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Introduction: A primer on information and influence in animal communication

ULRICH E. STEGMANN

> What is surprising is that, despite this intensive study, the whole subject [of animal communication] is extremely confused, largely because of the definitions of the various terms that have been used. While this was already true when the first edition of this book was written, the confusions have now reached monumental proportions, with leading theorists even disagreeing as to what should properly be called 'a signal' or 'communication'.
>
> Marian Dawkins (1995, p. 72)

> [T]here is widespread and often unrecognized confusion about the kinds of signal that exist, the mechanism responsible for their evolution, and the terms to be used to describe them . . . So it may be that a disagreement about terminology in a particular case is not about theories, or the words used to describe them, but about what the world is like.
>
> John Maynard Smith and David Harper (2003, p. 2)

Introduction

A midsummer evening in a temperate forest: male fireflies emit pulses of light from specialised organs as they fly about in search of females. Females respond by emitting their own light pulses, which prompt males to approach them. A dialogue of light pulses ensues until the males have located the females (Lewis & Cratsley, 2008). Mate recognition in fireflies illustrates some basic features of animal communication: a *sender* sends a physical *signal*, which is perceived by a *receiver* who responds to it. In fireflies the initial sender is the male, whose signal is the light pulse, and the receiver is the responding female.[1]

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[1] The roles of sender and receiver reverse when the female emits her own light pulse.

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Signals are physical events, behaviours or structures to which receivers respond. Yet they are more than that, according to the standard view in ethology (e.g. Hauser, 1996; Bradbury & Vehrencamp, 2011a). As the colloquial meaning of 'signal' suggests, animal signals are events that convey *information* to receivers, where information is the *content* of a signal, or what the signal is about. For instance, the light pulses of fireflies reveal information about location, motivational state and species identity; the light pulses of a male convey, "Here I am in time and space, a sexually mature male of species X that is ready to mate. Over." (Lloyd, 1966, p. 69).

However, such explicit specifications of information contents are rare (e.g. Owren & Rendall, 1997), not least because identifying specific contents is difficult (Cheney & Seyfarth, 1990; Hauser, 1996). Normally contents are circumscribed in vaguer terms, such as 'information about food', or they are invoked indirectly by classifying signals as, for instance, predator or alarm calls. Yet the underlying assumption is always that signals carry information in the sense of having some more or less specific content. Unsurprisingly then, information has found its way into formal definitions of signals and communication: *communication* is often defined as the process of conveying information from senders to receivers by means of signals, and *signals* as the behaviours or structures that senders evolved in order to convey information (Table 1).

Table 1 *Examples of informational and non-informational definitions of animal signals and communication. Note that both Wilson (1975) and Maynard Smith and Harper (2003) excluded information only for the purposes of defining signals and communication; they did not reject the idea that both phenomena involve information.*

	Informational	Non-informational
Signal	"[Signals are] behavioral, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms." (Otte, 1974, p. 385)	"We define a 'signal' as any act or structure that 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 & Harper, 2003, p. 3)
Communication	"I consider communication to be any sharing of information between entities – in *social* communication, between individual animals." (Smith, 1997, p. 11)	"Biological communication is the action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell) in a fashion adaptive to either one or both the participants." (Wilson, 1975, p. 176)

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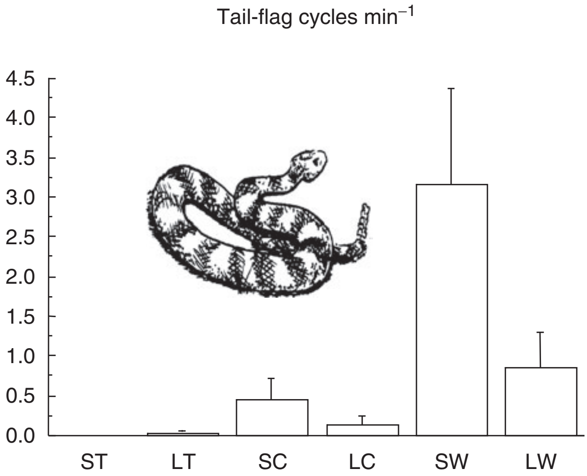

Figure 1 Mean rate (+SE) of tail flagging by squirrels during the first 2 minutes following playback of soft and loud tones (ST and LT, respectively) and of rattling sounds of small (S) and large (L) as well as cold (C) and warm (W) rattlesnakes. Squirrels flagged their tails significantly more in response to rattles than to tones, and more to rattles from warm snakes than to rattles from cold snakes. Warm snakes produce rattles that are both louder and have a higher click rate than those produced by cold snakes, which are less dangerous to squirrels. Graph reproduced with permission from Swaisgood *et al.* (1999); rattlesnake reproduced with permission from Richard Coss.

As structures that *evolved* to convey information, signals are typically contrasted with *cues*, which are behaviours or structures that convey information without having evolved for this purpose (e.g. Otte, 1974; McGregor, 1993; Hasson, 1994; but see Hauser, 1996). Rattling by rattlesnakes has probably evolved to ward off predators by conveying the information that the snake is venomous, i.e. rattling is a signal. But rattling can be a cue as well (Swaisgood, Rowe & Owings, 1999). The click rate and dominant frequency of the rattling sound of Pacific rattlesnakes correlate with a snake's body temperature and size, respectively (Rowe & Owings, 1990). California ground squirrels use these sound properties to adjust their degree of vigilance. Squirrels become more vigilant in response to rattling sounds from warmer snakes (Figure 1; Swaisgood *et al.*, 1999), which are more agile and therefore more dangerous. For the squirrels, click rate and dominant frequency thus carry information about snake temperature and size, and they are cues because they did not evolve in order to convey such information.

Although information is a central and entrenched concept in animal communication studies, it seems possible to describe communication without it. The first paragraph of this introduction sketched firefly communication simply

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in terms of what some individuals do (emitting a light pulse) and how others respond (emitting another light pulse/approaching). We can even *define* signals and communication without appeal to information (Table 1). Why then introduce apparently intangible postulates such as content, message, meaning or information? Why not do without them? Doing away with information concepts, minimising their role or supplementing them with concepts like manipulation is what some ethologists advocate (Dawkins & Krebs, 1978; Johnstone, 1997; Owren & Rendall, 1997; Owings & Morton, 1998; Rendall, Owren & Ryan, 2009; Carazo & Font, 2010). Questions about the legitimacy of information will be addressed later in this chapter. The following section focuses on the concept of information itself.

Information

Colloquial information

Signals are taken to convey information in the sense that they are about something, or have content (e.g. Halliday, 1983; Dawkins, 1995). But what does it mean to say that signals *have* content? This question is rarely addressed explicitly. Yet judging by how terms such as 'information' are employed in practice, it appears that much work in animal communication is based on three distinct but closely related answers (I will refer to these as 'content 1' etc. later in this introduction).

(1) Predictions and knowledge

Many authors use 'information' interchangeably with what receivers come to know (e.g. Krebs & Dawkins, 1984; Seyfarth & Cheney, 2003; Bradbury & Vehrencamp, 2011a), what they infer (e.g. Krebs & Dawkins, 1984; Slocombe & Zuberbühler, 2005) or what they predict when perceiving a signal (e.g. Smith, 1997; Seyfarth *et al.*, 2010). In other words, a signal's information content is often equated with what receivers predict, infer or learn from it. And this practice suggests a first answer to what having content consists in: signals have content (or, equivalently, carry information) when they enable receivers to predict something from their occurrence.

Predicting is frequently understood in a qualitative sense (e.g. Krebs & Dawkins, 1984; Smith, 1986; Seyfarth *et al.*, 2010). There is, however, a quantitative framework for modelling predictions: statistical decision theory (Bradbury & Vehrencamp, 2011a; see also Ch. 3). The basic idea in applying statistical decision theory is that animals constantly face decisions about how to act and that they use information (knowledge) to choose among alternative courses of action. Animals come equipped with some degree of background knowledge about the probability

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of certain events, which derives from earlier experiences and/or from heritable biases due to past selection. In order to achieve optimal decisions, animals continually update their prior information by attending to appropriate current events.

Consider contests among red deer stags over access to females. Frequent components of stag contests are roaring matches, which are usually won by the more frequently roaring male (Clutton-Brock & Albon, 1979). Faced with a roaring harem-holder, a challenger must decide whether to retreat or keep roaring. Stags base their decisions on an estimate of their opponent's fighting ability. Fighting ability comes in degrees, but let us assume for illustrative purposes that rivals categorise one another as being either weak (W) or strong (S). If prior knowledge suggests to a male that its rival is as likely to be weak as he is strong [$P(W) = P(S) = 0.5$], then such knowledge is of little help in deciding whether or not to retreat. However, fighting ability correlates with roaring: weak males roar less frequently than strong males (Clutton-Brock & Albon, 1979; Reby *et al.*, 2005). Males can use knowledge of this correlation to predict the fighting ability of opponents (Box 1).

Box 1 A simple application of statistical decision theory

According to statistical decision theory, predicting or inferring something from the occurrence of a signal amounts to calculating a *conditional* probability. A conditional probability is the probability of an event or state on the condition that some other event or state has occurred. Inferring something from a signal involves calculating the conditional probability of an event on the condition that the animal has observed that the signal has occurred. So, when a stag infers the fighting ability of a rival (the state) from his roar (the signal), he effectively 'calculates' the conditional probability that his rival has a certain fighting ability on the condition that he roars with a certain frequency.

Suppose that stags are either weak (W) or strong (S) and they either roar frequently (F) or infrequently (I). If a stag perceives his rival roar frequently, then the stag calculates two conditional probabilities: the probability that (1) the rival is weak on the condition that he roars frequently and the probability that (2) the rival is strong on the condition that (again) he roars frequently. To simplify matters, we will only consider how the stag calculates probability (1), which is written $P(W|F)$, where '|' means 'given' (not to be confused with '/', the symbol for division). One way to calculate $P(W|F)$ is to use Bayes' theorem:

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$$P(W|F) = \frac{P(W) \times P(F|W)}{P(W) \times P(F|W) + P(S) \times P(F|S)}$$

In order to calculate $P(W|F)$, the stag needs some background knowledge. First, he needs to know how probable it is to encounter rivals that are weak and rivals that are strong. These are the 'prior probabilities', $P(W)$ and $P(S)$. They are independent of having heard a rival's roar.

Second, the stag needs to know how strongly roaring correlates with fighting ability. Such correlations are estimated as the conditional probabilities that a certain type of signal will be produced by the sender (or perceived by the receiver) given a certain state of the world. With two types of signal and two states there are four conditional probabilities:

	State or event in the world	
Signal	Strong male (S)	Weak male (W)
Frequent roaring (F)	$P(F\|S)$	$P(F\|W)$
Infrequent roaring (I)	$P(I\|S)$	$P(I\|W)$

This table is a coding matrix. It specifies the degree to which a state or event in the world affects the probability that a signal will be produced (or perceived). For instance, it specifies how the fact that a male is weak affects the probability that he roars frequently, $P(F|W)$ (this is the converse of the probability the stag needs to calculate, $P(W|F)$).

The stag can now 'update' his prior probability that the rival is weak. This process can be modelled with Bayes' theorem. Suppose the stag's prior probability that the rival is weak is $P(W) = 0.5$. So, without having heard the rival's roar, the rival is equally likely to be weak or strong [$P(S) = 0.5$]. Suppose also that the stag knows about the following correlations between roaring and fighting ability: strong males roar frequently 80% of the time and infrequently 20% of the time [$P(F|S) = 0.8$, $P(I|S) = 0.2$], whereas weak males roar infrequently 95% of the time and frequently 5% of the time [$P(I|W) = 0.95$, $P(F|W) = 0.05$]. Inserting these values into Bayes' theorem yields:

$$P(W|F) = \frac{0.5 \times 0.05}{0.5 \times 0.05 + 0.5 \times 0.8} = 0.06$$

The result shows that the stag has learned something from the rival's frequent roaring. Hearing the rival roar frequently reduces the stag's estimate of the probability that his rival is weak from an initial 50% to a mere 6%. In other words, the stag can now be fairly confident that the rival is not weak. He can adjust his behaviour accordingly.

Two points are worth emphasising. First, when a receiver has used a signal to update its estimate of the probability of certain events, it has just made the first step. In order to use what it has learned to guide its behavioural response, the receiver also needs to take into account the fitness costs of making correct as opposed to incorrect choices of action (Bradbury & Vehrencamp, 2011b). Second, updating critically depends on what the receiver knows about the correlations between signals and world states (the coding). From the point of view of statistical decision theory, the signal by itself, without the coding, carries no information (J. Bradbury, personal communication). As mentioned in the main text, a signal's carrying information can be understood as enabling receivers to infer something from it. Since without coding receivers cannot infer anything from a signal, the signal itself carries no information.

Statistical decision theory is not only a quantitative tool for modelling how and what receivers predict from signals. Ecologists studying foraging behaviour, too, understand the idea that *cues* carry information/content as a matter of allowing predictions, and they employ statistical decision theory to model this process (e.g. Valone, 1989; Giraldeau, 1997; Danchin *et al.*, 2004; Stephens, 2007; Wagner & Danchin, 2010). Indeed, a rich and partly controversial taxonomy of types of information has been developed along these lines (e.g. Danchin *et al.*, 2004; Wagner & Danchin, 2010). One of the proposals is to distinguish between *private* and *public* information. European starlings probe the ground for insects and so acquire knowledge about patch quality, which is then used in foraging decisions, for instance when to leave the current patch for another (private information: knowledge of *x* gathered from direct contact with *x*). Instead of probing for insects themselves, individuals may also gain this information by observing their flockmates' probing success (Templeton & Giraldeau, 1996). The latter is public information: knowledge of *x* gathered from a cue of *x*.

It is tempting to believe that predictions, inferences and knowledge imply cognitive or psychological processing on the receiver's part, perhaps even conscious awareness. Indeed, key steps of decision-making have neural correlates (reviewed in Lee, 2010, and Bradbury & Vehrencamp, 2011c). But cognitive capabilities are implied in neither foraging ecology nor animal communication. Quantitative and informal work in these areas remains explicitly neutral on

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the mechanistic aspects of deriving predictions (Danchin *et al.*, 2004; Stephens, 2007; McNamara & Dall, 2010; Bradbury & Vehrencamp, 2011a). In some species, inferences from signals may just consist in simple learned associations or evolved dispositions (Krebs & Dawkins, 1984; Smith, 1997). Likewise, predictions from cues may consist in non-cognitive processes (Danchin *et al.*, 2004; McNamara & Dall, 2010).

(2) Mental representations

A more demanding view about the nature of signal content emerged in work on ‘referential’ signals. Referential signals allow receivers to infer features of the external environment instead of, or in addition to, features of the sender (variously labelled “semantic”, “referential”, “symbolic”; reviewed in Hauser, 1996). The alarm calls of vervet monkeys are a well-known example (Seyfarth, Cheney & Marler, 1980). Vervets emit three acoustically different types of calls in response to three different types of predators: leopards, eagles and snakes (Figure 2). Listeners respond to the calls in a way appropriate for the type of predator. For example, calls emitted in response to approaching eagles prompt vervets to seek cover in bushes, whereas calls emitted in response to snakes elicit upright posture and scanning of the ground. These calls appear to function like labels for things in the world, in this case types of predators, much like some words in human languages (Hauser, 1996; Cheney & Seyfarth, 2007).

Animal signals are called “functionally referential” when they function like labels (e.g. Marler, Evans & Hauser, 1992; Macedonia & Evans, 1993; Fischer *et al.*, 1995; Evans & Evans, 1999; Manser, Bell & Fletcher, 2001). This leaves open whether the signals are like words in the additional sense of eliciting mental representations of the referent in the minds of receivers, i.e. internal representations which mediate receiver responses. Such “representational” (Hauser, 1996; Evans & Evans, 2007) or “conceptual” signals (Zuberbühler *et al.*, 1999) are taken to be close to human words on the basis of assuming that human words refer to things indirectly, via something in the mind of receivers, an abstraction or concept (e.g. Cheney & Seyfarth, 1990; Hauser, 1998) or a mental representation (Evans, 1997; see also Box 2). According to the most demanding view of informational communication, referential signals have content only in the case that receivers infer or predict something from it by means of internal representations, or even mental “images” (Maynard Smith & Harper, 2003; Seyfarth & Cheney, 2003; cf. Fedurek & Slocombe, 2011; Wheeler *et al.*, 2011). Accordingly, the term ‘information’ is sometimes used to denote whatever a receiver’s mental representations encode (Maynard Smith & Harper, 2003; Seyfarth & Cheney, 2003).

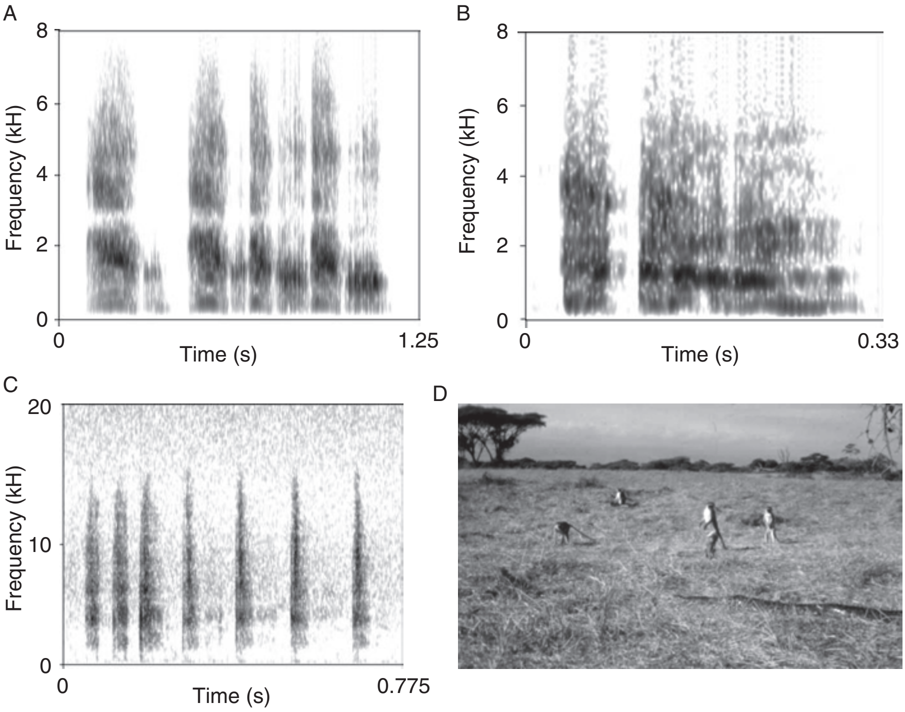

Figure 2 Vervet monkeys (*Chlorocebus aethiops*) give acoustically distinct alarm calls in response to leopards (A), eagles (B) and snakes (C). The acoustic features of alarm calls also differ from the predators' own vocalisations (e.g. vervet eagle alarm calls do not sound like eagle shrieks). When encountering one of these predators directly, vervets react in a manner specific and adaptive to the kind of predator involved, e.g. standing upright and scanning the ground when perceiving a python (D: python approaching from the lower right-hand side of the photo). Playback experiments in the wild showed that simply hearing an alarm call given in response to one type of predator, without perceiving the predator itself, triggers the appropriate behavioural response. Variations in acoustic features that may be associated with a sender's fear (e.g. call amplitude, or loudness) have no significant effect on the type of response. For these reasons, vervet alarm calls are considered to be "referential" or "semantic", i.e. "signs [that] refer to objects in the external world" (Seyfarth *et al.*, 1980, p. 1070). The study by Seyfarth *et al.* (1980) generated much interest in the presence of referential signalling in other species (reviewed in Seyfarth *et al.*, 2010; Fedurek & Slocombe, 2011; see Radick, 2007 for a history of playback experiments). A–C: Sonograms provided by Robert Seyfarth. D: Photo by Richard Wrangham.

(3) Correlation

What enable animals to make predictions from signals are correlations between signals and other states or events. In some contexts, correlations are deemed sufficient for signals to have content. The state or event with which the

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Box 2 Learning theory

Animals that repeatedly experience associations between two events can change their capacity for certain behaviours ("associative learning"; see Shettleworth, 2001, for terminological ambiguities). One of the best-known forms of associative learning is classical conditioning, which involves unconditioned reflexes. An unconditioned reflex is a behavioural response that is always triggered by a certain type of stimulus (such as salivation triggered by food). In classical conditioning experiments, animals are repeatedly exposed to pairings of the original (unconditioned) stimulus with a second type of event that does not normally trigger the reflexive response. After a while, animals perform the behaviour simply after perceiving the new event on its own. Pavlov famously exposed dogs to both food and a ringing bell, and the dogs eventually salivated in response to hearing the bell. What psychological and neural mechanisms are responsible for this change in the dogs' capacity to react?

According to associative theories of learning, training 'stamps in' the association between the new (conditioned) stimulus and the behavioural response. That is, animals acquire a rigid response to the conditioned stimulus by establishing an excitatory or inhibitory connection between them (S–R theories). Representational or cognitive theories of learning propose instead that training creates a connection between the conditioned stimulus and an 'expectation' of the unconditioned stimulus (S–S theories). The bell triggers a neural representation of food (or a representation of the relation between the two), and the animal reacts on the basis of this representation (reviewed in Lieberman, 2003; Shettleworth, 2010). The classic debate between associative and representational theories of learning is the background for the contrast some ethologists draw between rigid (or automatic) and representation-mediated responses (see 'Colloquial information').

Current research favours cognitive theories (Shettleworth, 2010). But it is acknowledged that there is evidence on both sides (Lieberman, 2003) and that the nature of the posited neural representations remains elusive (Gallistel, 2008). One of the strongest lines of evidence in favour of cognitive learning theories is thought to come from alarm calls in Diana monkeys (Shettleworth, 2001). Diana monkeys react in the same way to acoustically distinct vocalisations, e.g. to the shrieks of an eagle and to the eagle alarm calls of their conspecifics (see figure). This suggests that despite their differences, the two types of vocalisations evoke the same kind of mental