it is important to realise that this coordination might arise in very different ways in the ontogenetic development of individuals.

5.8 Selected reading

A very thorough review of evolutionary and other aspects of communication is provided by Green and Marler (1979). Parker (1974) develops the idea that, during aggressive interactions, animals use displays to assess the fighting ability of their opponents and use this information in deciding whether to terminate or continue a dispute. Maynard Smith (1976b) provides a concise account of the application of Games Theory to animal behaviour. He argues that, in interactions between two animals, there will usually be some conflict of interest and that what is best for one animal to do will depend on what the other does. These ideas are discussed by Caryl (1979) who suggests that they depart from a traditional ethological view that communication evolves for the mutual benefit of signaller and receiver. In a reply to Caryl, Hinde (1981) argues both that Caryl misrepresents many early ethological interpretations of communication, and that there is currently too much emphasis on the idea that communication is a means by which one animal may exploit or manipulate another, a view developed by Dawkins and Krebs (1978). The evolution of cooperative behaviour on the basis of reciprocity is discussed by Axelrod and Hamilton (1981), who analyse the Prisoners' Dilemma game outlined in this chapter. A critical discussion of the various ways that the word 'information' has been used is provided by Wiley and Richards (1983).