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Animal Signalling

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Synonyms

Animal communication; Signals

Definition

Signals are an important aspect of social behavior in the biological world, as they allow information and/or influence to be transmitted between organisms via intermediary signalling and response behaviors. This is often interpreted through an evolutionary lens, whereby the relevant behaviors are assumed to have co-evolved; however, alternative definitions and formalizations exist in the literature.

Introduction

The evolutionary science of animal signalling began with Charles Darwin's *The Expressions of the Emotions in Man and Animals*, published in 1872, and signalling has been central to the study of animal behavior (ethology) since then. In 1973, the Nobel Prize in Medicine was jointly awarded to three ethologists whose work was pioneering in this regard: Karl von Frisch, Konrad Lorenz, and Niko Tinbergen. This included work on the phenomena of imprinting by hatchling birds, and von Frisch's description of the complex, information-rich "waggle dance" of worker bees, by which the details of distant food sources are encoded and communicated to others in the hive. Since then, animal signalling has been the subject of laboratory and field studies on animals ranging from microbial life to large vertebrates including primates and cetaceans. Several bodies of theoretical literature have also been spawned, with cross-over applications to the human sciences.

Forms of Animal Signalling

Animal signalling occurs in a wide variety of forms and contexts. Striking cases occur across species boundaries and in highly asymmetric relationships, for example, between prey animals and their predators as in the case of the leaping (stotting) behavior of Thompson's Gazelles during pursuit by predators, and vivid coloration of some amphibian or insect species to advertise their toxicity. However, most animal signalling takes place between conspecifics and functions to regulate social behavior. Most signals are also biologically fixed and involuntary, in the sense of either being expressed developmentally (such as coloration) or reactively, e.g., via visual or audible

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cues of aggression, fear, and sexual arousal, and nonvisual signals such as pheromones and physical contact. Such traits and behaviors are typically innate and robust across a species, though there are known cases, such as whale song, where signal variants propagate by cultural transmission and social learning.

Many vertebrates also engage in behaviorally complex signalling systems, such as the alarm calls of several monkey species and the gestural systems of great apes. Vervet monkeys emit alarm calls that discriminate between different types of predator (e.g., snake, eagle, leopard, baboon) which in turn elicit "best response" avoidance behaviors from alerted conspecifics (e.g., climb a tree, hide under a bush, etc.) (Seyfarth et al. 1980). Communicative behaviors of chimpanzees and other great apes have been extensively studied and include both reflexive signals (such as baring teeth to communicate aggression) and dozens of vocalizations and gestures (such as clapping and beckoning) which facilitate social interaction. These appear to be intentional in performance but are also innate and robust with respect to usage, with many gestural signals being common across the great ape clade, including human children (Byrne et al. 2017). However, there is ongoing debate about the intentionality, ontogeny, and origins of these gestural systems, including the degree to which learning and ritualization plays a role, as well as the implications that can be drawn regarding the evolution and acquisition of human language (Tomasello and Call 2019).

Evolutionary Explanations

Several theoretical and formal approaches have been developed to explain the evolution of animal signalling. Amotz Zahavi famously proposed the "handicap principle," whereby costly or risky traits or behaviors can be interpreted as strategic signals of underlying qualities, for example, the spectacular tail of the peacock as a costly investment in advertising the male's quality as a mate. Though initially focused on sexual selection, Zahavi and others have argued that the handicap principle is broadly applicable to signalling throughout the biological world, and it has been formalized using evolutionary game theory as a signalling game by which "high-quality" senders can advertise themselves as such by sending a signal that is too costly for low-quality individuals (Grafen 1990; Zahavi and Zahavi 1997). The stotting behavior of Thompson's Gazelles during pursuit by predators is one putative illustration of this model: the high leaps are less risky if the animal already has a good chance of getting away, and can therefore serve as an honest signal for the predator to switch targets, to the benefit of both animals. If fitness benefits for receivers and high-quality senders align in this way, then conditional signals and responses can co-evolve.

However, there is disagreement about the degree to which the handicap principle and costly/strategic signalling underpins signalling ontogeny. An alternative proposal, especially in cases of sexual selection, is the "truth in advertising" principle (Kodric-Brown and Brown 1984), which states that some animal signalling takes place costlessly via traits which also serve the purpose they advertise. For example, an impressive set of antlers on a stag can both help their bearer compete for mating privileges but also deter weaker opponents from competing. In a seminal text on animal signalling, Maynard Smith and Harper also draw the distinction between handicap signals and "index signals," which are honest because of an intimate relationship between their method of generation and the trait being signalled for, such that they are difficult or impossible to fake. Their example is the roar of a stag, which is a costless-yet-honest signal of the stag's size and strength, because these qualities are what determine the tone and volume of the roar (Maynard Smith and Harper 2003). Other theoreticians have emphasized game-theoretic models and interpretations which are more general and nuanced than the classic handicap formulation, including signalling games where senders and receivers have more common interest, and there is scope for richer communication (Skyrms 2010). Importantly, these different signalling models have different implications with respect to costs and benefits, and resulting evolutionary trajectories. Alternative frameworks have also been developed by theoretical biologists which

are more closely linked to the specifics of ecological context (e.g., Hebets et al. 2016).

Information, Influence, and Evolution

Given the diversity of signalling forms and explanatory approaches, the scientific study of animal signals is spread across many disciplines. It can involve observational studies of animals (in the wild and in captivity) and experimental studies, but there is also a considerable body of theoretical and formal work on biological signalling, e.g., carried out via evolutionary game theory and other modelling approaches.

This means that working definitions of signalling do not always agree. One common criterion for a signal is that it encodes and transmits information, so any observable trait of an organism that is correlated with an unobservable trait could be a "signal" of it to some other organism. More commonly, however, as outlined by Maynard Smith and Harper (2003), signalling is seen by evolutionary biologists as an evolved *mutualistic* relationship, where the sharing of information improves the fitness of both senders and receivers. This definition is narrower and more precise: "any act or structure which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (Maynard Smith and Harper 2003, p. 3). For example, bleeding did not evolve to attract sharks, so blood in the water, while informative, is not a signal in this co-evolutionary sense and is instead a *cue*.

Cues are one way of breaking the co-evolutionary condition: receivers adapt to take advantage of information that the sender reveals in a way that was not itself selected for. Conversely, senders might adapt to take advantage of preexisting receiver responses in order to *manipulate* them. One cross-kingdom example is the *Ophrys speculum* orchid, which attracts male *Campsoscolia ciliata wasps* by mimicking the chemical signals of a sexually receptive female wasp so effectively that males preferentially copulate with the flower rather than with actual females (Ayasse et al. 2003). Cues and dishonest manipulation are both one-sided phenomena where an exploitative adaptation in either the sender or the receiver was not responded to by counter-adaption in the other. Given there is no selection for the cue or manipulable trait, its persistence therefore requires additional explanation particular to the case; e.g., for the wasp species, remaining vulnerable to the orchid's manipulation is probably less costly than altering the relevant parts of its mating strategy.

However, the co-evolutionary definition is not universally accepted. In an early dissent, Dawkins and Krebs (1978) described it as the "classical ethological" approach to signalling and proposed their own definition of signalling as *influence*. On this view, what is essential to signalling is that the sender intervenes on the receiver's behavior by triggering conditional responses. This bundles together as signals both co-evolved signals and dishonest manipulation, as in the orchid-wasp case. Notably, this fits with how the term is used by at least some biologists; for example, throughout the Ayasse et al. paper describing the orchid-wasp case, the authors describe the deceptive pheromones manufactured by the *Ophrys speculum* orchid as "chemical signals."

Three distinct uses of "signal" can therefore be found in the literature: (i) a narrow sense where signals are both informative and influential, contrasted against cues and manipulations, (ii) the signals-as-information sense which includes cues but not manipulation, and (iii) the signals-as-influence sense which includes manipulations but not cues. In many contexts, the differences are merely semantic, but in others, the three uses would imply different evolutionary narratives regarding which behaviors (sender and/or receiver) have been selected for and why.

Animal Signalling and Human Behavior

Other than language, many attempts have been made to explain distinctively human traits via applications of animal signalling theory. These are often speculative and controversial. Some early theorists and popularizers of sociobiology ascribed evolved, innate, non-intentional signalling functions to exaggerated morphological features such as turned-out lips and enlarged ear

lobes, breasts, and penises. A range of signalling explanations have also been proposed for intentional behaviors as diverse as conspicuous consumption, generosity, suicide bombing, grief, regret, and religion. Many proposals state that the costliness of such behaviors can be explained via the handicap principle or other signalling mechanisms but few attempts to interpret and quantify the relevant costs and benefits in a way that plausibly fits the relevant game-theoretic models (Grose 2011). Evidence for testable predictions (where these exist) has also been mixed or difficult to obtain, compounded by the additional modes of selection and transmission which human enculturation enables.

Conclusions

Animal signals are a common object of study in the biological sciences, where there is a large body of both case studies and theoretical literature. However, there are disparate approaches to describing and explaining animal signalling, with ongoing debates at both the conceptual and empirical level. Evidence of evolutionary causation also becomes problematic outside of cases where (i) innate sender and receiver behavior means there is a one-to-one mapping between stimulus and response and (ii) fitness differences are readily discernible. Signalling theory, as developed in the study of animal signals, is therefore an intriguing and potentially powerful tool for crafting evolutionary explanations, but moving beyond simple verbal models of signalling requires a challenging degree of engagement with the complexities of both the signalling explanations and their application.

Cross-References

- ▶ Communication, Cues, and Signals
- ▶ Costly Signaling
- ▶ Costly Signaling and Altruism
- ▶ Costly Signaling Theory
- ▶ Dishonest Signals
- ▶ Evolution of Communication
- ▶ Grief as Social Signal
- ▶ Manipulation and Dishonest Signals
- ▶ Sexual Signaling
- ▶ The Handicap Principle

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