5

The evolution of signal form

So far, we have had rather little to say about the form of signals. In Chapter 2, we were concerned primarily with the cost of producing a signal, and the relation between the cost and reliability of the signal, but its form was ignored. In contrast, the form of an index, discussed in Chapter 3, is crucial, since an index only works if its intensity is causally tied to the quality being signalled. But many signals are not indices; we now turn to various ideas that have been proposed to explain their form.

5.1 Ritualization

Most signals probably evolved by the ritualization of cues that other individuals were already using to gain information (Chapter 1). The idea of ritualization has two aspects. First, the origin of a signal in a pre-existing cue, and second, the fact that the signal is often more stereotyped and repetitive than the original cue: we discuss these two aspects in turn.

Morris (1956) divided the cues that one animal might provide to another into those resulting from changes in physiological state and those that are behavioural. There are a variety of physiological responses that appear to have provided cues that have been ritualized into signals. In all the following examples the hypothetical cue was under the control of the autonomic nervous system:

1. *Thermoregulation.* Birds and mammals raise and lower their feathers or hair to help control their body temperatures. Usually their plumage or pelage is slightly raised away from the body, trapping an insulating layer of air. If the feathers or hair are erected, however, this layer is lost and heat is dissipated. Social interactions must often involve an increase in body temperature as a result of increased activity. There is thus scope for changes in feather and hair posture to provide cues suitable for ritualization into signals. Although many displays do indeed involve dramatic changes in feather or hair erection (e.g. Andrew 1972), it remains unclear how many evolved in this way. In particular, by erecting its feathers or hair in a display an animal makes itself appear larger. Thus, this component of the display may be an 'exaggerator' (as discussed in Section 4.1) of body size. If so, receivers would have been trying to evaluate body size rather than using thermoregulatory changes as a cue to increased body temperature.

2. *Respiration.* The increased activity likely in many social interactions may prompt an increased respiration rate. Rapid breathing might be loud enough to provide a cue that can be ritualized into a call. Similarly, the associated movements may provide the raw material for signals. For example, many fish displays highlight the gill covers which are often coloured or decorated with protuberances.

3. *Urination and defecation.* Extremely frightened mammals often relieve themselves. The use of urine and faeces to mark territory boundaries might have evolved from this because territory owners relieved themselves with fear at the edge of their range but were willing to fight intruders (Lorenz 1970). On the other hand, this is not the only possible explanation. Mammals have to relieve themselves at intervals, whether frightened or not. If potential intruders began to use urine and faeces as a cue that an area was occupied, it might pay owners to relieve themselves at territory boundaries.

4. *Pupil dilation.* The diameter of the pupils in the eyes does not vary only with light levels. For example, an African Grey Parrot constricted her pupils when saying a word that she had learned and when she heard the same word spoken (Gregory and Hopkins 1974). Humans are unconsciously aware of this cue in other individuals, assessing dilation of the pupils as a friendly gesture (Hess 1965). Women have in the past exploited this fact by adding drops of belladonna (an antimuscarinic drug) to their eyes to dilate their pupils. A side-effect of belladonna is that it inhibits the lens muscles of the eye and so increased attractiveness to men may have been accompanied by reduced discrimination of their suitors. The size of the pupil is more obvious if the surrounding iris is pale. Iris colour often varies between birds of the same species, but of different age or sex. For example, female Galahs (an Australian cockatoo) have pink irises against which their pupil diameter is easy to assess. Males, however, have very dark irises, almost as if they are trying to conceal their pupil diameter (Rogers and Kaplan 1998): the meaning of these signals is unknown.

5. *Yawning.* This is a puzzling case. In primates, the yawn is a signal of aggression. This makes good sense—the yawn bares the canine teeth, and may well have originated by ritualization. But what of human yawns? They are certainly not signals of aggression. There is evidence that yawning is unrelated to prior amount of sleep, but that it acts to maintain or increase arousal when the environment provides little stimulation (Baenninger 1997). This suggests that, as our ancestors ceased to use their teeth to fight with, the yawn ceased to be a signal that had an obvious, iconic meaning (although it is not clear why it could not continue to function as a symbol of aggression), and which was, therefore, free to acquire a physiological role. However, the human yawn may still have some role as a signal: like laughter, it appears to be infectious.

The range of behavioural cues that seem to have been ritualized into signals is as diverse as that of physiological cues. For example:

1. *Intention movements.* Before birds take off, they often crouch down on flexed legs, withdraw their head and raise their spread tail. The legs are then straightened, launching the bird into the air as it opens its wings. If a human or a predator slowly

approaches a bird, it may make several 'false starts' before fleeing. The movements could, therefore, act as a cue that the individual is likely to take off. Many species make such intention movements before leaving a flock without being disturbed; if they do so their companions usually ignore their departure, but if they do not the flock often flees in panic.

A wide variety of displays seem to be derived from these flight intention movements (Andrew 1956). Sky-pointing by gannets, boobies and some of their relatives (Fig. 5.1) is a well-studied example (van Tets 1965; Kennedy *et al.* 1996). In the Atlantic Gannet, the display precedes take-off from the nest site: the bird stretches its neck, pointing its bill vertically, while slightly moving its wings away from the body and lifting its feet alternately from the ground. Among boobies, however, sky-pointing occurs during courtship and is more complicated. The most extreme version is that of the Blue-footed Booby: the wings are opened and rotated at the shoulder so that their upper surface points forward and the tail is cocked until it also leans forward. The posture is so distorted that the outstanding ethologist Michael Cullen initially thought that it was mythical (Nelson 1978). As the displaying bird moves away, it raises its feet in a highly exaggerated manner, flaunting their bright blue webs. Thus, as Krebs (1987) said of ritualization in general, 'an ancestral dither may have evolved into a dance akin to that of a whirling dervish'.

2. *Protective movements.* When approaching each other primates often flatten their ears, retract their scalp and partially close their eyes. These behaviours, which tend to be most marked in subordinates, seem best interpreted as protecting vulnerable parts of the head. In some species these protective movements seem to have been ritualized into signals. For example, in many Ceboid and Cercopithecoid monkeys scalp retraction exposes brightly coloured skin under the eyebrow ridge (Andrew 1963).

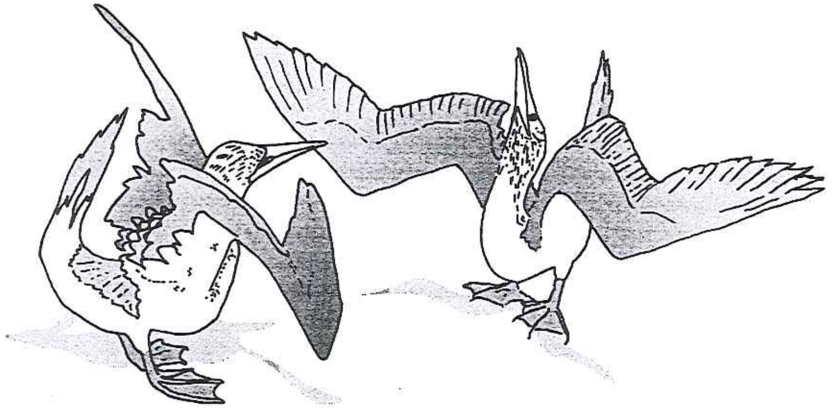

Fig. 5.1 Ritualized flight intention movements in the Blue-footed Booby (from Cramp and Perrins 1994).

3. *'Displacement' behaviour.* Animals often interrupt one behaviour with another apparently irrelevant one. We agree with Dawkins (1986) that the term 'displacement' is unfortunate because the behaviour might be a relevant one misinterpreted by the observer. The behaviours are however very striking and tend to occur when the animal appears uncertain what to do or is thwarted from doing something. For example, a European Robin encountering a large beetle may dither beside it as if unsure whether to attack or flee, and then briefly preen itself. Bird feeders in which the food is temporarily unavailable induce similar behaviour. Social interactions provide many opportunities for a conflict within an individual about whether to approach or flee or for an individual to become thwarted.

Lorenz (1970) argued that 'displacement' preening during courtship had become ritualized into some of the mating displays of ducks. Such preening is often made more conspicuous by being targeted at colourful feathers. These often form a speculum—a panel on the upper surface of the secondary flight feathers—with a species-specific colour pattern (females usually have a duller version). For example, that of the Mallard is iridescent blue, bordered by white bands. Courting males expose their speculum and place their beak behind the wing as if preening. In some species the speculum is exaggerated in size because adjacent feather tracts are the same colour. For example, the iridescent blue-green greater coverts and tertials of Wood Ducks roughly double the size of the colour patch. Males of the closely related Mandarin Duck have a normally sized speculum of a similar colour to that of Wood Ducks, but have a greatly elongated central tertial feather which can be erected during courtship. The male mock-preens by placing its bill behind the sail, which then appears contiguous with the large orange patch on their cheeks, which are adorned with elongated feathers.

Turning now to the kinds of change that occur, ritualized signals differ from cues in four main ways (Wiley 1983; Johnstone 1997): they tend to be more conspicuous, redundant, and stereotyped, and they are often preceded by alerting components. We will illustrate each of these features in turn and then assess what, if any, light they shed on signal evolution.

1. *Conspicuousness.* Signallers depend on receivers being able to detect their signals, so it is unsurprising that ritualized signals tend to be more conspicuous than cues.

2. *Redundancy.* This can involve simple repeating a signal or giving complex displays containing many elements. Both types of redundancy are well illustrated by the courtship display of Musk Ducks (Fig. 5.2). Males raise their spread tails and bend their heads back, exposing a grotesquely large flap of skin under their bill, while

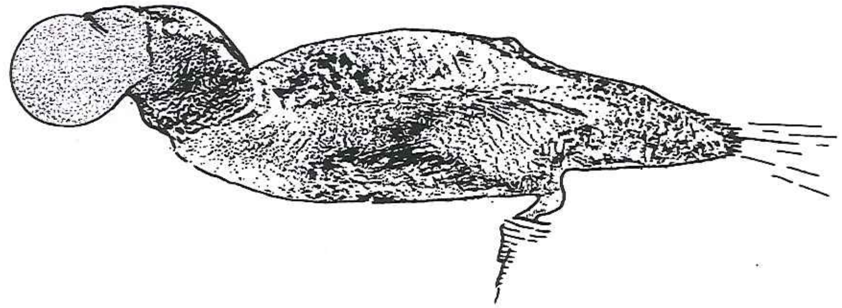

Fig. 5.2 Courtship display of male Musk Duck *Biziura lobata*; after del Hoyo *et al.* (1992).

splashing noisily around in the water with their feet. They give shrill whistles and loud grunts, the latter being accompanied by vigorous up-and-down pumping of the head with a raised crest. There may well be an olfactory component to the display as well: as noted by Darwin (1871), during the breeding season male Musk Ducks stink, hence the common name.

3. *Stereotypy.* Many displays are remarkably stereotyped. Courting male Common Goldeneyes repeatedly give Head-Throw displays. Each display starts with the head held low, almost on the bird's shoulders, and consists of three movements: (a) the neck is then extended vertically; (b) the head is flung backwards until the nape touches the rump; (c) the head moves forward to its starting position. Despite this complexity, Head-Throws vary little in duration with 95% lasting between 1.13 and 1.44 s (Dane *et al.* 1959).

4. *Alerting components.* Many visual signals start off with conspicuous movements; for example, head-bobbing in many lizards begins with fast movements of large amplitude, but is concluded by more subtle, species-specific movements (Fleishman 1992). Similarly, vocalizations are often preceded by loud calls or other sounds: in Section 7.6.4, we describe how male orang-utans sometimes introduce their calling displays by pushing a large piece of dead wood out of a tree, making a loud crash.

These four features of ritualized signals tell us rather little about signal evolution because they can be explained in several ways. Thus, Zahavi (1977) overstated the case when arguing that signals evolve as they do because ritualization increases costs and so ensures honesty. In this context, stereotypy might provide a standardized situation in which subtle differences between signallers become more obvious; an analogy would be the way in which athletes are asked to undertake the same task rather than being allowed to choose how to demonstrate their speed or strength. Ritualization could, however, have entirely different functions, to which we now turn: it may increase signalling efficacy (Section 5.2), or the ability of signallers to manipulate receivers (Section 5.3).

5.2 Efficacy

The term 'efficacy' was introduced by Guilford and Dawkins (1991), in a paper drawing a distinction between two design requirements influencing the form of signals: 'strategic design', that is, the features of a signal required to ensure honesty, and those features influencing 'the probability that the signal, once given, will reach its target destination and elicit a response at all'. They coined the term efficacy to refer to the latter features: the idea is best explained by examples.

A simple example is the observation (Morton 1975) that birds living in a forest environment tend to have lower frequency songs, a tendency that can be seen even within a species (Hunter and Krebs 1979, for Great Tits), essentially because high frequency sounds are dispersed by twigs and leaves. A second simple example is that alerting components at least sometimes really do draw attention to the message that follows, as their name suggests. For example, this was confirmed by experimental manipulation of playback for the introductory tonal elements of the subsequently trilling song of Rufous-sided Towhees (Richards 1981). Thus, ritualization does sometimes function to increase efficacy: for examples involving other aspects of ritualization, see Wiley (1983).

A remarkable example of a signal that has evolved to be effective in difficult circumstances has been described by Aubin *et al.* (2000) in the Emperor Penguin. These birds nest in the Antarctic winter. No nest is made. The single egg, and later the chick, is carried on the feet of one or other parent, while the other goes to sea to collect food. When the chick is older it remains on the ice while both parents feed. This system requires that the adult birds can find each other, and their own chick, in a colony of several thousands, when the birds are clumped together to keep warm, and in the total absence of landmarks. They do so acoustically. In birds, sound is produced in the syrinx, a two-part organ located at the junction of the bronchi. The two parts can be controlled separately. The result is a 'two-voice system'. In the Emperor Penguin, the beat generated by interaction between the two parts results in a sequence of 'syllables' of varying length, resembling a bar code, in the apt analogy suggested by the authors. Playback experiments demonstrated that, provided the two-voice system was being used, birds were able to identify their chick, or partner, at a distance. The two-voice system also occurs in the King Penguin, which has a similar method of raising its chicks, but not in nesting penguins. In this fascinating case a highly complex signal has evolved in a cooperative system to meet the requirements of efficacy.

It may require careful analysis to determine what type of signal is most likely to reach its target. Endler (1983, 1991) has emphasized that it is not sufficient that a colour pattern should look conspicuous against an artificial background to a human observer. Parrots, tanagers, orioles, and titmice can be hard to see against their usual bright background, as can a brightly coloured butterfly flying in flickering sunlight. Endler has worked on poeciliid fishes, in which males are faced with the contradictory requirements of being conspicuous to females but cryptic to predators. He treats the colour pattern of the background as consisting of a mosaic of patches varying in size, shape, colour, and brightness. A fish is cryptic if its own pattern resembles one drawn at random from the background, allowing for lighting conditions and the visual sensitivity of potential predators (e.g. two poeciliid species use red patches for communication, because their main invertebrate predators are red-blind). In guppies large and highly reflective spots are more conspicuous: they occur mainly on males from regions with low predation.

In some cases, the optimal design of a signal depends on its function. Marler (1955) described a particularly convincing example. Alarm calls can be divided into different categories according to the response to the signal. 'Flee' alarm calls, given to a cluster of individuals in immediate danger of attack, for example from a hawk, and causing all individuals rapidly to disperse, we would expect to be hard to locate, and not necessarily audible from a distance. 'Assembly' alarm calls cause hearers to assemble from a wide area, perhaps to mob a potential predator: we would expect them to be easy to locate, and audible at a distance. Figure 5.3 shows that these expectations are confirmed.

Guilford and Dawkins (1991) emphasized the importance, for some types of signal, of 'receiver psychology'—in particular, the efficacy of a signal will be increased if its meaning can be easily learnt and remembered (Roper 1990). For example, domestic chicks learn to avoid a visual signal more rapidly if it is paired with an auditory stimulus (Rowe 2002), consistent with the idea that redundancy increases efficacy.

5.3 Arms races, manipulation and sensory bias

5.3.1 Introduction

A more cynical view of animal signals was taken by Dawkins and Krebs (1978), and developed further in Krebs and Dawkins (1984). This view sees a signal, not as a means of transmitting information, but as a means whereby one animal exploits another's muscle power. The signaller is seen as 'manipulating' the receiver, and the receiver as 'mind-reading'—that is, as deducing, by experience or instinct, how the signaller will behave. The result is an evolutionary arms race. Krebs and Dawkins (1984) point out that the features of ritualized signals are those used by the advertising industry to persuade us to do something to their benefit and—all too often—to our cost.

In ESS models, it is usually assumed either that the signaller can choose one of a small number (often only two) alternative signals, or that the signal varies continuously along a single dimension. For such models, there is usually an ESS, characterized by the fact that each party to the interaction is choosing the optimal behaviour—signal or response—given what the other party is doing. But there is an alternative kind of situation in which, whatever the present state of the population, there is always a better signalling policy, and always a better policy for the receivers;

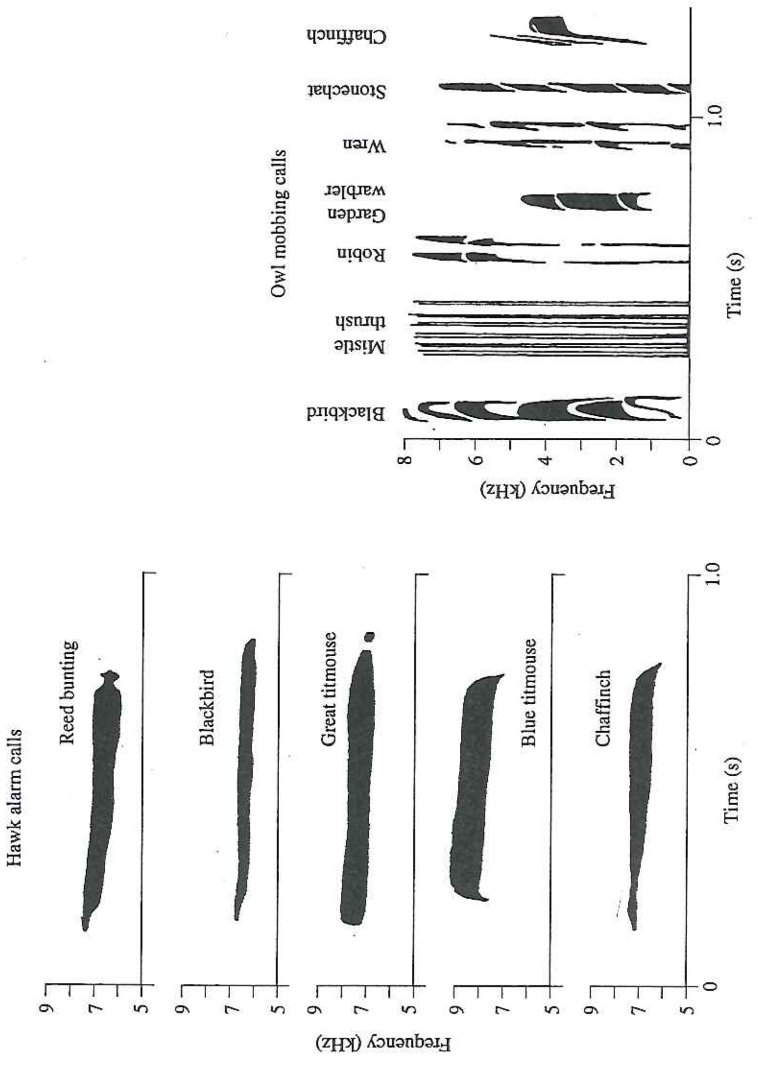

Fig. 5.3 Alarm calls eliciting flight and mobbing in various passerine birds (from Marler 1955).

there can be no stable equilibrium, and the population will evolve continuously. The crucial feature of such situations is that, whatever the current state of the population, there is always a possible signal that will extract more from the receiver than the signal that is currently being given.

We now discuss this alternative. We will do so in three stages, First, we describe a simple model that leads to continuing evolution, and an example in which it has been shown experimentally that a population is not in equilibrium. We then ask what evidence there is suggesting that, whatever signal is now being given, there is always a possible improvement, extracting more from the receiver. Finally, we discuss comparative data that point to non-equilibrium dynamics.

5.3.2 A model, and an experiment

Enquist (2002) considers the following simple model. An 'actor' gives a single signal, saying in effect 'I am here, and want something'; a 'reactor' responds by transferring a gift of value x, which can vary from 0 to 1. The actor's fitness is maximized if he receives $x = 1$; the reactor's optimum is $x = 0.5$. Thus there is a conflict of interest. In the first version of the model, Enquist assumes that, depending on genotype, the actor can choose any one of a number of unique signals, and that, again depending on genotype, reactors have a 'look-up table' indicating the response to every possible signal. Mutation of an actor causes him to choose a different, randomly chosen signal; mutation of a reactor causes him to alter the response to a random signal (usually, of course, one that is not at present being given) to a new value, randomly chosen between 0 and 1. If the number of possible signals is reasonably large, it will always be the case that there is some mutant signal that will extract a value of x close to 1 from most reactors, and that it will be some time before an appropriate mutation in reactors, giving x close to 0.5 to the new mutation, can arise and spread. It is therefore not surprising that, in simulations, actors evolve so as to extract a reward substantially larger than the value of 0.5 that is optimal for reactors. In other words, reactors are being manipulated, or exploited.

Enquist recognizes that the model is implausible mechanistically. It is not plausible that reactors should have a genetically determined look-up table for responses to many unique signals, most of which are not being received. He therefore simulated a revised version of the model in which the responses of the reactor are determined by an evolvable neural net. Behaviourally, this differs from a look-up table in that it 'generalises'; that is, if two signals are similar, then the responses to those signals will also be similar. In simulations, if both actor and reactor populations were able to evolve, the degree of exploitation was small ($x < 0.51$), although there was continuing evolution of both. However, if only the actor population could evolve, the degree of exploitation increased. Thus, although with coevolution the outcome was close to the reactor's optimum, we are not looking at an ESS; at an ESS, even if one participant could no longer evolve, there would be no inducement on the other to change.

Turning to the real world, the following experiment (Rice 1996) illustrates such non-ESS behaviour beautifully, albeit in a non-signalling context. In *Drosophila melanogaster*, male seminal fluid reduces the competitive ability of sperm from other males, thereby increasing the male's fitness. It also reduces the female's propensity to remate, and increases her egg-laying rate. However, it is toxic to females, reducing their survival. Rice allowed males to evolve in adaptation to females of a particular strain, but prevented the females from coevolving (by continuing the female strain from females that had not been exposed to the selected males). The result was an increase in the toxicity of the seminal fluid of the selected males in the unselected females. It seems, therefore, that in nature males are continually evolving in an arms race with other males, and that females respond to the changes in males so that the seminal fluid does not become increasingly toxic; if females are prevented from coevolving, the seminal fluid does become more toxic. Perhaps this will be seen as the coevolution of chemical weapons rather than of signals, but it does show how coevolution can lead to an ever-changing balance.

5.3.3 The response to novel signals

In the models described in the last section, the evolution of the population depended on the response to novel signals. If the response to a novel signal is arbitrary, and unrelated to the present signal to which reactors have had a chance to adapt, then the outcome is dramatic and unpredictable, and most of the time the signallers are exploiting the sensory preferences of the reactor. But if, as simulated by a neural net, responses are positive to novel signals that resemble the present one to which reactors have adapted, but negative to wholly new signals, then continuing evolutionary change still occurs, but the degree of exploitation of signallers is small. How do animals in fact react to novel signals?

Experiments suggest that the usual response to novel signals, rather than being arbitrary as in Enquist's first model, are more likely to be positive to signals resembling the one to which the receiver is already adapted: see Mackintosh (1974) for a review. This phenomenon, known as 'generalisation', has in the main been established by first training an animal to respond positively to some stimulus, X, and observing that its responses to new signals falls off with their difference from X (see Fig. 5.4a). However, similar results have been obtained for instinctive responses, although the experiments are harder to design and interpret, because the relevant features of the signal often concern pattern rather than some continuous variable such as intensity or pitch (Ghirlanda 2002). Note that, if the response to the initial signal X was already optimal for the signaller, then there would be no continuing evolution. But this is not always so: reactors may prefer a signal differing somewhat from that to which they have been trained (or have evolved) to respond—a phenomenon known as 'peak shift' (see Fig. 5.4b). If so, although not arbitrary, the response to a novel signal is such as to cause continuing evolutionary change. In some cases, animals may prefer signals of substantially greater intensity, a phenomenon referred to by Tinbergen (1951) as a 'supernormal stimulus' (see Fig. 5.5).

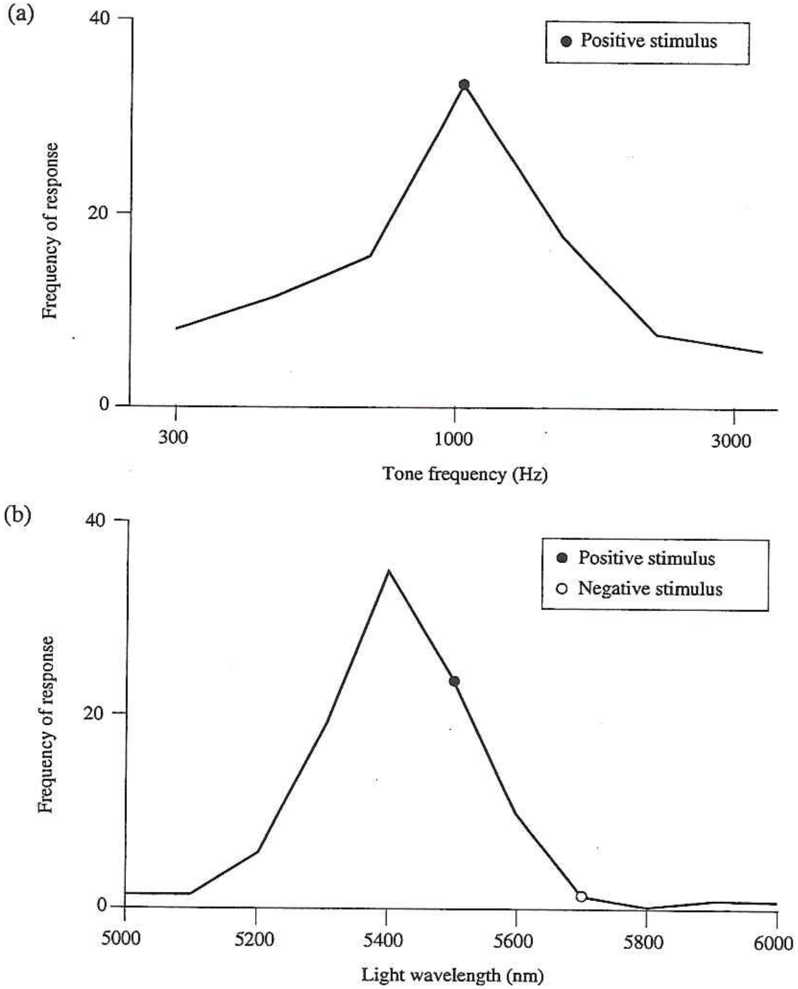

Fig. 5.4 Generalization and peak shift (after Enquist 2002). (a) Generalization: response of pigeons as a function of tone frequency. The birds had previously been rewarded for responding to a frequency of 1000 Hz (Jenkins and Harrison 1960). (b) Peak Shift: response of pigeons as a function of light wavelength. The birds had previously been rewarded for responding to a wavelength of 5500 nm, but not for responding to 5700 nm (Hanson 1959).

What of qualitatively novel signals? There is evidence for two kinds of novelty:

1. A cue that is relevant in one context evolves into a signal in a wholly different one. An example is described in Section 5.4.3: in guppies, there is evidence that orange colouration, which is used as a positive cue by both sexes when foraging, has evolved into a sexually selected male trait. A similar process has occurred in water mites feeding on copepods (Proctor 1991; see Section 5.4.1).

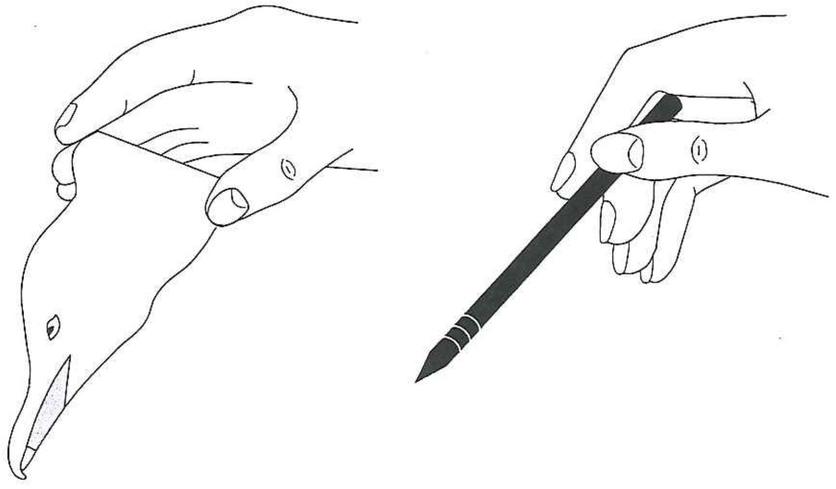

Fig. 5.5 Example of a supernormal stimulus: Herring Gull *Larus argentatus* chicks aim 26% more pecks at a thin red rod with three white bands at the tip than at a more realistic cardboard model of an adult's head; after Tinbergen (1953).

2. A qualitative change may occur in a signal, without a change of context; for example, there may be a change in the location of a patch of colour influencing female choice in courtship. This has been most intensively studied in relation to colour rings attached to the legs of birds, perhaps because ornithologists are worried that the rings they use for identification may have unintended consequences. Zebra Finches have a red bill, brighter in the male. Males with red colour rings have been reported to be more attractive as partners, both in captivity (Burley 1981) and in the wild (Burley 1988). In a freely breeding population, red-banded males were more successful in obtaining extra-pair copulations than males with green bands, and females mated to red-banded males resisted extra-pair copulations (Burley *et al.* 1994). However, the phenomenon is controversial: Jennions (1998) failed to detect a preference for red bands in cage choice experiments. Female preference for males with leg bands similar in colour to that present elsewhere in his plumage has been reported in some other species (e.g. American Goldfinches, Johnson *et al.* 1993) but not in others (e.g. Bluethroat, Johnsen *et al.* 2000).

The phenomenon is not confined to leg bands. Zebra Finches and the related Long-tailed Grass-finch belong to a lineage devoid of crested species, yet females prefer males wearing artificial white crests (Burley and Symanski 1998). In the Zebra

Finch this might reflect transference from the white 'moustaches' of the male: the Long-tailed Grass-finch does have a white rump, but in this case transference is perhaps less plausible.

Transference can also occur when the initial preference is learnt, not genetic. Plenge *et al.* (2000) raised female Javanese Munias under two conditions. Some were raised by normal unadorned birds, while others were reared by birds with a red feather added to their foreheads. Once mature, the females were allowed to choose between a normal unadorned male and a male ornamented with three different kinds of artificial ornament, which differed from the learned red feather on the forehead. These novel traits were: (a) a blue feather on the forehead; (b) red stripes on the tail; (c) blue stripes on the tail. Females whose parents had red feathers on their foreheads preferred males with red stripes on their tail, but not males with either sort of blue ornament. Thus, there appeared to be transference of a learned preference for the colour red. This kind of transference could play an important role in the evolution of conspicuous male traits. The control females, raised by unadorned parents, showed no consistent preference for unadorned or adorned males. This shows that females could recognize males with a phenotype different from their father as conspecifics. It also suggests that selection for mating with a conspecific would not necessarily prevent the evolution of novel sexually selected traits.

Thus, it is impossible to be dogmatic about the nature of the response to novel signals. However, it seems likely that the common pattern will be of generalization, perhaps with a small degree of peak shift, resulting in continuing evolutionary change, but not of a rapidity to result in serious exploitation of the receiver of the signal. But, occasionally, non-adaptive bias in favour of a wholly novel signal may have more dramatic results, less favourable for the receiver. Note that these conclusions depend on two assumptions:

1. There is a conflict of interest between signaller and receiver over the optimal response to a signal.
2. The signal is not an index.

In the next section we discuss the empirical evidence for this type of non-equilibrium dynamics.

5.3.4 The comparative data

If the appropriate image of signalling systems is a shifting balance, rather than a stable equilibrium, there is one clear prediction. Since a shifting balance is predicted as a consequence of conflict between signaller and receiver, we would expect the form of aggressive signals to evolve more rapidly than cooperative ones. Andersson (1980), using data from Sebeok (1977), argued that this was the case. He explained it, not in terms of sensory exploitation, but by suggesting that a novel threat display is usually a reliable predictor of attack, but later is increasingly used as a bluff and so loses its effectiveness, and is then replaced by yet another new display.

We would also expect aggressive signals whose form is not causally linked to quality to evolve more rapidly than indices of RHP used in aggressive encounters. Enquist (2002) quotes aggressive signals in cichlid fishes in support of this prediction. Colour patterns are often used in aggressive encounters; these almost always differ between closely related species. In contrast, tail-beating and mouth-wrestling are indices of quality, and are shared by many species.

5.3.5 Conclusions

In contrast to the ESS picture, in which the population evolves to a stationary equilibrium, at which it would not pay either signallers or receivers to change their behaviour, given what the others are doing, the 'arms race' picture supposes that there is always a 'mutant' signal possible that elicits a more favourable response for the signaller, and concludes that, if this is so, the result will be continuing evolutionary change and exploitation of receivers by signallers. Formal models have confirmed this intuition, but have shown that much depends on how receivers respond to wholly novel signals. If responses to novel signals are such that there is always some signal possible that elicits a substantially more favourable response, then the result will, as predicted, be continuing evolution, and serious exploitation of receivers. However, experiments on the response of animals to novel signals suggests that the typical behaviour is one of 'generalization': that is, the more similar a novel signal is to the one at present preferred as a result of training (or, if responses are innate, to the signal commonest in the present population), the more favourable will be the response. If generalization is perfect, then there is no selection for change, and hence no continuing evolution. But if there is some degree of 'peak shift'—that is, if the most favoured signal differs to a small extent from the one that has been optimal during training—then there will be continuing evolution, but the degree of exploitation will be small. However, it should be emphasized that most of the evidence concerning generalization and peak shifts is based on experiments in which the responses to signals are the result of training rather than instinct. Finally, there is empirical evidence that, if receivers are prevented from evolving, serious exploitation can result.

This 'arms race' picture makes two predictions that are confirmed. First, we would expect signals used in aggressive encounters to evolve more rapidly than those used in cooperative interactions. Second, in aggressive interactions, purely conventional signals (e.g. colour patterns) should evolve more rapidly than indices of RHP, for example of size.

5.4 Sensory manipulation

5.4.1 Frogs and swordtails

A related idea has been proposed by Ryan (1990, 1998), and Basolo (1990, 1995). They suggest that a signal may evolve whose form depends on a pre-existing bias in the sensory system of receivers. The form of such signals may appear arbitrary, but it is not a necessary feature of the idea that there should be a continuing arms race between signaller and receiver.

In the Túngara Frog (Ryan 1990) the male mating call has two components, a high-pitched whine and a series of low-pitched chucks. The whine is always given and is sufficient to provoke a female response. Chucks are not always produced, but increase the attractiveness of calls to females: they are also risky, attracting frog-eating bats (Ryan 1985). Larger males make a lower frequency chuck, and females prefer lower-frequency calls. Low frequencies are perceived by the basilar papilla, and the tuning of the papilla is such that it is more sensitive to frequencies lower than that of typical male chucks; thus the female preference is probably a direct consequence of this bias in sensory sensitivity. Ryan argues that this 'sensory bias' existed in the genus *Physalaemus* before the evolution of the chuck call (Fig. 5.6). The *P. pustulosus* species group consists of two sister clades, one on each side of the Andes. Chucks are part of the mating call only in two of the eastern clade: the Túngara Frog *P. pustulosus* itself and an undescribed species that is a sister to *P. petersi*. Yet the basilar papilla (see earlier) is present throughout the genus, and measurement of sensitivity in a species from the western clade, *P. coloradorum*, which lacks the chuck call also revealed a sensory bias towards low frequencies. Moreover, females of that species prefer conspecific whines to which chucks have been digitally added (Ryan 1997). This suggests that the sensory bias did indeed precede the evolution of the chuck call, although an alternative possible explanation is that predation by bats has led to the secondary loss of the chuck in some species (Shaw 1995).

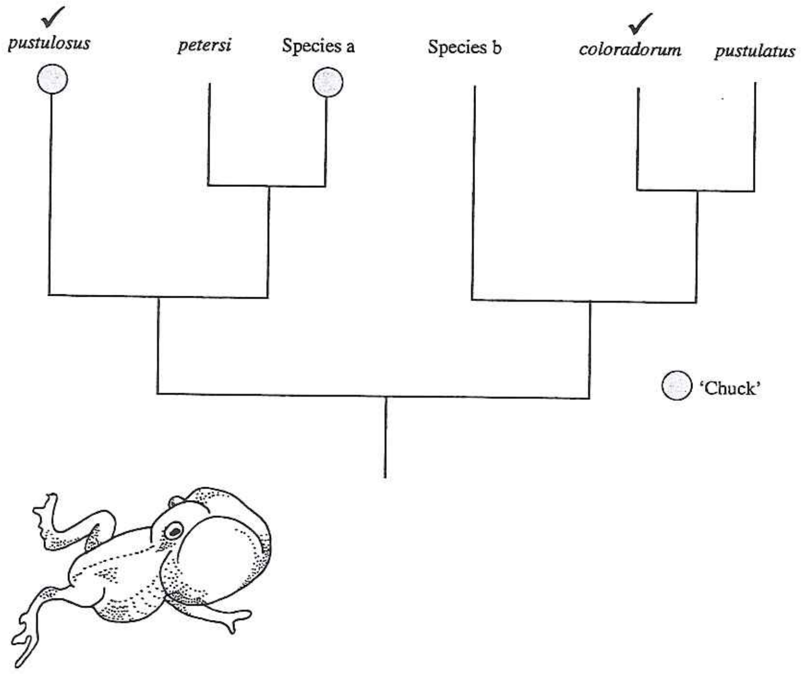

Fig. 5.6 Phylogeny of the Túngara Frog *Physalaemus pustulosus* clade, based on morphological and molecular data; after Ryan (1997). Males of the species labelled with filled circles often add a chuck to their advertisement call. Females of the two species labelled with ticks prefer recordings with chucks added to those without.

A similar argument has been made for the 'sword' in the fish genus *Xiphophorus* (Basolo 1990). This genus includes both swordtails, with a sword-like extension of the caudal fin, and platyfish, with no such extension. Basolo found that platyfish prefer conspecific males with a 'sword' to the same males without. If the presence of a sword is a derived character in the genus, then this suggests that the female preference for a sword preceded the male structure. Meyer *et al.* (1994) presented a molecular phylogeny suggesting that the absence of the tail in platyfish is the derived character within the genus. This makes the traits of the sister genus, *Priapella*, critical. They lend support to the sensory bias hypothesis: males lack a sword, but females prefer conspecific males with one added artificially (Basolo 1995).

Thus in *Physalaemus* and *Xiphophorus*, female preference preceded the male trait. This observation is relevant to Fisher's (1930) 'runaway' theory of sexual selection. Ryan (1998) points out that, in both the 'runaway' and the 'good genes' theories of sexual selection, female preferences evolve indirectly because they are genetically correlated with male traits that are under direct selection: the preferences themselves are not under direct selection. This is correct. For example, in the runaway theory, a female that mates with a male with, for example, a long tail does not therefore have more offspring; but the gene that causes her to do so will, in the next generation, tend to be associated with genes for long tails, and males with long tails *do* have more offspring (provided, of course, that most females prefer such males). Thus, the spread of a gene causing females to prefer males with long tails occurs because of 'genetic correlation' with long-tail genes. A problem with the theory, therefore, has always been to explain why most females come to prefer such males in the first place. Fisher himself thought that, typically, females would select as mates males of high general fitness, and that sometimes such preferences would be exaggerated by his 'runaway' process. The theory of sensory bias provides an alternative answer: the preference was originally an accident of sensory physiology. However, this does not invalidate Fisher's theory. Given an initial preference, for whatever reason, selection may lead to an exaggeration both of the preferred trait, and of the preference. Sensory bias would also help to explain why preferences tend to be for larger, brighter, or otherwise more conspicuous traits: Fisher's theory by itself predicts the evolution of tiny tails, for example, just as readily as large ones.

These two examples have in common that the signal elicits a positive response in species lacking it. In neither case is there any reason to see the signal as exploitative, or as the first step in an arms race. It is not obvious why the chuck, or the sword, should have appealed to receivers in the first place. A possible answer is that the novel trait was relevant to some cue or signal already influencing female choice. For example, female fish might favour a sword because of a pre-existing preference for large males: in other words, swords were initially exaggerators of body length. This hypothesis is not supported, however, by a study of the swordless species *Priapella omaecae*: females prefer males with a sword added, but do not discriminate between males of different size (Basolo 2002). A second type of explanation for sensory bias is that there was a pre-existing response that was adaptive in a different context. For example, water mites, *Neumania papillator*, locate their copepod prey by detecting water vibrations. Proctor (1991) showed that males attract females by moving their legs so as to mimic these vibrations.

We now discuss a context in which it seems that a signal that initially elicited an adaptive response from females can evolve into one that is effective only because females have evolved to respond to it, despite the fact that they no longer gain any direct benefit from doing so.

5.4.2 Nuptial gifts in insects

Male insects often offer nuptial gifts to females. There is a bewildering variety of systems, reviewed by Vahed (1998). The following summary is based on how females may benefit from the gift, and what the male gains from offering it.

5.4.2.1 The female benefits nutritionally

We describe two examples. Mating in the scorpionfly *Bittacus apicalis* was described by Thornhill (1976). Males capture an arthropod prey, and then attract a female pheromonally. The male presents the prey to the female, which feeds on it during copulation. After copulation is ended there is a struggle for the prey; the male usually wins, and either eats it or uses it in a second courtship. The female benefits from a large prey item through an increase in her subsequent fecundity. A second case in which females benefit nutritionally was described by Steele (1986*a*,*b*) in *Drosophila subobscura*. During courtship a male often produces on his proboscis a drop of liquid regurgitated from his crop. A starved female, but not a well-fed one, will extrude her own proboscis and take the drop. The food thus obtained increases her subsequent fecundity. Steele showed that wild-caught females usually behaved like starved laboratory females.

In both these cases there is evidence that the nuptial gift increases the female's fecundity; there is no reason to speak of 'exploitation'. But the benefits to the male are quite different in the two cases. In *Bittacus*, as in most insects in which nuptial gifts are exchanged, a female will eat and copulate at the same time. The larger the prey item, the longer the duration of copulation, and the more sperm are transferred. The male does not increase his chance of mating by his gift—the female mates anyway: he increases his fecundity. In *D. subobscura*, Steele found that starved females are more likely to mate if offered a nutritious drop: the male is increasing his mating success. It may also be relevant that female *D. subobscura* typically mate only once, so, by increasing the fecundity of the female, the male is also increasing the number of his own offspring.

5.4.2.2 Sensory exploitation

Sakaluk (2000) argues that the evolutionary origin of nuptial gifts in the cricket *Grylloides* is sensory exploitation. In these crickets, the male deposits on the female genital aperture a spermatophore consisting of two parts, an ampulla containing sperm, covered by a jelly containing free amino acids, called a spermatophylax. During copulation the female eats the spermatophylax; the quantity of sperm transferred depends on its size. There is phylogenetic evidence that this system is derived from that in *Gryllus*, in which there is no spermatophylax, and the female terminates copulation by eating the ampulla; she may then mate again with the same male. Females of three species of *Gryllus* readily eat the spermatophylax of *Grylloides* if offered it, showing that the sensory response preceded the structure. Sakaluk suggests that the system in *Gryllus* evolved into that in *Grylloides* because it pays the male to prolong copulation by offering a gift that is equally attractive but cheaper to produce.

If this interpretation is correct, then *Grylloides* has taken the first step on the evolutionary path from a nutritionally valuable gift to the sensory exploitation of the female, although it is important that the signal is by no means arbitrary in form. Empid flies (also known as Dance Flies) have travelled further along this path: see Cumming (1994) for a review. In typical Empids the males form a mating swarm, each carrying a prey item as a gift. During copulation the female eats the prey; copulation ceases when she has completed her meal. In some species the prey is lightly wrapped in silk: in others it is partly encased in a silken balloon. In *Empis geneatis*, the balloon contains a minute, dessicated prey item, useless as food (Fig. 5.7). In two species of *Hilara*, the gift consists of an inedible silk ball containing no prey at all. Although there is no direct phylogenetic evidence, it seems plausible that evolution has led from a system analogous to that of *Bittacus* to one in which the female responds to a signal, but gains no direct benefit in return. She may, however, receive benefits of the kind proposed by Fisher (1930): by mating with a male that offers an inedible balloon, she will have sons that offer a balloon, and that is what females like.

5.4.3 Further examples of sensory manipulation

Female guppies prefer to mate with males with bright orange spots. The degree of preference varies strikingly between different geographic regions, which has made guppies a favoured system for the study of mate choice, starting with Endler (1980). Until recently, the favoured hypothesis was that, by choosing males with bright spots, females choose males of high quality, for two reasons. First, the orange colouration of the spots depends on carotenoids, which must be ingested, and is therefore a measure of foraging ability. Second, the colour depends on parasite load (Houde and Torio 1992).

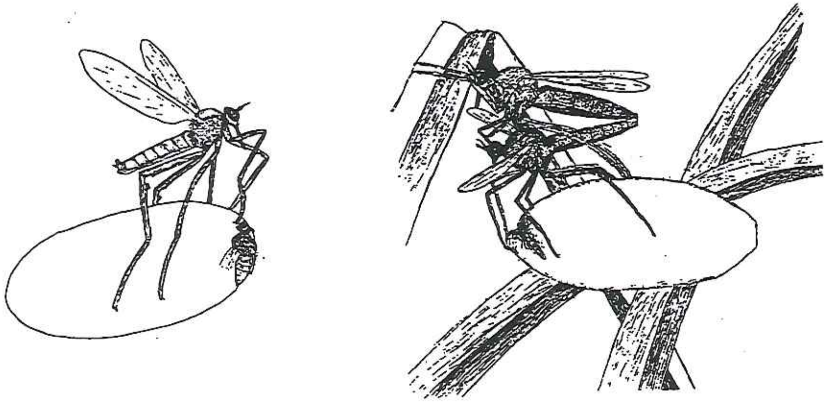

Fig. 5.7 Nuptial gift in *Empis*: the male carries a silk balloon containing a prey item (from Brown 1975).

The first reason for doubting this 'indicator' hypothesis was the observation (Grether 2000) that the strength of female preference is not greater in regions where carotenoids are hard to acquire. More recently, Rodd *et al.* (2002) have produced strong evidence for the view that males are exploiting a pre-existing sensory bias in favour of orange objects. They studied fish in the wild, and also fish derived from different regions, but raised in the laboratory on brown-coloured food. Colour preference was measured by recording the frequency with which fish pecked metal discs of various colours. In laboratory studies, males as well as females pecked at orange discs more frequently than at discs of other colours, and the degree of preference in males and females covaried in fish derived from different regions. They also found that male preference for orange discs, and female preference for males with bright orange spots, covaried geographically: astonishingly, male preference for orange discs accounted for 74% of the geographical variation in female mate preference.

5.5 Mimicry and cheating

It may be helpful to define what we mean by deception (Semple and McComb 1996). Consider a signal that is given in more than one circumstance, but always produces the same response in receivers. Receivers usually benefit from their response, but deception can occur if there is another circumstance in which the same response benefits the signaller at the receiver's expense. This definition makes no assumption about what goes on inside the brains of the signaller and receiver. Mimicry is a common form of deception, although the two terms do not cover an identical range of cases. Thus mimicry may be of a cue rather than a signal, and deception may involve an identical signaller giving an identical signal, but in inappropriate circumstances.

As an example, consider the jumping spider, *Portia fimbriata,* which preys on orb-web spiders such as *Zosis geniculatus* (Tarsitano *et al.* 2000). When first encountering a web, *Portia* manipulates it in a way that simulates the struggles of a prey insect. This usually provokes the resident to approach. But when moving close to the resident spider, *Portia* makes brief rocking movements, resembling the disturbance of the web by wind, thus masking its own movements. A third signal, resembling that made by a prey insect brushing the periphery of the web, is made if *Portia* estimates that the resident spider is large.

Perhaps the classic example of mimicry is that in which a distasteful and warningly coloured prey is mimicked by an edible mimic (Batesian mimicry). Such systems are usually in equilibrium, at least in the short run, because the mimic is rare relative to the model, so that it pays predators to believe the signal. The edible African Swallowtail Butterfly illustrates this point beautifully, males are non-mimetic, perhaps because of the role of colour in mate choice. Females mimic different distasteful butterflies in different parts of Africa: in regions where models are rare or absent, the females are non-mimetic (Sheppard 1958). This is a game two can play: some predators are also mimics—for example, Painted Redstarts (Jablonski and Strausfeld 2000). These birds exploit the fact that many insects, when they detect an approaching predator, jump and fly away. The redstarts spread their tails and wings, which are decorated with white patches, and pursue and feed on the insects they flush in this way. Experiments with models demonstrated that both the movement and colouration of the wing and tail increase their effectiveness. The method works only because redstarts form only a small part of the predator guild, and flight is an effective defence against most predators.

In Batesian mimicry, it may be true both that the system is in equilibrium, and that the responses of receivers have evolved in the context of signalling. A Batesian mimic is certainly deceiving, or exploiting, the receiver of the signal. But the receiver of the signal responds in the required way to the signal because the response has evolved as an adaptive response to an honest signal by genuinely distasteful prey. Provided that mimics are not too common relative to models, the system is in equilibrium. Evolutionary change can arise from selection on receivers for the ability to distinguish mimic from model, and on mimics to make such distinction impossible: there is little reason to expect such selection to lead to ongoing evolutionary change; in particular, there is no reason to expect an arbitrary change in the signal to be beneficial. Essentially the same argument applies to other cases of mimicry. Mimicry, therefore, is a clear example of exploitation, but not of either sensory bias or of non-equilibrium dynamics.

The inappropriate use of alarm calls is another clear case of deception. Matsuoka (1980) watched Great Tits, Marsh Tits, and Willow Tits at a bird table giving hawk-alarms in the absence of predators. When the other birds flew off, the caller seized some food. Møller (1988) used playback of tape-recordings to confirm that the hawk-alarm calls of Great Tits given in the absence of a predator caused the same fleeing response as those recorded when a predator was present. Although the caller usually benefited at the receivers' expense, it probably paid birds to flee whenever they heard an alarm call: the costs of being killed far outweighed losing a few minutes of feeding time. Even so, there must be limits on how often deceptive alarm calls can be used before they lose their effect. Great Tits seem to ration their use in at least three ways. First, they did not use them when confronting an individual subordinate to themselves. Second, they were most likely to use them when food was likely to be unusually valuable (during snow storms, early and late in the day). Finally, birds gave fewer deceptive calls if food was dispersed, so that it was easier for birds to share it than if the same food had been clumped. Several other birds use alarm calls in similar ways (e.g. Munn 1986*a*,*b*; Tramer 1994).

Deceptive use of alarm calls during fights has also been suggested (e.g. Dale and Slagsvold 1995). Caution is required: the idea that the 'conflict call' of Eurasian Nuthatches was used both in fights and as a hawk-alarm (Cramp and Perrins 1993) arose because two very similar calls were confused (Matthysen 1998).

Courtship is a common context for deception. For example, female Dance Flies cannot hunt for food, and receive all their protein in the form of nuptial gifts from males. They compete for these gifts at leks which form at dusk. Experiments using model flies show that males prefer to give their gifts to and then copulate with females with extended abdomens. In some species (e.g. *Rhamphomyia sociabilis*) abdomen swelling is a reliable index of egg maturation. But before female *R. longicauda* join a lek they swallow air, inflating pouches along the edges of their abdomen. They then wrap all three pairs of legs—which are heavily scaled—around the abdomen. These two exaggerations completely mask the state of egg development, so that males are regularly deceived into handing over food to females whose offspring they are unlikely to father (Funk and Tullamy 2000). But it is not only males that are deceived in Dance Flies: as described in Section 5.4.2, these flies have long been known for a case of apparent deception in which males hand over empty silken shrouds rather than prey. It is intriguing that a system that originated as an honest trade, in which males supply food and females supply eggs ready to be fertilized, has, in different lineages, evolved into deception of males by females, and of females by males.

Adams and Caldwell (1990) studied the threat display given by the stomatopod crustacean, *Gonodactylus bredini*. Individuals in the process of moulting continue to give the display, although they are in fact vulnerable and unable to attack. The rarity of the cheating relative to the honest signal is ensured by the fact that only a small proportion of individuals are moulting at any one time. A similar case is described by Backwell *et al.* (2000) in a fiddler crab, *Uca annupiles*. Male fiddler crabs have a large claw which is used as a signal both in attracting mates and in contests with other males: in the latter context it is also used as a weapon. In most species, a male that loses a claw regenerates a new one identical in form to the original. In *U. annupiles*, in contrast, the replacement claw is lower in mass and less effective as a weapon. The authors found that males with original claws are not more likely to fight with males with regenerated claws, and females when choosing mates do not discriminate against males with regenerated claws. Surprisingly, they found that up to 44% of males in natural populations may have regenerated claws. These observations lead them to suggest that the apparent rarity of cheating may be an artefact of the difficulty, in most cases, of detecting cheats, and that dishonesty may be quite common.

This case raises a hard question. Are we looking at a stable equilibrium of the kind investigated theoretically in Chapter 2, or at a signalling system which, in this species, is on the way out? If it is really impossible for other males to distinguish between original claws and regenerated claws that are cheaper to produce but less effective as weapons, why do males produce effective but expensive claws in the first place? If the present system is a stable one, there must be some disadvantage to the replacement claw. Presumably this arises in the context of escalated fights.