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## Introduction

Whether signals are reliable or deceptive has been a central question in the study of animal communication in recent years. The crux of the issue is whether animal signals are honest, in the sense of conveying reliable information from signaler to receiver, or deceitful, in the sense of conveying unreliable information, the falsity of which somehow benefits the signaler. This issue arises in a variety of contexts. When a male courts a female, do his signals honestly convey his quality relative to other males? Or does he exaggerate his quality in order to win over females that would otherwise choose some other male? When one animal signals aggressively in a contest over a resource, does the signaler honestly convey its likelihood of attack? Or does the signaler exaggerate that likelihood in order to intimidate competitors that would otherwise defeat him? The question of reliability versus deceit arises even in interactions that, on the face of things, seem to be predominantly cooperative. When an offspring begs for food from its parents, does it honestly convey its level of need? Or does the offspring exaggerate its need in order to get more food than the parents would otherwise provide?

The issue of reliability and deceit in animal communication resonates with human observers for a variety of reasons. One is that the occurrence of deceit is fraught with moral implications. In the view of many, human communication is permeated with deceit. Do humans stand apart in this regard, or are other animals as bad or worse? The answer might have considerable effect on how we view ourselves, as well as on how we view other animals. A second reason for interest in this issue is that the occurrence of deceit, if deceit is defined appropriately, can have considerable implications for our understanding of animal cognition. Some definitions of deceit are framed so as to require cognitive processes of considerable sophistication, such as the ability to form intentions and beliefs and to attribute beliefs to other individuals. If we employ such a definition, and if we can then determine that nonhuman animals deceive each other according to this definition (a big "if"), then we have provided support for a greater level of cognitive capacity than many earlier views of animal behavior have allowed.

Our own interest in reliability and deceit revolves around neither morality nor cognition, but instead derives from the evolutionary implications of the issue. The way one expects animal communication systems to function in terms of reliability and deceit depends on how one views the operation of natural selection. Early students of animal behavior often assumed implicitly that selection operates at the level of groups, so that behavior evolves toward

what is best for the population or species as a whole, leading to the view that animal communication consists primarily of the cooperative exchange of reliable information. The predominant view nowadays, however, is that selection acts largely at the level of the individual, so that behavior evolves toward what is best for the individual performing the behavior, and not toward what is best for the group. If behavior is commonly selfish, in this sense, then it is not always obvious why animals should exchange information cooperatively. Instead, one might expect many instances in which signalers would attempt to profit individually by conveying dishonest information. But because individual selection works on the receiver as well as the signaler, receivers ought to respond to signals only if doing so is to their advantage, on average. Therefore, if dishonesty is common, it also is not obvious why receivers should respond to signals.

Taking the argument one step further, if receivers fail to respond to signals, it is not obvious how signaling systems can exist at all. Thus if one accepts the view that selection acts predominantly at the level of the individual, as we do, and if one at the same time accepts the idea that animals do communicate with each other, as seems obvious, then one is left with a series of evolutionary puzzles. Are animal signals in reality reliable or unreliable? If animal signals are reliable, what mechanisms maintain reliability despite the tempting advantages of dishonesty? If animal signals are deceitful, do receivers respond to them anyway, and, if so, why? Our principal purpose in this book is to work through possible answers to evolutionary puzzles such as these.

## Definitions

Before we get to these puzzles, we need to define some terms. First, we need to define what we mean by "signal," in order to delimit the set of traits whose honesty and dishonesty we will examine. In one of the first rigorous evolutionary analyses of communication, Otte (1974, p. 385) defined "signals" as "behavioral, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms." Otte explicitly rejected group-selectionist explanations for the evolution of traits, so in his view the transmission of information had to confer some reasonable advantage on the signaler itself in order to satisfy the definition. Thus Otte excluded as signals those traits that convey information to predators or parasites without any benefit to their possessors; he cited the chemicals in human sweat that attract disease-carrying mosquitoes as a possible example. Otte also rejected as signals those traits, such as body size, that may be used by other individuals of the species to assess their possessors but did not evolve for that function. Clearly included under Otte's definition would be vocalizations, color patterns, and body movements that have evolved be-

cause they transmit information in a way that benefits the individual that exhibits those traits. More ambiguous are traits, such as the form of a bird's tail, that originally evolved for some other function but have been modified by selection for information transmittal. We will regard such traits, or more precisely their modified properties, as signals; thus the bird's tail itself is not a signal but the tail's length is, if that length has been exaggerated beyond its aerodynamic optimum in order to influence receivers.

This brings us to our definitions of reliability and deceit. In everyday English, "reliable" means that "in which reliance or confidence may be put; trustworthy, safe, sure" (Little et al. 1964). An animal signal, then, would be reliable if one could have confidence in its veracity, or truthfulness—if, that is, one could trust the signal to convey whatever it is supposed to convey. The difficulty with this formulation is in ascertaining what the signal is "supposed to" convey. "Supposed to" in this context must be interpreted from the viewpoint of the receiver rather than the signaler; what matters is whether the signal conveys something that the receiver would benefit from knowing. If we are certain what it is that the receiver benefits from knowing, such as some attribute of the signaler or its environment, then we can ascertain the reliability of the signal by measuring the correlation between the signal and the attribute of interest.

Suppose, for example, that we think that female frogs are interested in the size of conspecific males, and we find that calls communicate information on male size by a negative correlation between call frequency and caller size (males with deeper croaks are larger). We can then determine the reliability of this information by measuring the correlation between call frequency and caller size. The trouble is that we can never really be certain that caller size is what the females "want" or "need" to know. Even if we can show that call frequency is well correlated with caller size, and that the females show a behavioral preference for calls of lower frequency, we cannot be sure that their true interests are not in some other characteristic—perhaps, in this example, male age. The best we can do is to measure as carefully as we can the benefits that the receivers obtain from different types of information. If we can show that female frogs benefit from mating with larger males but not from mating with older ones, we at least can have some confidence that size is what matters to the receivers, and then evaluate reliability of call frequency in terms of its correlation with signaler size.

To formalize this definition, we suggest that an animal signal is reliable if:

1. Some characteristic of the signal (including, perhaps, its presence/absence) is consistently correlated with some attribute of the signaler or its environment; and
2. Receivers benefit from having information about this attribute.

A remaining problem is how to specify what we mean by "consistently correlated." We can never expect a perfect correlation between signal characteristic

and the attribute being signaled. Even if signalers are striving for perfect honesty, errors must be expected in the production of the signal and in our measurements of it, either of which would prevent our observing perfect reliability. How good, then, does the correlation have to be for us to conclude that the signal is on the whole reliable? One answer is provided by the concept of "honest on average" (Johnstone and Grafen 1993, Kokko 1997). A signal can be considered honest on average if it contains enough information, sufficiently often, that the receiver on average is better off assessing the signal than ignoring it. Consider again the example of male frogs communicating their size to females via the frequency of their call. The correlation between male size and call frequency can never be expected to be perfect, and in reality is often rather low (see chapter 4). The male's call can be considered honest on average if the correlation between male size and call frequency is good enough that the female benefits on average from using the call to assess male size, instead of ignoring this signal feature. In practice, it will be difficult to determine whether this criterion is being met, but at least it provides a theoretical standard against which reliability can be judged.

A simple way to define "deceptive" would be as the opposite of reliable, but for many the concept of deception carries more baggage, and consequently requires a more complex definition. A relatively simple definition of deception is provided by Mitchell (1986, p. 20), who suggested that deception occurs when:

1. A receiver registers something Y from a signaler;
2. The receiver responds in a way that is appropriate if Y means X; and
3. It is not true here that X is the case.

Note that the definition requires specifying what the signal (Y) means to the receiver. The meaning of Y to the receiver is judged by the response of the receiver to Y together with an observed correlation between Y and X, across many such signals. In other words, we infer that Y means X to the receiver because signalers usually produce Y in association with X, and because the receiver responds to Y in a way that is appropriate if X is true. To make this more concrete, let Y be an alarm call given by the signaler. The alarm call is usually produced when a predator (X) is present, and the receiver typically responds to the alarm call by fleeing, an appropriate (i.e., beneficial) response if a predator is indeed nearby. Deception occurs if the signaler produces the alarm and the receiver reacts by fleeing when in fact no predator is present.

A difficulty with Mitchell's (1986) definition, which he himself points out, is that deception so defined cannot be distinguished from error on the part of the signaler. If the signaler has produced an alarm in error, would we want to call such an action deceptive? This problem can be solved if the definition of deception further stipulates that the signaler benefits from the receiver's response to the signal. Mitchell (1986) himself is uncomfortable with the notion

of benefit, remarking that the "idea of benefit is taken from human affairs" and when applied to nonhuman animals typically refers to what a human observer "believes is good for them." For an evolutionary biologist, however, "benefit" has a straightforward meaning—an individual benefits from an action if that action increases the individual's fitness, in the sense of the representation of the individual's genes in subsequent generations. Benefit in this sense is not an anthropocentric idea, but one that applies equally well to all organisms. With the added stipulation about a benefit to the signaler, we will define deception as occurring when:

1. A receiver registers something Y from a signaler;
2. The receiver responds in a way that
  - a. benefits the signaler and
  - b. is appropriate if Y means X; and
3. It is not true here that X is the case.

Deception defined in this way has sometimes been termed "functional deception" (Hauser 1996), meaning that the behavior has the effects of deception without necessarily having the cognitive underpinnings that we would require of deception in humans.

Other definitions specify that deception must have more complex cognitive underpinnings, that is, that the signaler has an "intention" to cause the receiver to form a false "belief" about the true situation (Russow 1986, Miller and Stiff 1993). Deception defined in this way has been termed "intentional deception" (Hauser 1996). "Intentions" and "beliefs" are mental states, and as such are difficult to measure in nonhuman animals, to say the least. Whether animals possess such mental states, and whether they can ascribe them to others, is of great interest to philosophers (Dennett 1988) and cognitive ethologists (Cheney and Seyfarth 1990, Seyfarth and Cheney 2003, Byrne and Whiten 1992), as well as to the general public. A major goal of some researchers studying deception in nonhuman animals is to use this type of interaction as a window onto the mental states of those animals, in an effort to determine whether they do indeed form intentions, beliefs, and so forth. Although we applaud such efforts, we repeat that our own interests lie elsewhere, in the analysis of reliability and deceit from a functional, evolutionary viewpoint. Another way of saying this is that we are interested in how natural selection shapes animal communication to be either honest or dishonest. From this viewpoint, the question of mental states is largely irrelevant; the costs and benefits to the signaler of giving a false alarm, and to the receiver of responding, ought to be the same whether or not the signaler is able to form an intention and the receiver to form a belief.

Another issue in defining deception is whether to include the withholding of signals. Some authors have argued in favor of this inclusion, suggesting that under certain circumstances, a failure to signal can be considered just as



deceptive as producing a dishonest signal (Cheney and Seyfarth 1990, Hauser and Marler 1993a, Hauser 1996). Hauser (1996), for example, states that if an animal fails to produce a signal in a certain context in which that signal is typically produced, and if the animal benefits from failing to signal, that failure constitutes functional deception. This idea seems to us to have little application to a large majority of signaling contexts, such as those involving aggression or mate choice, in which cooperation is not expected from the interactants. In practice, the idea that withholding information is deceptive has most often been applied to cooperative interactions, most notably to interactions in which an animal signals the discovery of a food source to others of the same species (Hauser and Marler 1993a,b). Even here, the concept seems to us to be problematic. Say, for example, that a signaler follows the convention of calling when it finds a large amount of food, more than it can eat itself, and not calling when it finds a smaller amount. The signal then is consistently correlated with an aspect of the environment that receivers benefit from knowing, and so meets our criteria for reliability. Of course the receivers would be even better served by knowing more (i.e., from hearing about the small amount of food as well), but the signaler has not broken its convention in denying them this information.

Before we move on, let us reiterate in less formal terms the definitions of reliability and deceit we plan to use. Reliability requires that there be a correlation between some characteristic of the signal and some attribute of the signaler or its environment that the receiver benefits from knowing about, and that the correlation be good enough that the receiver on average benefits from assessing the signal rather than ignoring it. Deceit requires not only that the correlation between signal characteristic and external attribute be broken at times, but that the signaler benefits from this breakdown. Therefore, if a breakdown occurs in the correlation between signal characteristic and external attribute from which the signaler does not benefit, this would constitute unreliability but not deceit. A breakdown of this type we would describe as "error."

### Some History

Opinions about the prevalence of reliability and deceit in animal communication have swung back and forth in recent decades. A convenient place to enter this history is with a seminal paper published by Richard Dawkins and John Krebs in 1978 titled "Animal signals: Information or manipulation?" In writing this paper, Dawkins and Krebs were reacting to what they labeled as the "classical ethological" view of animal communication, which in their opinion treated communication as a cooperative interaction between signaler and receiver. The ethological view assumed that receivers (reactors) were "selected to behave as if predicting the future behaviour" of signalers, while the signalers were "selected to 'inform' reactors of their internal state, to make it easy for reactors to

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## Signaling When Interests Overlap

The interests of two individuals overlap in an evolutionary sense when the fitness of one depends, at least in part, on the fitness of the other. Such a positive fitness relation occurs whenever two individuals are genetically related; because they share genes, the overall success of one relative's genes depends to some extent on the success of the other's. Additional causes of convergent interests are possible, for example when the members of a mated pair depend on each other's continued survival and good health for successful reproduction, or when the members of a group depend on each other for safety from predation or to obtain food or other resources. Genetic relatedness, however, is the cause of overlapping interests that has been most emphasized in signaling research.

We begin by considering theory, which in practice means models of signaling between relatives. These models provide two basic explanations for signal reliability: it may result from the absence of conflict of interest between signaler and receiver, or it may be maintained by signal costs. We then consider empirical evidence from studies of three rather different types of signals: solicitations, alarms, and food calls. In solicitation, or "begging," one individual appears to ask another for some resource. Success in soliciting resources would seem to require overlapping evolutionary interests, and in practice successful solicitation most often occurs between genetic relatives, especially between offspring and their parents. Alarms are signals in which one individual warns others of the approach of some danger, such as a predator. One explanation for the occurrence of alarm signals is that they evolve to aid genetic relatives, although (as we will see) this explanation is controversial. We next consider the information available on food calls, calls that are given when food is discovered and that often have the effect of recruiting others to the food source. Food calls in some cases are given between individuals with overlapping interests, but they are also given between individuals with diverging and opposing interests. Our discussion of food calls leads us to consider another type of explanation for the maintenance of signal reliability: memory by receivers of the past performance of individual signalers with whom they interact multiple times.

### Signaling Between Relatives: Theory

Much of the theoretical work on signaling between relatives can be traced back to a short paper in which John Maynard Smith (1991a) introduced the "Sir

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## Signaling When Interests Diverge

This chapter concerns mating signals, those signals used by individuals of one sex to attract individuals of the other sex with the goal of inducing them to mate. In most mating systems, one sex does the bulk of the signaling, or "advertisement," while the other sex exercises choice among the signalers. A large literature exists that seeks, with considerable success, to explain why it is usually males that signal and females that choose (Bateman 1948, Trivers 1972, Clutton-Brock and Vincent 1991). Exceptions occur, but we shall take the usual pattern as a given, and as a shorthand we will speak in terms of males as the signalers and females as the receivers. The signaling models that we discuss ought in general to apply equally well to cases in which the usual pattern is reversed, so that females signal and males choose.

In the most general case, females are the more discriminating sex and are interested in mating with the best available male, whereas males are less discriminating and are interested in mating with any female. Male and female interests, then, are identical only in the singular case of the one male who is the best available; a female benefits from choosing him and he benefits from being chosen. For males of lesser quality, the interests of the sexes cease to be identical, in the sense that these lesser males would benefit from being chosen by females who would do better to choose someone else. It is in this sense that the interests of signaler and receiver diverge. Because of this divergence in interests, most signalers would benefit from exaggerating their quality, and questions of reliability and deceit become germane.

The literature on mating signals and the information these signals are thought to encode is voluminous. As in our treatment of signals where evolutionary interests overlap, we will confine our discussion here to a few kinds of signals that have been studied in considerable depth and that illustrate problems of reliability and deceit: carotenoid-based coloration, male bird song, and elongated tail plumage in birds. We begin with a review of the relevant theory.

### Mating Signals: Theory

Grafen (1990b) offers a general argument for the stability of honest signaling of mate quality. Suppose that males possess some quality,  $q$ , that is important to females, but which females cannot observe directly. In addition, males pos-



enough that the system is "honest on average," in the sense that females are more likely to obtain a high-quality mate by attending to the signal than by choosing randomly.

### Songs in Oscine Birds

"All those who have attended to the subject, believe that there is the severest rivalry between the males of many species to attract by singing the females." (Darwin 1859, *On the Origin of Species*, 1st Edition, pp. 88-89)

Songs can be defined in general as long, complex vocalizations produced mainly in the breeding season (Catchpole and Slater 1995). Vocalizations that meet this simple definition can be found in a number of animal groups, including most frogs and toads, certain insects, whales, and primates, as well as several orders of birds. The best-known singers are the oscine birds, a subset of the order Passeriformes (passerine birds or "perching birds"), defined taxonomically by the complex musculature of their vocal organ, the syrinx. Although a great deal is known about the function of song in many of those other groups (Gerhardt and Huber 2002, Greenfield 2002), we confine ourselves in this section to the songs of oscine birds.

In most temperate species of oscines, songs are produced exclusively, or nearly exclusively, by males. Singing by females seems to be considerably more common in tropical species than in temperate ones (Stutchbury and Morton 2001), and given the diversity of tropical avifaunas, many more oscines are tropical than are temperate. Nevertheless, we will treat song as a male phenomenon, simply because the available data on song as a signaling system comes almost exclusively from temperate species where male song predominates.

Male song is thought usually to have dual functions, one in male-male aggression, and the other in attracting and courting females. Both functions apply in oscines (Catchpole and Slater 1995) as well as other taxa (Searcy and Andersson 1986). Here we will concentrate on the mate attraction and courtship function, but the possibility of male-male aggressive effects must be kept in mind when interpreting certain types of results, such as correlations between song features and mating success.

### RECEIVER RESPONSE TO BIRD SONG

Song is a complex behavior that varies dramatically between species, and as a consequence a great many song features exist to which female oscines might respond (Searcy and Nowicki 2000). Most of the features for which there is evidence of female response can, however, be assigned to one of four categories: song output, song complexity, local song structure, and vocal performance.

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## Signaling When Interests Oppose

When two unrelated animals compete for some resource, generally speaking one must win and the other lose—one will get the food, the mate, or the territory, and the other will not. A given outcome will benefit the winner and harm the loser, and in that sense the interests of the two are diametrically opposed. But it may be better for both contestants to settle the contest by signaling rather than by fighting, and therefore it is not surprising that a great deal of communication occurs in aggressive contexts. Questions of reliability and deceit seem particularly pressing in such contexts, for receivers should have no interest in attending to an opponent's signals of fighting ability or intentions unless those signals are honest. At the same time, deceiving a receiver might be particularly beneficial to a signaler in an aggressive context, given the absence of common interests.

The literature on aggressive signaling is again too vast for us to review comprehensively, so instead we have chosen particular systems to illustrate specific points of interest. First, we consider aggressive postural displays in birds, which were the focus of much of the early controversy on honesty in animal signals. Next, we examine "badges of status," a term that refers to plumage signals in birds that convey dominance status. Badges are intriguing because these features are simple and seemingly easy to produce, and yet appear to have a profound effect on fitness, raising the question of why deceit is not rampant. Third, we discuss weapon displays in decapod crustaceans, displays that exhibit the enlarged claws these animals use in fighting. Weapon displays in crustaceans are particularly interesting to us because they provide some of the best evidence for deception available for any animal signaling system. Finally, we review the role of the dominant frequency of frog calls in aggressive contests, a signal feature that some have argued is constrained to be honest because of its dependence on body size. Before we get to any of these signaling systems, however, we begin by reviewing theory relevant to signals of aggression.

### Signaling in Aggressive Contexts: Theory

Suppose two animals compete for some resource. The two are evenly matched in fighting ability, but one values the resource more, and so is willing to fight

Of course, the model did not predict the properties of this signaling system in advance, but rather was formulated to explain them post hoc; nevertheless, the model provides a convincing explanation for the evolutionary stability of aggressive signaling in stomatopods.

The case for deception in the open-chela display of snapping shrimp is very different, in the sense that the distinctions between honest and deceptive signalers are small and continuous, rather than large and discrete. In snapping shrimp, deception consists of having a larger chela for one's body size than predicted by the general chela size versus body size relationship. Animals with larger than predicted chelae definitely exist, and can be taken as signaling false information. A weakness in this case is that it has not been shown that these animals benefit from signaling falsely. Nevertheless, the evidence that those individuals with larger than expected chelae signal more than others provides support for the hypothesis that they are benefiting disproportionately, and that this higher level of signaling represents deception by our definition.

### Dominant Frequency in Calls of Frogs and Toads

During the breeding season, males of many species of frogs and toads produce loud, obvious vocalizations termed "advertisement calls" (Wells 1977). These vocalizations typically serve dual functions in attracting females for mating and in warding off and intimidating rival males (Gerhardt 1994). Advertisement calls thus are analogous to the songs of acoustic insects and passerine birds (Searcy and Andersson 1986, Bailey 1991). What is particularly interesting about anuran advertisement calls is that a single property of the calls, their dominant frequency, conveys information about a trait of overwhelming importance in resolving aggressive contests, namely body size.

"Dominant frequency" in these studies is defined as the acoustic frequency with the greatest energy in the signal. Within many species of frogs and toads, the dominant frequency of the advertisement call is inversely correlated with the body size of the caller; in other words, the largest males give the deepest croaks. Another widely recognized fact is that larger body size is of great advantage in winning fights in many anuran species (e.g., Davies and Halliday 1978, Howard 1978, Arak 1983, Robertson 1986). The dominant frequency of an anuran call depends to some extent on the size, especially the weight, of the vocal cords (Martin 1971, 1972), and the size of the vocal cords must in turn be constrained by overall body size. The argument thus runs that dominant frequency depends on size of vocal cords, size of vocal cords depends on body size, and body size determines fighting ability; therefore, dominant frequency is constrained to be an honest signal of fighting ability. In the following, we consider the extent to which this constraint actually operates.