

Signal Reliability and Intraspecific Deception

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Abstract

A signal is considered to be reliable if (1) some feature of the signal is consistently correlated with an attribute of the signaler or its environment and (2) receivers benefit from knowing about that attribute. Signaling systems that do not provide reliable information may exist if signal features exploit a sensory bias of the receiver. At evolutionary equilibrium, however, signals are expected to be reliable on average, meaning that they are reliable enough that a receiver benefits overall from responding to them rather than ignoring them. When there is a conflict of interest between signaler and receiver, signal reliability requires some mechanism to be maintained. Proposed mechanisms include (1) physical and informational constraints on signal production; (2) signal costs that differentially affect signalers of varying quality (the handicap mechanism); (3) differential benefits, which produce honest signals of need; and (4) receiver-dependent costs, which produce conventional signals whose meaning is not related to their physical structure but rather results from an arbitrary convention. The requirement that signals be reliable only on average allows the possibility of some admixture of intra-specific deception, which has been observed in various types of signals, including signals used in aggression, courtship, predator warning, and begging.

Keywords

Conventional signals; Dance language; Deception; Developmental stress hypothesis; Handicap principle; Handicaps; Index signals; Matching; Quorum sensing; Receiver-dependent costs; Sensory exploitation; Signal reliability; Signals of need; Song type matching

Introduction

Signal reliability essentially means honesty: signals are considered to be reliable if they are honest about something of interest to the intended receivers of the signal. More formally, a signal is reliable if (1) some feature of the signal is consistently correlated with an attribute of the signaler or its environment and (2) receivers benefit from knowing about that attribute (Searcy and Nowicki, 2005). In signaling systems that are at evolutionary equilibrium, signals are expected to be reliable, at least on average. A system is at evolutionary equilibrium if natural selection does not favor further change in the behavior of any of the participants. In a simple signaling system, this requirement means that signalers must be doing the best they can given what the receivers are doing, and receivers must be doing the best they can given what signalers are doing. The latter stipulation means that at equilibrium a signal must be reliable enough that it is of net benefit to receivers to respond to it; otherwise, receivers would stop responding to the signal, and the signalers would then cease to give it.

Although some degree of reliability is required for signals to achieve evolutionary stability, reliability is by no means a given in such systems. To the contrary, signal reliability presents a puzzle whenever a conflict of interest exists between signaler and receiver. The puzzle is most easily seen with regard to aggressive signals, as aggression is the context in which the most extreme conflicts of interest occur. Suppose that two animals are contesting for a non-shareable resource, and that the two are equal in fighting ability. Suppose further that one of the two is willing to fight harder to gain the resource; if the animals escalate to a physical fight, this more aggressive individual will win. Given that both winner and loser are likely to experience some costs if they fight, both individuals may rather reliably signal their level of aggressiveness, with the individual giving the lower signal then conceding defeat. In this way, the resource would be allocated to the same individual as if there had been a fight, and both participants avoid the costs of fighting. The problem with this solution is that it is vulnerable to cheating: an individual that exaggerates its aggressiveness stands to benefit by winning more contests and more resources than honest signalers will win. Consequently, natural selection will favor exaggeration, which erodes signal reliability as it spreads. Once reliability has been sufficiently reduced, receivers will be selected to cease responding to the signal, and signalers to cease giving it. Other types of signaling systems are vulnerable to similar problems. In mate choice, for example, signalers may benefit from exaggerating their individual quality in order to attract potential mates, while in systems in which young beg for food from their parents, offspring may benefit from exaggerating their level of need in order to get more food. The fact that all these types of signaling systems exist and persist implies that mechanisms must be present in each system that act to maintain signal reliability. A variety of such mechanisms have been proposed, appropriate for different types of signals (Fig. 1).

Non-Equilibrium Systems

The requirement that signals be reliable on average applies only to signaling systems that are at evolutionary equilibrium, and not to non-equilibrium systems. One mechanism that can produce a non-equilibrium system is sensory exploitation, in which signals are used to manipulate receivers to respond in a manner that benefits the signalers rather than the receivers. In such cases, receivers are

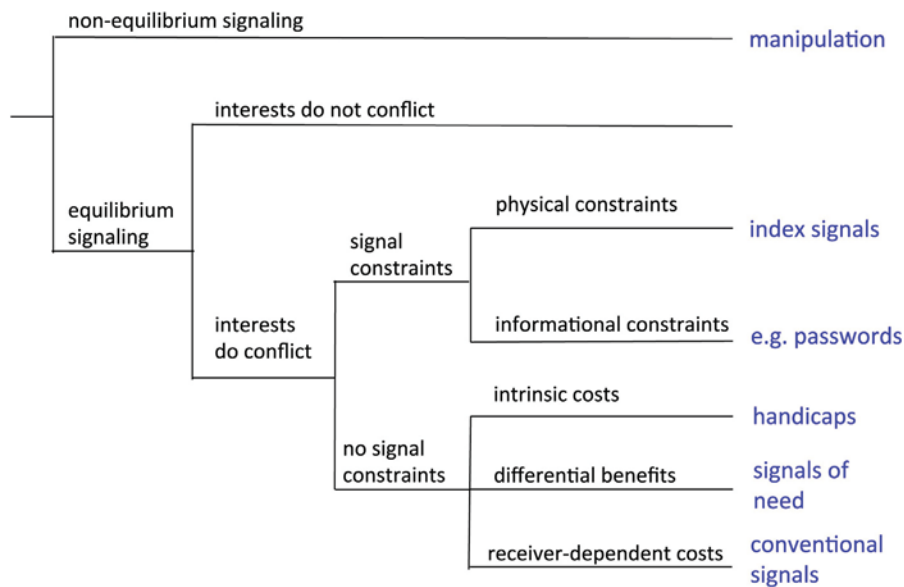


Fig. 1 A taxonomy of animal signals (based in part on Hurd, P.L., Enquist, M., 2005. A strategic taxonomy of biological communication. *Animal Behaviour* 70, 1155–1170). Signals are classified mainly according to the mechanism that maintains reliability. The first division is between signals that are or are not at evolutionary equilibrium; non-equilibrium signals are not informational so reliability is not an issue. A second division is between systems in which the interests of signalers and receivers do or do not conflict. No general term exists for signals given when interests do not conflict, but this category includes many signals given between genetic relatives. A third division is between signals whose production is or is not constrained. Constraints can be physical, producing index signals, or informational, producing signals such as passwords. Signals not subject to constraints are subject to a mix of costs and benefits, and are termed handicaps if their use is determined mainly by intrinsic costs, signals of need if determined mainly by differential benefits, and conventional signals if determined mainly by receiver-dependent costs.

not doing the best they can from an evolutionary perspective, in that they have not evolved responses that are adaptive for themselves. Sensory exploitation can evolve via pre-existing biases in the sensory or neural systems of receivers. Túngara frogs (*Engystomops pustulosus*) provide an example that illustrates the sensory bias hypothesis. Females of this species show a preference for complex male calls consisting of a whine plus one or more chucks over simple calls consisting of a whine only (Rand and Ryan, 1981). This preference can be explained at a mechanistic level by the properties of the female frogs' auditory system, which contains two inner ear organs sensitive to sound: the amphibian papilla, sensitive to low frequency sound (<1200 Hz), and the basilar papilla, sensitive to higher frequencies. The whine component of the male call stimulates primarily the amphibian papilla, while the chuck portion stimulates the basilar papilla; thus the enhanced attractiveness of the complex calls can be explained by its stimulating both inner ear organs (Ryan and Rand, 1990). The sensory exploitation interpretation then is that the female preference for complex calls arose via males evolving call features that exploit pre-existing properties of female hearing, producing a female preference that benefits certain males but that has no benefit for females. Under this interpretation, reliability is not an issue, as the signal provides no relevant information, reliable or unreliable, to receivers. Whether such a non-equilibrium state can be maintained indefinitely is questionable: that is, it is questionable whether females would go on being exploited indefinitely without evolving a response. Another interpretation of the túngara frog case is that complex calls provide better information on the location of the caller than do simple calls, as has been shown to be the case for bats that prey on the frogs (Page and Ryan, 2008) and that also prefer to approach the complex calls (Ryan *et al.*, 1982).

Signaling When Interests do not Conflict

In some signaling systems, the interests of signalers and receivers do not conflict, so the issue of unreliability is moot. Instead, selection can act in such systems to maximize information transfer between signaler and receiver, as was once thought to occur in animal communication as a whole (Dawkins and Krebs, 1978). Conflicts of interests are most likely to be lacking in cases in which signals are exchanged between close genetic relatives. Good examples of such systems can be found in the social insects, notably in the honeybee *Apis mellifera*.

In honeybee colonies, the workers are all females, daughters of a single queen, which typically has mated with multiple males. Workers rarely reproduce directly, and instead help raise the queen's new offspring, which are their sibs and half-sibs. In the absence of worker reproduction, conflicts of interest between workers are minimal. Under these conditions, there has evolved what is perhaps the most remarkable system of communication known for any non-human animal: the "dance language" of honeybees (von Frisch, 1967). Honeybees use dancing to communicate in two contexts: choice of a new nest site and choice of foraging sites. In the foraging context, dancers are workers that have found a food source and then returned to the hive, where they dance in the

dark on a vertical surface. A dancer moves in a figure 8 pattern, wagging her abdomen during the center segment or “waggle run.” Aspects of the dance such as the number of dances performed and the liveliness of each dance reliably signal the quality of food, as measured for example by its sugar content (Seeley *et al.*, 2000). The duration of each waggle run correlates with the distance to the food source (Seeley, 1997). Most remarkably, the direction of the food is indicated by the direction of the waggle run relative to the vertical, with the convention that straight up represents the direction of the sun (von Frisch, 1967). Thus if the food is located 30 degrees to the left of the sun, the waggle run is directed 30 degrees to the left of vertical. There are limits to the precision of the dance, particularly in communicating direction, but imprecision seems to be explained by error rather than by attempts to mislead. Some error seems inevitable, for example in estimating angles relative to the vertical using only gravity as a cue (Preece and Beekman, 2014).

The importance of genetic relatedness in promoting signal reliability has been demonstrated experimentally for quorum sensing systems in bacteria (Diggle *et al.*, 2007). In quorum sensing, bacteria release small molecules into the environment to be taken up by other bacterial cells. These signaling molecules have the effect of promoting the performance of cooperative behaviors such as the secretion of mutually beneficial chemicals. The function of quorum sensing is thought to be to allow bacteria to sense when local densities of cells are high enough to make cooperative behaviors advantageous. Typically reception of the signal leads to greater production of the signal (“autoinduction”), so that signal production accelerates in a positive feedback loop at high cell densities. In the gram negative bacteria *Pseudomonas aeruginosa*, a “signal blind” mutant occurs that produces low levels of the signal but does not show autoinduction and does not respond to the signal with cooperation. Because signal blind mutants do not increase signal production at high densities, they are less reliable in signaling high density than are normal wild type cells. When signal blind and wild type quorum sensing cells were competed against each other in laboratory experiments, the signal blind genotype increased in frequency over time under low relatedness conditions, whereas quorum sensing forms increased when relatedness was high (Diggle *et al.*, 2007). Thus as theory predicts, signal reliability is higher when conflicts of interest between signalers and receivers are minimized.

Signal Constraints

Signal constraints comprise one mechanism that can maintain signal reliability when conflicts of interest exist between signalers and receivers (Fig. 1). Two categories of constraints can be important, physical and informational. In the case of a physical constraint, some individuals are unable to produce particular signals or signal features because of physical limitations on their signal production. In the case of an informational constraint, some individuals are unable to produce particular signals because they lack information that is necessary to do so.

Signals that operate under a physical constraint are termed “index signals.” Such signals are constrained to be reliable, in that the physical mechanisms of signal production generate inescapable correlations between signaler morphology and signal attributes (Maynard Smith and Harper, 2003). The calls of male frogs and toads are often cited as an example. A crucial attribute of frog calls is their dominant frequency, the frequency component with the greatest amount of energy. Receivers of both sexes respond to this feature in ways that can benefit a caller: rival males are deterred by calls with low dominant frequencies, whereas females are attracted to such calls when seeking a mate. Martin (1971) showed that a strong correlation exists between the mass of a frog’s vocal cords and the fundamental frequency at which the cords vibrate. This relationship presumably occurs largely for purely physical reasons and so is largely inescapable. Because body size seems likely to play an important role in determining vocal cord mass, there is a strong causal pathway leading from body size to call frequency: body size determines vocal cord mass, which determines fundamental frequency of vocal cord vibration, which determines dominant frequency of calls. Consequently, the fundamental frequency of male calls should be a reliable indicator of male body size, which has proved to be true for a variety of anuran species (e.g., Davies and Halliday, 1978).

Despite the argument for inescapable reliability, evidence suggests that cheating on the dominant frequency signal has occurred on two time scales. Over evolutionary time, males of many toad species have acquired fibrous masses near the centers of their vocal cords, where the extra mass is particularly effective in lowering dominant frequency. Presumably, these masses evolved gradually, with selection favoring individuals that inherited any slight increment in mass because it made them sound slightly larger than they actually were. On a behavioral time scale, males in species such as cricket frogs (*Acris crepitans*) and green frogs (*Rana clamitans*) lower their dominant frequencies in aggressive situations (Wagner, 1989; Bee and Perrill, 1996), when appearing large is especially beneficial. Using artificial airflow across the vocal cords, Martin found that one way to lower dominant frequency is to lower the pulmonary air pressure, but that doing so leads also to a drop in amplitude. In green frogs, the drop in frequency of calls in aggressive contexts is accompanied by a drop in amplitude (Bee and Perrill, 1996), which may impose a cost by limiting the active space of the call over which females are attracted.

An informational constraint is illustrated by the case of song type matching in songbirds. Matching occurs in songbird species in which individuals possess repertoires of multiple, distinctive song types, allowing them a choice of which song type to sing at a given moment. In such species, matching occurs when one individual chooses to reply to another with the same song type that the other has just sung. In some species, such as song sparrows (*Melospiza melodia*), matching occurs at frequencies well above those predicted by chance (Stoddard *et al.*, 1992), suggesting that matching is deliberate. In western populations of song sparrows, matching is a strong predictor that a male will escalate to more intense signals of aggression and a weak predictor of physical attack (Akçay *et al.*, 2013). One interpretation of these results is that matching is a signal of attention; that is a signal that conveys that the matching individual is paying attention to the individual that it matches. The signal is constrained to be reliable, because matching at

above chance levels is only possible if the matcher is indeed paying attention to the other's songs. The constraint producing reliability is an informational one because it is information that limits ability to match, rather than physical ability to produce the signal.

Handicaps

Handicaps (Fig. 1) are a subset of "free strategic choice" signals: "free" because the signals are not subject to constraints, so any individual is able to produce them, and "strategic choice" because individuals choose whether to produce the signals in response to the costs and benefits of doing so (Hurd and Enquist, 2005). The relationships between signal costs and benefits on the one hand and attributes of the signaler or its environment on the other can then combine to make such signals reliable. The "handicap principle" of Amotz Zahavi is the most widely known hypothesis on how such a mechanism might work.

In his original formulation of the handicap principle, Zahavi (1975) suggested that if mating signals impose a cost to survival, only individuals of high quality will be able to survive their display, and an association is therefore produced between the signal and individual quality. Zahavi (1977) subsequently amended the idea to allow the display's development to adjust to individual quality during a signaler's lifetime, removing the requirement that death cull through signalers to produce reliability. A signal whose development depends on individual quality in this way is termed a "condition-dependent handicap."

The handicap principle was viewed with considerable skepticism until a game theory model by Grafen (1990) confirmed mathematically that, at equilibrium, signal costs can produce displays that are reliable about signaler quality. A graphical version of the model by Johnstone (1997) illustrates the logic (Fig. 2). The model plots the fitness costs and benefits of a signal against its intensity, which for a vocal display might be measured as amplitude or rate, or for a visual display as hue or brightness. The model assumes that the fitness benefits increase with increasing signal intensity, for example because a more intense courtship display attracts more mating partners. The benefit curve eventually levels off, signifying for the courtship signal that there is some upper limit to the number of matings that the signaler can achieve. Two cost curves are shown, one for high quality and one for low quality signalers. Both cost curves are straight lines, with costs increasing more rapidly with intensity for low quality than for high quality signalers. With these assumptions, the optimal signaling level can be found as the value of signal intensity that maximizes the difference between signal benefit and signal cost. As illustrated in Fig. 2, optimum signal intensity is higher for signalers of good quality than for signalers of poor quality. Cheating is not favored, because any signaler that raises its signal intensity beyond its optimum level experiences a greater increase in signal costs than in signal benefits. The model thus produces signals that are both reliable about quality and evolutionarily stable.

Under this scheme, signals are predicted to be reliable only along the dimensions in which they are costly. An illustration of this principle is provided by the contrast between stotting in antelope and calling in frogs. Stotting is a display performed by antelope such as Thomson's gazelles (*Eudorcas thomsonii*), in which the animal bounds high into the air while holding all four of its legs stiff. Stotting is most often performed in the presence of a predator and is thought to be directed to the predator rather than to other antelope. One cost proposed for stotting is that it reduces forward speed (Estes and Goddard, 1967); if so, the message it might convey is that the stotting animal is a speedy one, not worth attempting to chase down. Calling in male frogs, by contrast, is costly in terms of increased energy consumption (Taigen and Wells, 1985), but obviously does not have a cost in reduced speed. Producing calls at a high rate thus signals, presumably to female conspecifics, that the caller is in good condition in terms of energy balance, but not that it is in any way fast.

Although a large array of signals have been proposed to be handicaps, very few have been shown to have all the attributes needed to make the handicap principle work. One of the exceptions is courtship drumming in the wolf spider *Hygrolycosa rubrofasciata*. Males of this species attract females by drumming their abdomens against dry leaves, generating substrate vibrations and an air-

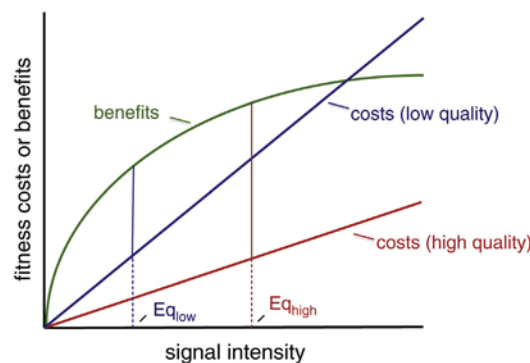


Fig. 2 The handicap model in graphical form (based on Johnstone, R.A., 1997. The evolution of animal signals. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioural Ecology. Oxford: Blackwell, pp. 155–178). The model assumes that the fitness costs of the signal increase linearly with increasing signal intensity, with a more rapid increase for low quality signalers (blue line) than for high quality ones (red line). Fitness benefits increase in a decelerating curve that is the same for both categories of signalers (green curve). The optimum signaling level is at the point where the difference between benefit and cost is maximized; this equilibrium signaling level is greater for a high quality signaler ($E_{q_{high}}$) than for a low quality one ($E_{q_{low}}$).

borne sound. Females chose males drumming at higher rates over males drumming less frequently (Kotiaho *et al.*, 1996) and show the same preference in response to playback of recorded drumming (Parri *et al.*, 1997). Captive males that are fed more drum at higher rates than do males fed less, showing that drumming is condition-dependent (Kotiaho, 2000). Males induced to drum at a higher rates lose weight more quickly and suffer higher mortality than males drumming at lower rates (Mappes *et al.*, 1996), demonstrating that drumming has not only an energy cost but the kind of fitness cost assumed by handicap models. Results were equivocal, however, on whether fitness costs increased more rapidly with drumming rate for low quality signalers than for high quality ones, with the predicted pattern holding for large males but not for small (Kotiaho, 2000).

The energy costs of drumming in wolf spiders and of calling in male frogs can be considered production costs because they are experienced at the time that the signals are generated for use in communication. Other signal costs, by contrast, may be experienced long before signal production, at the time when a signal structure or behavior is developing. According to the developmental stress hypothesis, learned aspects of bird song have developmental costs because song learning requires considerable investment in the brain structures that support song, and this investment is made during a period early in life when resources are limited and other aspects of the phenotype also require investment (Nowicki *et al.*, 2002a). In song sparrows, song repertoire size is a reliable indicator of a number of aspects of male quality, including degree of inbreeding and overall fitness (Reid *et al.*, 2005a,b). Female mating preferences are influenced by both repertoire size (Searcy, 1984) and quality of song learning, as measured by the accuracy with which young males copy adult song models (Nowicki *et al.*, 2002b). Nutritional limitation early in development has a negative effect on adult song repertoire size and on song learning accuracy (Schmidt *et al.*, 2013) as well as on adult body size (Searcy *et al.*, 2004). If song development has nutritional costs, as these results strongly suggest, and some males are better able than others to pay these costs in the face of developmental stresses, then song becomes a reliable indicator of male quality, with its reliability maintained by developmental costs.

Signals of Need

Many animals use signals to solicit resources or other forms of assistance. The begging of baby birds provides a familiar example. When an adult bird visits a nest containing nestlings, the young birds in many species respond with a variety of signaling behaviors, stretching their heads upwards, opening their bills to reveal colorful markings, and producing high-pitched vocalizations. Parents appear to respond to these signals by feeding the young. That provisioning is indeed a response to begging has been confirmed experimentally in a few species, for example by using playback to show that increasing the intensity of begging calls stimulates increased parental feeding (Burford *et al.*, 1998). Begging displays that similarly communicate need from offspring to parents are also found in some mammals, such as seals (Smiseth and Lorentsen, 2001) and meerkats (Manser *et al.*, 2008).

Begging has costs, for example through increased energy expenditure, leading to lower growth (Kilner, 2001), or through predator attraction, leading to higher mortality (Haff and Magrath, 2011). Given the existence of such costs, the reliability of begging might be explained by the handicap model. Note, however, that this model predicts that young in greater need, and thus of lower quality, should beg less intensely than young whose need is lower. This counter-intuitive prediction is confirmed in at least one begging system. In the strawberry poison frog (*Oophaga pumilio*), females deposit newly hatched tadpoles in rearing sites such as water-filled leaf axils. The females then visit these sites once every few days to feed their young with trophic eggs. When a female visits, the tadpole appears to beg by stiffening its body and vibrating. Better-fed tadpoles in general beg more, and tadpoles respond to experimental food deprivation by decreasing their time spent begging and their speed of vibration (Dugas *et al.*, 2017). Begging time and intensity thus appear to be reliable signals of quality rather than of need.

Most begging systems, however, do not work this way. In reed warblers (*Acrocephalus scirpaceus*), for example, nestlings respond to experimental food deprivation by increasing, not decreasing, their intensity of begging (Kilner *et al.*, 1999), and this pattern seems to be general across birds. The reliability of this pattern of begging is best explained not by the handicap model as in Fig. 2, but by a second version of Grafen's general model, depicted in graphical form (Johnstone, 1997) in Fig. 3. Here we assume a single cost line that applies to all signalers and two different benefit curves, one for signalers of high need and a second for signalers of low need. Individuals whose need is high, so that they are nearing starvation, experience a greater fitness benefit from receipt of a certain amount of food than do individuals that are already well fed, and thus of low need. The equilibrium signaling level can again be found for each category of signaler as the signal intensity that maximizes the difference between signal benefit and signal cost. It can be seen from Fig. 3 that the resulting optimum signaling intensity is higher for signalers in greater need than for signalers in lesser need, matching the pattern observed in most birds.

Whether we should label this new model a handicap model is unclear. Signal costs are needed to stabilize the signaling system, but it is really the relationship between benefits and needs that creates the expected relationship between signal intensity and signaler attributes. Therefore this hypothesis is better labeled a differential benefits model.

Conventional Signals

Receiver dependent costs provide a final category of explanations for signal reliability (Fig. 1). Such costs are produced by the responses of receivers and are sometimes alternatively labeled as "social" or "socially enforced" costs. When signals are subject to a physical constraint (e.g., frog calls) or a production cost (e.g., wolf spider drumming), the physical nature of the signal determines its meaning: low frequency in calls means a large frog, and rapid drumming means a well-nourished spider. By contrast, signals that are subject only to receiver dependent costs can have meanings that are arbitrary with respect to their physical nature

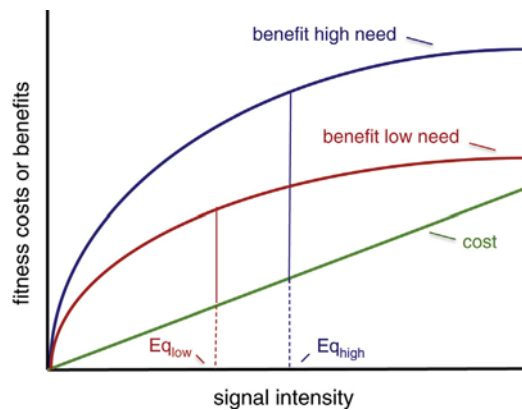


Fig. 3 A differential benefits model in graphical form (based on Johnstone, R.A., 1997. The evolution of animal signals. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology*. Oxford: Blackwell, pp. 155–178). The model assumes that the benefits of signaling increase more rapidly with increasing signal intensity for signalers of high need (blue curve) than for those of low need (red curve). Signal costs follow the same line for both categories of signaler (green line). The optimum signaling level is at the point where the difference between benefit and cost is maximized; this equilibrium signaling level is greater for signalers of high need ($E_{q_{high}}$) than for signalers of low need ($E_{q_{low}}$).

and that are instead determined only by convention. Signals of this type are therefore often termed “conventional signals” (Guilford and Dawkins, 1995). Receiver-dependent costs operate differently than handicap costs, because they do not have to be realized to maintain reliability. As long as cheating has potential costs, reliability can be maintained, even if the potential costs are hardly ever realized (Számádó, 2011).

Game theory models have been used to demonstrate the logic by which receiver-dependent costs might work. In the first of such models, Enquist (1985) assumed that two signals are possible: A, a signal of strength, and B, a signal of weakness. In honest signaling, an individual gives A if strong and B if weak. Individuals that produce B are assumed to give up if their opponent produces A and to fight if their opponent produces B. Individuals that produce A wait for their opponent to give up if it produces B and attack if the opponent produces A. Under these assumptions, weak individuals may be tempted to cheat by producing the signal of strength, because doing so will induce other weak individuals to give up, allowing a cheater to win more contests than it would if it were honest. The cost of cheating in this way is that producing the signal of strength will induce strong opponents to attack, thus embroiling dishonest signalers in fights that they will necessarily lose and that are avoided by weak signalers that are honest. Enquist’s analysis shows that cheating will not have a net advantage if the cost of fighting stronger opponents is high relative to the benefits of winning contests. Honest signaling therefore has a net advantage with some sets of parameter values, but not all.

The facial patterns of the paper wasp *Polistes dominulus* provide an example of a conventional signal (Tibbetts and Dale, 2004). The clypeus (a hardened plate in the front of the head) in these wasps is yellow with 0–3 black spots. The variability, or “brokenness,” of the black pattern, is positively associated with dominance. Wasps avoid challenging individuals whose faces have been experimentally painted to have more spots, demonstrating that the signal has a causal effect on dominance (Tibbetts and Lindsay, 2008). At the same time, subordinates painted to have the facial pattern of dominants receive increased aggression (Tibbetts and Dale, 2004), supporting the receiver-dependent cost hypothesis.

Deception

Although the hypotheses given above explain how reliability can be maintained in animal signaling systems, it remains possible that deception nevertheless occurs in animal communication, and is perhaps even common. When applied to communication between humans, the term “deception” implies that one individual has acted with the intention of causing another to form a false belief. “Intentions” and “beliefs,” however, are mental constructs that are not measurable in other animals and which are therefore not useful in analyzing their behavior. Accordingly it is important to formulate a definition of deception for animal communication that does not rely on these mental constructs. One such definition is as follows: deception occurs when (i) a signaler produces a signal Y that is usually associated with condition X, (ii) a receiver gives a response to Y that benefits the receiver and is appropriate under condition X, and (iii) condition X does not hold (Searcy and Nowicki, 2005). As an illustration, suppose that signal Y is an alarm call usually given when the signaler observes a predator nearby (condition X); that the receiver responds by stopping all activity; and that this freezing response is appropriate when a predator is nearby because freezing lowers the chance that the predator will detect the receiver. In this case the alarm is deceptive if it is given when no predator is present and in a context in which the signaler benefits from causing the receiver to freeze. Note that with this definition the requirement that deception is intentional is replaced by a requirement that the actor benefits in an evolutionary sense from giving a false signal.

Instances meeting this definition have long been known and accepted as deception in interspecific communication. In Batesian mimicry, for example, a harmless prey species evolves a resemblance to a harmful species, as when a harmless king snake evolves the red, yellow, and black pattern of a venomous coral snake (Greene and McDiamid, 1981). Some predators will avoid attacking the

king snake because of its coral snake appearance, thus benefiting the king snake. The red, yellow, and black pattern is usually associated with coral snakes, predators react to the signal in a way that would be appropriate if the signal did represent a coral snake, and king snakes benefit from this response, thus satisfying all our criteria for deception. Predators can also use deception against prey, as when female fireflies of the predatory genus *Photuris* mimic the flash patterns of females of another firefly genus, *Photinus*, to attract male *Photinus* and then consume them (Lloyd, 1965).

The existence of intra-specific deception has been slower to gain acceptance. One of the first cases to be widely recognized involves the meral spread display of the stomatopod *Gonodactylus bredini* (Steger and Caldwell, 1983). These marine crustaceans have a pair of enlarged second maxillipeds, the “raptorial appendages,” which are used in smashing shelled prey and in fighting with conspecifics. In the meral spread display, the raptorial appendages are spread outward, exposing conspicuous spots on their largest segments, the meri. Normally meral spreads are used during aggressive competition for burrows to threaten opponents with impending blows. Where they are deceptive is when used by newly-molted individuals, whose exoskeletons are so soft that they are unable to deliver an effective blow and will in fact injure themselves if they do strike another individual. Even though newly-molted stomatopods cannot follow through on such threats, they actually use meral spreads more often in defense of their burrows than do individuals that are between molts (Steger and Caldwell, 1983). Newly-molted individuals that use meral spreads experience less escalation from opponents and are more likely to retain their burrows compared to newly-molted individuals that neither threaten nor flee (Adams and Caldwell, 1990). Bluffing using meral spreads thus affects receivers in a way that benefits bluffing individuals, satisfying that criterion for deception.

Other cases of intra-specific deceit involve false alarm signals, as in our hypothetical example illustrating the definition of deceit. False alarms are used by male antelope to retain sexually receptive females on their territories (Bro-Jørgensen and Pangle, 2010), by birds (Møller, 1988) and monkeys (Wheeler, 2009) to draw competitors away from food, and by male squirrels (Tamura, 1995) to immobilize rival males. Deception is also known to occur in signals used in mate attraction. In the fiddler crab *Uca annulipes*, males that lose their signaling claws replace them with ones that are lighter, more slender, and cheaper to use, but which seem to be equally effective in attracting females (Backwell *et al.*, 2000). In the nursery web spider *Pisaura mirabilis*, males provide a nuptial gift of an insect prey wrapped in silk to help induce females to mate, but sometimes substitute an empty insect exoskeleton or plant part likewise wrapped in silk (Ghislandi *et al.*, 2014). These deceptive gifts are just as effective in inducing females to mate as legitimate gifts, but lead to briefer copulations, as females seemingly cut copulation short when they discover the deception (Albo *et al.*, 2011). Even signals exchanged between genetic relatives can be deceptive to some extent. Nestling birds increase the intensity with which they beg when competing with siblings for food, so that begging is less reliable about need when nestlings beg with siblings than when they beg alone (Caro *et al.*, 2016).

Conclusion

That intraspecific deception is known to occur in many forms demonstrates that the requirement that signals be reliable in equilibrium systems must not be an absolute one. Instead, it appears that signals need only be “honest on average,” meaning that signals need only be reliable enough that a receiver is better off attending to them than ignoring them (Kokko, 1997). Thus the presence of honest signalers can provide the selective benefit that maintains receiver response to the signal, which is then exploited by a subset of dishonest signalers. One might expect this subset to be small, as is the case for deception in the stomatopod *Gonodactylus bredini*, in which it is estimated that at any one time only 20% of the population has the weakened, newly-molted exoskeleton that leads to deceptive threat displays. In other cases, the subset of dishonest signalers is surprisingly large, for example in the fiddler crab *Uca annulipes*, in which as many as 44% of the males in a population have the deceptively cheap, regenerated signaling claws.

Even in those systems in which dishonesty seems most common, some mechanism must still be in place to make the signals at least honest on average. Those mechanisms include those reviewed above: shared evolutionary interests, physical and informational constraints, the handicap principle, differential benefits, and receiver-dependent costs. Future research may reveal additional mechanisms.

See also: Cognition: Deception: Competition by Misleading Behavior. **Evolution:** Methodology: Cost and Benefit Analysis. **Overview Essays:** Game Theory and Animal Behavior.

References

- Adams, E.S., Caldwell, R.L., 1990. Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Animal Behaviour* 39, 706–716.
- Akçay, C., Tom, M.E., Campbell, S.E., Beecher, M.D., 2013. Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proceedings of the Royal Society London B* 280, 20122517.
- Albo, M.J., Winther, G., Tunii, C., Toft, S., Bilde, T., 2011. Worthless donations: Male deception and female counter play in a nuptial gift-giving spider. *BMC Evolutionary Biology* 11, 329.
- Backwell, P.R.Y., Christy, J.H., Telford, S.R., Jennions, M.D., Passmore, N.I., 2000. Dishonest signalling in a fiddler crab. *Proceedings of the Royal Society London B* 267, 719–724.
- Bee, M.A., Perrill, S.A., 1996. Responses to conspecific advertisement calls in the green frog (*Rana clamitans*) and their role in male-male communication. *Behaviour* 133, 283–301.

- Bro-Jørgensen, J., Pangle, W.M., 2010. Male topi antelopes snort deceptively to retain females for mating. *American Naturalist* 176, e33–e39.
- Burford, J.E., Friedrich, T.J., Yasukawa, K., 1998. Response to playback of nestling begging in the red-winged blackbird, *Agelaius phoeniceus*. *Animal Behaviour* 56, 555–561.
- Caro, S.M., West, S.A., Griffin, A.S., 2016. Sibling conflict and dishonest signaling in birds. *Proceedings of the National Academy of Sciences of the United States of America* 113, 13803–13808.
- Davies, N.B., Halliday, T.R., 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* 274, 683–685.
- Dawkins, R., Krebs, J.R., 1978. Animal signals: Information or manipulation? In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology*. Blackwell, Oxford, pp. 282–309.
- Diggle, S.P., Griffin, A.S., Campbell, S.E., West, S.A., 2007. Cooperation and conflict in quorum-sensing bacterial populations. *Nature* 450, 411–414.
- Dugas, M.B., Strickler, S.A., Stynoski, J.L., 2017. Tadpole begging reveals high quality. *Journal of Evolutionary Biology* 30, 1024–1033.
- Enquist, M., 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour* 33, 1152–1161.
- Estes, R.D., Goddard, J., 1967. Prey selection and hunting behavior of the African wild dog. *Journal of Wildlife Management* 31, 52–70.
- Ghislandi, P.G., Albo, M.J., Tuni, C., Bilde, T., 2014. Evolution of deceit by worthless donations in a nuptial gift-giving spider. *Current Zoology* 60, 43–51.
- Grafen, A., 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144, 517–546.
- Greene, H.W., McDiarmid, R.W., 1981. Coral snake mimicry: Does it occur? *Science* 213, 1207–1212.
- Guilford, T., Dawkins, M.S., 1995. What are conventional signals? *Animal Behaviour* 49, 1689–1695.
- Haff, T.M., Magrath, R.D., 2011. Calling at a cost: Elevated nestling calling attracts predators to active nests. *Biology Letters* 7, 493–495.
- Hurd, P.L., Enquist, M., 2005. A strategic taxonomy of biological communication. *Animal Behaviour* 70, 1155–1170.
- Johnstone, R.A., 1997. The evolution of animal signals. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology*. Blackwell, Oxford, pp. 155–178.
- Kilner, R.M., 2001. A growth cost of begging in captive canary chicks. *Proceedings of the National Academy of Sciences of the United States of America* 98, 11394–11398.
- Kilner, R.M., Noble, D.G., Davies, N.B., 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature* 397, 667–672.
- Kokko, H., 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology* 41, 99–107.
- Kotiaho, J.S., 2000. Testing the assumptions of conditional handicap theory: Costs and condition dependence of a sexually selected trait. *Behavioral Ecology and Sociobiology* 48, 188–194.
- Kotiaho, J.S., Alatalo, R.V., Mappes, J., Parri, S., 1996. Sexual selection in a wolf spider: Male drumming activity, body size and viability. *Evolution* 50, 1977–1981.
- Lloyd, J.E., 1965. Aggressive mimicry in *Photuris*: Firefly femmes fatales. *Science* 149, 653–654.
- Manser, M.B., Madden, J.R., Kunc, H.P., English, S., Clutton-Brock, T., 2008. Signals of need in a cooperatively breeding mammal with mobile offspring. *Animal Behaviour* 76, 1805–1813.
- Mappes, J., Alatalo, R.V., Kotiaho, J., Parri, S., 1996. Viability costs of condition-dependent sexual male display in a drumming wolf spider. *Proceedings of the Royal Society London B* 263, 785–789.
- Martin, W.F., 1971. Mechanics of sound production in toads of the genus *Bufo*: Passive elements. *Journal of Experimental Zoology* 176, 273–294.
- Maynard Smith, J., Harper, D., 2003. *Animal Signals*. Oxford University Press, Oxford.
- Møller, A.P., 1988. False alarm calls as a means of resource usurpation in the great tit *Parus major*. *Ethology* 79, 25–30.
- Nowicki, S., Searcy, W.A., Peters, S., 2002a. Brain development, song learning and mate choice in birds: A review and experimental test of the “nutritional stress hypothesis”. *Journal of Comparative Physiology A* 188, 1003–1014.
- Nowicki, S., Searcy, W.A., Peters, S., 2002b. Quality of song learning affects female response to male bird song. *Proceedings of the Royal Society London B* 269, 1949–1954.
- Page, R.A., Ryan, M.J., 2008. The effect of signal complexity on localization performance in bats that localize frog calls. *Animal Behaviour* 76, 761–769.
- Parri, S., Alatalo, R.V., Kotiaho, J., Mappes, J., 1997. Female choice of male drumming in the wolf spider *Hygrolycosa rubrofasciata*. *Animal Behaviour* 53, 305–312.
- Preece, K., Beekman, M., 2014. Honeybee waggle dance error: Adaption or constraint? Unravelling the complex dance language of honeybees. *Animal Behaviour* 94, 19–26.
- Rand, A.S., Ryan, M.J., 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Zeitschrift für Tierpsychologie* 57, 209–214.
- Reid, J.M., Arcese, P., Cassidy, A.L.E.V., et al., 2005a. Fitness correlates of song repertoire size in free-living song sparrows (*Melospiza melodia*). *American Naturalist* 165, 299–310.
- Reid, J.M., Arcese, P., Cassidy, A.L.E.V., et al., 2005b. Hamilton and Zuk meet heterozygosity? Song repertoire size indicates inbreeding and immunity in song sparrows (*Melospiza melodia*). *Proceedings of the Royal Society of London B* 272, 481–487.
- Ryan, M.J., Rand, A.S., 1990. The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* 44, 305–314.
- Ryan, M.J., Tuttle, M.D., Rand, A.S., 1982. Bat predation and sexual advertisement in a neotropical anuran. *American Naturalist* 119, 136–139.
- Schmidt, K.L., Moore, S.D., MacDougall-Shackleton, E.A., MacDougall-Shackleton, S.A., 2013. Early-life stress affects song complexity, song learning, and volume of the brain nucleus RA in adult male song sparrows. *Animal Behaviour* 86, 25–35.
- Searcy, W.A., 1984. Song repertoire size and female preferences in song sparrows. *Behavioral Ecology and Sociobiology* 14, 281–286.
- Searcy, W.A., Nowicki, S., 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press, Princeton, New Jersey.
- Searcy, W.A., Peters, S., Nowicki, S., 2004. Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*. *Journal of Avian Biology* 35, 269–279.
- Seeley, T.D., 1997. Honey bee colonies are group-level adaptive units. *American Naturalist* 150, S22–S41.
- Seeley, T.D., Mikheyev, A.S., Pagano, G.J., 2000. Dancing bees tune both duration and rate of waggle-run production in relation to nectar-source profitability. *Journal of Comparative Physiology A* 186, 813–819.
- Smiseth, P.T., Lorentsen, S.-H., 2001. Begging and parent-offspring conflict in grey seals. *Animal Behaviour* 62, 273–279.
- Steger, R., Caldwell, R.L., 1983. Intraspecific deception by bluffing: A defense strategy of newly molted stomatopods (Arthropoda: Crustacea). *Science* 221, 558–560.
- Stoddard, P.K., Beecher, M.D., Campbell, S.E., Horning, C.L., 1992. Song-type matching in the song sparrow. *Canadian Journal of Zoology* 70, 1440–1444.
- Számadó, S., 2011. The cost of honesty and the fallacy of the handicap principle. *Animal Behaviour* 81, 3–10.
- Taigen, T.L., Wells, K.D., 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *Journal of Comparative Physiology B* 155, 163–170.
- Tamura, M., 1995. Postcopulatory mate guarding by vocalization in the Formosan squirrel. *Behavioral Ecology and Sociobiology* 36, 377–386.
- Tibbetts, E.A., Dale, J., 2004. A socially enforced signal of quality in a paper wasp. *Nature* 432, 218–222.
- Tibbetts, E.A., Lindsay, R., 2008. Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. *Biology Letters* 4, 237–239.
- von Frisch, K., 1967. *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge, MA.
- Wagner, W.E., 1989. Fighting, assessment, and frequency alteration in Blanchard's cricket frog. *Behavioral Ecology and Sociobiology* 25, 429–436.
- Wheeler, B.C., 2009. Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society London B* 276, 3013–3018.
- Zahavi, A., 1975. Mate selection – A selection for a handicap. *Journal of Theoretical Biology* 53, 205–214.
- Zahavi, A., 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* 67, 603–605.

Further Reading

- Dugas, M.B., Strickler, S.A., Stynoski, J.L., 2017. Tadpole begging reveals high quality. *Journal of Evolutionary Biology* 30, 1024–1033.

- Enquist, M., 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour* 33, 1152–1161.
- Grafen, A., 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144, 517–546.
- Guilford, T., Dawkins, M.S., 1995. What are conventional signals? *Animal Behaviour* 49, 1689–1695.
- Hurd, P.L., Enquist, M., 2005. A strategic taxonomy of biological communication. *Animal Behaviour* 70, 1155–1170.
- Maynard Smith, J., Harper, D., 2003. *Animal Signals*. Oxford University Press, Oxford.
- Mokkonen, M., Lindstedt, C., 2016. The evolutionary ecology of deception. *Biological Reviews* 91, 1020–1035.
- Nowicki, S., Searcy, W.A., Peters, S., 2002. Brain development, song learning and mate choice in birds: A review and experimental test of the "nutritional stress hypothesis". *Journal of Comparative Physiology A* 188, 1003–1014.
- Scott-Phillips, T.C., 2008. Defining biological communication. *Journal of Evolutionary Biology* 21, 387–395.
- Searcy, W.A., Nowicki, S., 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press, Princeton, New Jersey.
- Steger, R., Caldwell, R.L., 1983. Intraspecific deception by bluffing: A defense strategy of newly molted stomatopods (Arthropoda: Crustacea). *Science* 221, 558–560.
- Tibbetts, E.A., Dale, J., 2004. A socially enforced signal of quality in a paper wasp. *Nature* 432, 218–222.
- Zahavi, A., 1975. Mate selection – A selection for a handicap. *Journal of Theoretical Biology* 53, 205–214.