Animal signals

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The study of animal signals began in earnest with the publication in 1872 of Charles Darwin's *The Expressions of the Emotions in Man and Animals*, which laid the basis for a comparative study of signals across all animals, including humans. Yet even before Darwin, the exceptional diversity of animal signals has gripped the attention of natural historians and laymen alike, as these signals represent some of the most striking features of the natural world. Structures such as the long ornamented tail of the peacock, the roaring sounds of howler monkeys, audible kilometers away, and the pheromone trails laid by ants to guide their nestmates to resources are each examples of animal signals (Figure 1). Indeed, because signals evolved for the purpose of communicating (Box 1),

their prominence can be hard for even a casual observer to overlook. Animal signals therefore raise many scientific questions: What are their functions? What information do they transmit? How are they produced? And why did they evolve?

Pioneering empirical work on animal signals was carried out by Karl von Frisch, Konrad Lorenz, and Niko Tinbergen, three ethologists who were awarded the Nobel Prize in 1973. Karl von Frisch decoded the famous 'waggle dance' of honey bees, showing that seemingly insignificant dancing motions that bees make inside the hive can tell other colony members the precise location of distant food sources. Lorenz integrated himself into the daily activities of geese, allowing them to imprint on him, and he thereby identified many of the nuances of their communication. Niko Tinbergen, an astute field observer, disentangled signals that gulls and other animals use in territorial conflicts. Tinbergen was also responsible for bestowing an essential framework for studying animal signals — his 'four questions' about the phylogeny, function, development and mechanism of

signals or any other behavior. Together, these three scientists emphasized the importance of entering the perceptual world of animals to fully analyze and understand animal signals. Their work underlies much of the current scientific research on animal signals.

Subtleties of animal signals
Many animal signals may 'jump out' at the human observer, because they utilize sensory modalities to which humans are highly attuned, but other signals can be harder to detect, involving modalities that are outside our species' sensory perception. For instance, electric fish utilize discrete pulses of electric discharge in aquatic environments to communicate. Given the diverse channels through which animals communicate — encompassing chemical, electric, acoustic, optical, and tactile modalities — there are clearly abundant avenues for signaling, as well as ample biological raw material that can be co-opted for signaling functions. This underscores an important lesson for researchers: not all animal signals are necessarily prominent, and so acute sensitivity
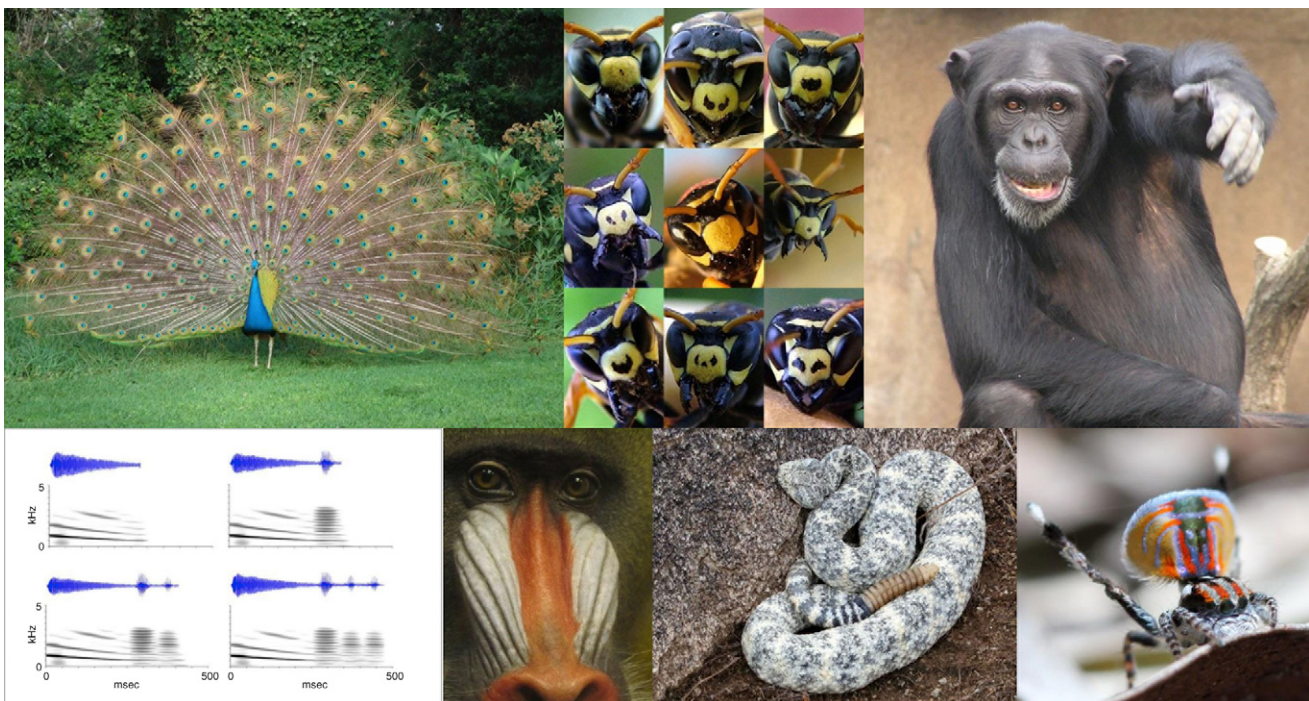

Figure 1. Diversity of animal signals.
From top left: peacock (*Pavo cristatus*) displaying its elaborate tail feathers (courtesy of Jessica Yorzinski); wasp (*Polistes dominulus*) variation in facial 'badges of status' (courtesy of Elizabeth Tibbetts); chimpanzee (*Pan troglodytes*) gesturing (courtesy of Michael Tomasello); Túngara frogs (*Physalaemus pustulosus*) spectrograms of chuck calls (courtesy of Michael Ryan); mandrill (*Mandrillus sphinx*) colorful red face (courtesy of Mark Laidre); southwestern speckled rattlesnake (*Crotalus mitchellii*) with rattle exposed (courtesy of Harry Greene); peacock spider (*Maratus volans*) raising its legs and abdomen in display (courtesy of Madeline Girard).

Box 1.

Defining signals and a framework for their investigation.

Signals can be defined in a four-part definition:
(1) acts or structures produced by signalers, which
(2) evolved for the purpose of conveying information to recipients, such that
(3) the information elicits a response in recipients, and
(4) the response results in fitness consequences that, on average, are positive for both the signaler and the recipient.

For example, when a hermit crab raises its claw, performing a threat signal, it provides information about its intention to attack, which a recipient can then respond to by fleeing, which ultimately results in both the signaler and the recipient benefiting by avoiding an escalated fight.

Signal	Information	Response	Fitness consequences

Threaten

Signaler's intention to attack → Recipient flees from signaler →

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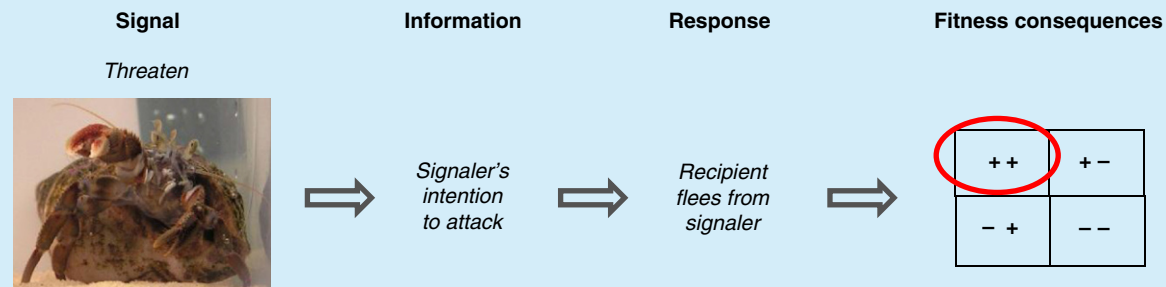
Each part of the definition of a signal provides a guide to key empirical measurements that must be made to fully understand the signal. First, the form of a signal must be precisely described and quantified, often requiring specialized equipment (e.g., a spectrometer for reflected light signals or audio recording equipment for acoustic signals). Second, a consistent correlation must be established between the use of a signal and the particular contexts (*e.g.*, signaler attributes or environmental parameters) that have relevance to the recipient, to show that the signal is reliably informative. Third, the probability of the recipient's behavior changing between different states must be quantified after (compared to before) it received the signal, to show the signal alters the recipient's response. And fourth, and perhaps most difficult, the impact on reproductive success that such signaling interactions entail must be established for both the signaling and recipient parties, to determine whether each party — as expected — is benefiting on average. Each of these objectives should ideally be examined both observationally during natural interactions as well as in experimentally controlled situations.

to the perceptual world and the environmental constraints faced by one's study organisms is vital, otherwise many of the subtleties of animal signals may be overlooked.

Constraints and contexts
Even when signals occur in modalities familiar to humans, they may still prove challenging to detect due to selection pressures that favor subtlety over conspicuousness. Signals can thus vary along a continuum on a variety of axes, from 'conspiratorial whispers' (close-range, understated, and directed to a single recipient) to extremely prominent signals (broadcast over long distances to a large audience of recipients). Where a given signal falls on this scale will depend on many factors, including the social context in which signaling occurs, the chance of unintended eavesdroppers (*e.g.*, predators) intercepting the signal and the environment through which the signal must travel. The environment, for instance, can impose strong

constraints on the efficacy of signal transmission, distorting or degrading the signal as it travels to its target. Certain modalities may thus provide a superior solution for communicating in a given environment — *e.g.*, acoustic signals for communicating in dense forests where visual signals would be inadequate. The duration of the signal also places constraints on which modality is optimal: viscous chemical signals that last for extended periods can serve well as long-lasting territorial markers, whereas rapidly fading acoustic calls will serve well as alarms that designate momentary external threats. Overall, environmental constraints shape the design of signals, especially a signal's modality and form.

The social contexts of signaling, however, also matter, and animal signals are used in a variety of contexts, both between different species (*e.g.*, signals used by prey to deter predators) and within a species (*e.g.*, signals use for mate attraction, intimidating rivals,

altering group mates to an external danger, or begging for food from one's parents). In all these contexts, different types of information are conveyed (Box 2), which may at times necessitate different forms of signals to accomplish the communicative goal. For instance, Darwin pointed out that signals with opposite meanings often have opposite forms. This 'principle of antithesis', as he called it, explains why a dog approaching with hostile intentions instead of affectionate intentions exhibits such different signals: the hostile dog is prepared to attack and so assumes a posture that is in accordance with its readiness to aggress, whereas the affectionate dog does exactly the opposite to guarantee its lack of hostility is not mistaken. Thus, a signal's design is also shaped by the information it must convey.

Cues vs. signals and the evolutionary origins of signals
An important distinction can be made between a cue and a signal. Like

signals, cues can provide information to others. For instance, the rustling of a mouse as it forages in the undergrowth is a cue that may convey information to a predator about the mouse's location. However, this information is purely a by-product of the mouse's foraging activity: the rustling was not shaped by natural selection to convey that information. In contrast, signals have been shaped by natural selection for the specific purpose of conveying information and thereby influencing others' behavior, ultimately impacting both the signaler's and the recipient's fitness.

While cues differ from signals, many signals may have evolved from what once were cues. For instance, a number of species exhibit threat signals involving prominent postures or bodily movements that indicate an individual's aggressive motivation or fighting ability. These threat signals are often abbreviated forms of a species' natural attack pattern, with individuals exposing their weaponry or positioning themselves in preparation for conflict. Over evolutionary time, such intention movements appear to have been ritualized into prominent and highly stereotyped displays, which can convey the likelihood of an animal attacking. As such, animals need not always undertake an all-out escalated fight, but can potentially use relevant signals to make critical assessments beforehand. In a similar manner, Darwin first pointed out that many vocal signals that animals perform appear to have originated from altered breathing patterns that initially may have been cues, correlated with the types of physical action the breather was preparing to undertake.

The evolutionary process by which signals evolve from cues is known as the 'signaler precursor route'. In this case, the signals originate from behaviors or structures that originally were informative aspects of the signaler and then were further specialized over evolutionary time to convey information more effectively. There is also another route for the evolution of signals: 'recipient precursors'. In this case, recipients may have preexisting sensory biases that are either accidental or have been selectively favored in contexts independent of communication. For instance, females of a certain species might prefer and be attracted to the color red because their preferred

food source is red. When such biases exist it may then favor the evolution of signaling traits that exploit the bias (*e.g.*, males may develop red coloration to attract females for mating). Such sensory exploitation appears to have occurred in mate choice for many species, one example being the chuck call of Túngara frogs, which is extremely attractive to females, even females in species where males have never evolved the call. However, signals that have originated through recipient precursors need not remain entirely uninformative. Recent evidence in splitfin fish shows that even when signals originate from such 'sensory traps' they can later become reliable indicators of key aspects of male quality.

Signals as information or manipulation

Sensory exploitation as an evolutionary source of signals raises a more general question: are signals fundamentally informative (providing the recipient with useful information that helps it choose the right response) or are they instead manipulative (deceiving the recipient by inducing a response that is good for the signaler, but not necessarily for the recipient)? If signaler and recipient have aligned interests, then this problem of manipulation does not arise; but if signaler and recipient have conflicting interests, then manipulation can be a problem. In a seminal paper, Richard Dawkins and John Krebs suggested that, from an evolutionary perspective, signals should be viewed as manipulative, as natural selection will always favor signalers that elicit responses that are in their own selfish interests, regardless of the fate of the

recipient. Dawkins and Krebs went so far as to suggest that the idea of signals bearing information should be abandoned entirely.

The logic of this 'manipulation argument' was elegantly modeled with evolutionary game theory by John Maynard Smith. Maynard Smith envisioned a population of animals in which a certain signal reliably provides information to recipients, for instance by honestly indicating the likelihood of a signaler attacking. Now consider the consequences of a mutant that performed this same signal even when it did not intend to attack. This dishonest mutant would invade the population, because it could drive opponents away from precious resources despite having no intention to follow through with its signal. Eventually, the entire population would exhibit this dishonest signal, making the signal worthless and uninformative.

The problem of dishonest mutants seemed intractable until Amotz Zahavi suggested a solution: the 'handicap principle'. The handicap principle suggested that some signals might be too costly for a signaler to fake. For instance, certain mate attraction signals might only be produced by males that are of sufficiently high quality, because the costs to lower quality males of displaying these signals would be prohibitive. Parallel concepts had arisen independently in economics, where 'conspicuous consumption' and 'extravagant wastefulness' were suggested to reliably signal wealth among humans. For the handicap principle, in particular, the long train of the peacock seemed to provide a plausible example, given the expense

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Box 2.

Some types of information conveyed by animal signals.

Internal environment – signaler's attributes
- Species, sex, age, group membership, kinship, individual identity
- Location (*e.g.*, direction or distance from recipient)
- Condition or quality (*e.g.*, weight, body size, age, health, mating receptivity)
- Fighting ability, strength, resource holding potential, or dominance status
- Motivational or affective state, emotions (*e.g.*, fear or hunger), subjective resource valuation, willingness to escalate a contest, aggressive intentions, probable future actions (*e.g.*, attack)

External environment – features of the outer world
- Referential designation of objects or events (e.g., predator presence or type, danger level, or quantity or quality of food sources), either immediately present or remote in space or time

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Box 3.

Factors guaranteeing signals remain reliable despite signaler–recipient conflict.

Index: these signals (sometimes referred to as 'unfakeable' or 'assessment' signals) are intrinsically anchored to an animal's anatomy or physiology by physical constraints. Such signals are usually based on some structure that has been grown over an extended period and which allows recipients to assess the signaler's resource-holding potential. The cost that stabilizes reliability is thus paid over the course of development, such as through investment in size or generation of a specific bodily organ. An example of index signals is the frequency of vocalizations in frogs, where pitch depth is constrained by the mass of the vocal chords, providing a reliable indicator of size.

Quality handicap: these signals are the type first envisioned by Zahavi in which the cost that stabilizes honesty is paid as the signal is produced. These signals 'use up' the quality being advertised — often because they are energetically costly — so only 'high quality' individuals can afford them. An example of quality handicap signals is the roaring of red deer, where the production of roars requires significant and prolonged movement of chest muscles and thus quickly exhausts 'low quality' individuals.

General handicap: these signals incur a production cost, but this cost is the same for all signalers. What differs between signalers is the benefits they stand to gain from success-fully eliciting a response with the signal. Signalers that will benefit more (*e.g.*, hungrier off-spring) are more likely to signal (*e.g.*, beg more often for food from their parents), indicating their greater need. An example of general handicap signals are the gaping mouth displays produced by begging chicks of many bird species.

Convention and vulnerability: these signals can be produced with minimal production costs and negligible difficulty. Their reliability is guaranteed by the fact that recipients frequently test signalers, probing them for weaknesses. Performance of some of these signals thus places the signaler at risk, either by exposing a vulnerable part of the body or precipitating attack. Individuals that perform these signals probabilistically suffer the potential for severe injury, so those who would be unable to bear the associated risk would find dishonesty unprofitable. An example are the black facial patterns (so-called 'badges of status') of paper wasps.

Reputation: these signals are not necessarily difficult or costly to produce, nor are they associated with attacks from recipients. These signals require only that signalers and recipi-ents have prior knowledge of one another's past signaling record, which occurs if individuals recognize one another, interact repeatedly, and remember the outcome of prior interactions. Signals produced by individuals who were dishonest in the past will be devalued or not responded to at all. Potential cheaters thus experience a tradeoff between the immediate benefits of successful dishonesty and the future consequences of losing their long-term credibility. An example of a reputation signal is alarm calling in vervet monkeys, where indi-viduals whose alarms have been unreliable in the past fail to evoke responses later on.

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of growing and displaying such a costly structure for its bearer. Yet, the question remained whether the handicap principle could solve other cases of conflicts-of-interest between signalers and recipients; and if not, whether there might be other solutions for signal reliability.

Solutions for signal reliability
Recent work has indicated that the handicap principle is not the only possible explanation for the reliability of animal signals and, in fact, several mechanisms — not all of which require excessive production costs — may guarantee that signals continue to

be informative over evolutionary time (Box 3). Indeed, when signalers and recipients are highly related to one another, or when they have minimal conflicting interest, then signals may be cost free, with certain types of 'pooling equilibria' emerging in which some signalers of different types employ the same cost-free signal. And even when signalers and recipients have strong conflicts of interest, theoretical models indicate that honesty itself need not be costly: all that is required is that each instance of lying that deviates from the honest equilibrium be met with high costs. Mechanisms for reliability in conflict

situations, therefore, typically hinge on the fact that recipients of signals have their own evolutionary interests, so if signals do become unreliable, then it will no longer pay recipients to attend to them. The tendency of recipients to ignore unreliable signals should consequently put pressure on signalers to use only the types of signals that can be readily validated, based on differential signaling costs or benefits or based on the past signaling record of the signaler. Signalers and recipients will thus be dynamically coupled over time — even if one party attains an advantage for some period, over the long haul we should expect signalers to provide reliable information, and recipients to make use of this information, with both parties benefiting overall from their co-evolutionary relationship.

An important subtlety though is that while signals are predicted to be generally reliable they need not be perfectly reliable for recipients to still pay attention to them. As long as signals are 'honest on average' — that is, they contain enough useful information for recipients to be better off attending to them than ignoring them — then the signaling system can remain evolutionarily stable. Consequently, there is still scope for signalers to occasionally misrepresent their signals, with at least some dishonesty occurring at equilibrium. As Wolfgang Wickler noted, "We can really learn the truth about the evolution of signals best from the liars." Thus, as long as deception either remains at a low enough frequency, is difficult for recipients to detect, or does not harm recipients' fitness too drastically, it can persist. Interestingly, in stomatopod crustaceans, high levels of threat displays are observed when signalers are molting — a life stage in which the signaler is unable to follow through with its threat, so that the threat amounts to a bluff. Recipients nevertheless still flee from such bluffs. The reason bluffing remains stable is because only a small proportion of individuals are molting at any one time; threat displays overall are therefore still worth heeding, particularly because the costs to recipients of challenging true threats can be extremely high. Interestingly, in other systems, such as paper wasps, where black facial spots of varying size and shape are 'badges of status' that signal dominance, wasps whose facial patterns do not

reliably reflect their true dominance are severely punished; and because high status individuals are frequently tested in this system, bluffing is rare.

Sexually-selected signals with multiple components

Given the mechanisms favoring signalers that provide reliable information, an important goal of studying animal signals is to isolate the specific information content of signals. This goal is perhaps most challenging in mate choice, where elaborate signaling traits have been shaped by sexual selection and can involve multiple components and modalities (*e.g.*, males courting females by producing bright visual colors, sounds, substrate-borne vibrations, and pheromones, all simultaneously). An important question for such signals is how recipients integrate all this complexity and how they use this information to select mates. Two important hypotheses have been proposed for such multi-modal sexual signals: different signals might each convey different information (the 'multiple message' hypothesis) or different signals might convey the same information (the 'backup message' hypothesis). It is also possible that some sexually selected signals might not provide information at all, because they are still in a 'runaway' process of exploitation that has not yet stabilized. Researchers are beginning to understand how these different explanations might apply across animal species by experimentally altering certain signal components and determining what information recipients glean from them and how they alter their response. Another useful approach has been to carefully measure the specific signal components that recipients attend to most. For instance, researchers recently developed a portable eye-tracking system to examine which elements of a peacock's multi-ornament display are visually attended to by females. Interestingly, females selectively attended to specific components of male's courtship displays and largely ignored other components, which suggests some components might be differentially informative. Notably though, the interaction between different signal components sometimes functioned to more effectively capture and maintain

female attention, so combinations of signals might synergize and exceed the effectiveness of any single signal component.

Interactive experimental approaches

While observation remains an essential first step in describing animal signals, experiments are critical for testing the accuracy of these conclusions and fully understanding the complexity of animal signals. A wide range of experimental approaches have been used to study animal signals, though perhaps most useful are those involving the interactive presentation of signals to live animals — what Donald Griffin has called "an experimental dialogue". Such dialogues can be accomplished for signals from any modality by presenting the signal to recipients in controlled conditions (for instance, through acoustic playback of sound signals). Interactive models and robots, in particular, offer a powerful means of isolating the responses that signals elicit in recipients as well as the conditions under which signals are most likely to be produced. For instance, the development of an interactive female sage grouse robot, with a camera and microphones implanted inside the robot, has enabled researchers to examine how male sage grouse change their courtship signals based on a female's orientation and postures. Such research can give insights into how signalers coordinate their signaling with moment-by-moment feedback from recipients.

From animal signals to human language

While animal signals can be complicated, they are dwarfed in complexity by human language. Language allows our species to transmit vastly more information than any animal signaling system and to communicate on any topic, new or imaginary. Humans can accomplish this feat because we are able to semantically reference anything around us with words and then create new meanings based on the unique syntax of altered word-orderings. In contrast, animal signals are often, though certainly not always, single isolated signals or repeated sets of the same signal, and they are generally dedicated to specialized functions that provide just a few categories of information.

It is notable that many aspects of human communication still have parallels with animal signals, being based on non-verbal gestures or facial expressions that are also found in our primate relatives. Some researchers have even suggested that gestures might have provided the first proto-languages during human evolution; and it is interesting in this respect that attempts to teach aspects of language to nonhuman primates first met with success only after American Sign Language — a gesture based system — was used. Nevertheless, human language is far richer in its communicative potential than any nonhuman species can attain, even after dedicated training with human teachers, and this therefore raises an important challenge for research at the interface of animal signals and human language: how and why did language arise as a communication system and why is it that no other animal signaling system has the power of human language?

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