

Discuss the evolution and function of honest and dishonest animal signals and illustrate with examples

Introduction

An animal signal is a morphological or behavioural feature of one individual, the sender or signaller, which will modify the behaviour of another, the receiver or recipient (*Davies, Krebs & West, 2012*). The nature of signalling across the animal kingdom is extremely diverse, whereby the specific signals and responses at hand may take place over a range of different spatial and temporal scales with differing degrees of subtlety within both interspecific and intraspecific levels. This variety in signals is due to the diverse range through which animals are able to communicate, including chemical, tactile and optical modalities as well as the potential to co-opt biological raw material for signalling functions (*Laidre & Johnstone, 2013*). One way in which animal signals can be divided into different subsets is by assessing whether they are 'honest' or 'dishonest'. Honest signals are those that are fundamentally informative by providing a recipient with correct information regarding the sender or an aspect of their knowledge to illicit an appropriate response. Dishonest signals are manipulative, they convey information about the sender which might not be a true indication of their biology, thus deceiving the recipient into a response that may lead to a decrease in fitness relative to the sender (*Laidre & Johnstone, 2013*). While the behavioural aspect of such signals have been widely observed and studied, more recently the literature has focussed on the evolution of signals, particularly with regard to how the balance of honest and dishonest signals might prevail in populations. This essay will assess their evolution before looking at two specific examples of animal signals.

Evolution of Animal Signals

When assessing the evolutionary origins of honest and dishonest animal signals, it makes sense to look at other similar forms of animal behaviour. A cue is an aspect of animal behaviour that conveys information from one individual to another, much like signals. However, an important distinction between the two is that cues are merely by-products of another part of an individual's behaviour and therefore are not in themselves shaped by natural selection, but rather change concurrently due to selection upon a different trait. It is thought however, due to their similarities, that many signals may have evolved from what were originally cues. This evolutionary process is known as the 'signaller precursor route'. An example can be seen in many species' threat signals. These are movements and postures that denote the individual's intent to fight, as well as potentially giving an indication of their ability in the case of honest signals. This kind of signal is often an abbreviated form of the fighting behaviour itself, thus simplifying their attack pattern, for example, by positioning themselves in preparation for conflict (*Laidre & Johnstone, 2013*). An important difference in terms of evolution, therefore, between cues and signals is that while recipients may respond on an evolutionary scale in reaction to a cue, the cue itself is not being changed by selection due to the receiver's response. In contrast, a signal will be directly acted upon by natural selection leading to an influence in the behaviour and fitness of both the sender and the recipient, and thus the evolution is tightly associated with the interplay between both individuals involved in the interaction at hand.

As well as the signaller precursor route, signals may also evolve through an evolutionary process known as 'recipient precursors'. This is when a recipient might have a form of pre-existing sensory bias that will be favoured in the context of communication. For example, if individuals of a species mainly exploit a red food source, females of this species might prefer this colour to others in a different context, such as that of mate choice. This will, in theory, lead to selection in males of this species evolving red colouration (*Laidre & Johnstone, 2013*).

Once assessing how signals evolve in general, it should be considered what it is that promotes the evolution of dishonest signals. This concept of selection for dishonest signals revolves around the existence of conflicting interests between the recipient and sender. That is to say, when the interests are aligned there should be no problem of manipulation of signals arising throughout evolutionary history, but conversely if they have conflicting interests then signals may evolve to become deceiving (*Manning & Dawkins, 2012*). This idea was defended by Dawkins and Krebs leading to the 'manipulation argument', whereby they suggested that signals should be viewed as manipulative in general from an evolutionary scale because selection will favour signals that are in the sender's selfish interested irrespective of the recipient's fate. They suggested that signals bearing honest information should be completely abandoned by this logic (*Krebs & Dawkins, 1984*).

This theory does not stand much ground due to the observable maintenance of honest signals in many populations. Some work has been done on why natural selection doesn't drive dishonest signals to dominate, including the work of Amotz Zahavi. He suggested 'the handicap principle', which suggests that some signals may be too costly for individuals to fake and therefore cannot be dishonest (*Zahavi, 1975*). This can be seen in the example of the evolution of roaring in red deer during the rutting season. Males roar at each other to gain control of harems of females, with the winner being the male that can roar most vigorously, thus gaining control without the need for a physical fight. This roaring signal is an honest depiction of the male's ability to fight due to its exhausting nature and it is only the strongest males that are able to maintain the roaring for a prolonged period of time (*Clutton-Brock & Albon, 1979*). This demonstrates the fact that in some cases signals cannot evolve in senders such that they convey false information about the fitness of the individual.

Another important factor when assessing the evolution of dishonest signals, relative to honest signals, is that whether a signal will evolve or not is highly reliant on the receiver's response. It is the limits of accurate assessment by the recipient that makes it possible for dishonest signals to evolve (*Backwell et al, 2000*), however, the tendency of receivers to ignore such dishonest signals from the senders will put evolutionary pressure on them to produce signals that can be readily validated. From this co-evolutionary dynamic, it has been suggested that in order to evolve and prevail, signals must be 'honest on average'. To be evolutionary stable, the signals must contain enough information for receivers to generally benefit from responding to them than if they were to ignore them. Thus dishonest signals can exist but only at low frequencies or when they are difficult to detect (*Laidre & Johnstone, 2013*).

This essay has so far looked at the evolution of animal signals. To look deeper into this area of behavioural biology, two specific signal examples will be assessed from fiddler crabs and honeybees.

Fiddler Crabs

Fiddler crabs, *Uca annulipes*, are unusual in the sense that they display a high proportion of dishonest signalling. Males assess other male's fighting ability by observing the size of their claw, which they will display through a specific waving motion. It is the size of the claw coupled with the behaviour that is thought to be a fairly accurate predictor of mating success (*Backwell & Passmore, 1996*). This is significant with regards to dishonest signalling when coupled with an important part of the species' life history. Fiddler crabs will lose their brachychealous claws, and following this loss they will regenerate a new leptochelous claw, which is lighter, more slender and less robust. For any given claw length, the regenerated leptochelous claw will be weaker due to the change in muscular morphology and thus the length will be a less honest indication of their true fighting ability compared to brachychealous claws (*Backwell et al, 2000*). In short, this means that were a fight to take place, males with leptochelous claws of the same length as males with brachychealous claws are competitively inferior and thus are highly likely to lose the fight.

Despite this, in a study by Blackwell et al, it was found that there was no significant difference in the ratio of leptochelous to brachychealous males that attracted females to their burrows for mating, based on the proportion of the two claw types within the population. Further to this, it was found that once a female visited a male's burrow, she was just as likely to mate with both types of male (*Backwell et al, 2000*).

This is of evolutionary interest, because it means there is maintenance of a fairly high prevalence of dishonest signalling by a less fit version of the population: as many as 44% of the surface-active males were found to have leptochelous claws (*Backwell et al, 2000*). If a female chooses a leptochelous male, they are less reliably mating a male that provides a variety of benefits which are generally considered as being positively associated with their phenotypic condition and larger sexual traits (*Moller & Alatalo, 1999*), thus reducing the fitness of her future offspring compared to if she were to mate with a brachychealous male. If males are allowed to dishonestly cheat like this, then further questions arise such as why doesn't an even higher proportion of the male population cheat, and why do any males invest in the more costly brachychealous claw?

It is thought that this does not occur because of the male-male fighting dynamics. Younger, and therefore smaller, males are more likely to be involved in fights because there is a high proportion of males in the population that are slightly larger than them and therefore will challenge them to a fight. In this scenario, it would be detrimental for all young males to have leptochelous claws, as it would be highly likely that they would have a 100% loss rate in fights. But as they grow larger and older, the relative frequency of actually fighting decreases and thus the costly brachychealous claws may be less advantageous (*Backwell et al, 2000*). Therefore, the initial benefits of having brachychealous claws, but the cheating strategy leading to an

increase in fitness at a lower cost by regenerating leptochelous claws when older, may select for this aspect of the crab's life history.

Honeybees

Honeybees, *Apis mellifera*, have long been studied with regards to their behaviour. The ability of up to 10,000 bees to launch into flight simultaneously in under 60 seconds is an incredible feat of collective behaviour, and studies have been undertaken to assess how a subset of individuals might signal to the vast number of conspecifics when it is time to take-off (*Rittschof & Seeley, 2008*).

It is thought that a certain set of scout bees that have chosen the new site, which the entire colony will eventually swarm to, indicate the time to leave through two behavioural signals: piping signals and the buzz-run. The piping signal is communicated from the sender as she presses her thorax against the receiver to stimulate warming such that the threshold temperature of 35°C can be reached before flight (*Seeley TD & Tautz J, 2001*). The buzz-run is somewhat more complex, but light has been shed on the behaviour in a recent study by Rittschof & Seeley.

Using 7,500 bees, the two authors analysed the specific behaviour of the buzz-run and how this might translate as a signal to indicate take-off. In the hour before take-off, the number of surface bees that were 'buzz-running' steadily increased as they ran about with their wings spread and vibrating, producing a low-pitched buzzing sound. In the final forty minutes, the proportion of signalling bees performing a buzz-run compared to that of a piping signal also significantly shifted, with 80% of the excited bees performing a buzz-run in the final five minutes. The specific behaviour of the buzz-run was that of a short burst of agitated motion with their wings whirring as they butt through groups of motionless bees. It was found that this signal physically dispersed the recipient bees and made them noticeably more active (*Rittschof & Seeley, 2008*). While this is how the behaviour acts as a signal, it is interesting to therefore assess how it may have evolved.

Following the signal, it was observed that the sender bee briefly launches into flight before landing again after a few seconds. This is of interest with regards to how the behaviour evolved because it implies that the behaviour is still somewhat a ritualised form of normal take-off behaviour: the bee will spread her wings and beat them with a frequency of roughly 225 Hz, incidentally pushing past other bees (*Rittschof & Seeley, 2008*). It is clear therefore to predict how this signal evolved from a cue, and was further ritualised to activate a response behaviour in other individuals that are preadapted to detect such a cue.

Conclusion

Animal signals function as a form of communication between individuals, encompassing a huge range of different morphologies and behaviours. The term is fairly vague in the sense that it can refer to a number of elements of an animal's biology that acts on differing spatial and temporal scales, as well as having the potential to communicate hugely different points of information, at differing levels of subtlety, and to elicit vastly different responses. The interplay between the sender and receiver(s) and the nature of the signal will determine how the signal evolves, as well

as whether individuals can persist in a population over time when signalling dishonestly. For example, this can be demonstrated with the two signal examples discussed in this essay, whereby dishonest signals regarding fighting ability in fiddler crabs can persist due to the fitness gain in the sender and the specific life history of the species, but there is no reason for why dishonest buzz-runs would evolve as this would be of no advantage to any members involved in the interaction. Fundamentally, although much work has been done to assess animal signals, they are a complex combination of communicative animal traits that require more study in the future to truly understand how they evolve and function.

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