

## Essay

## What do animal signals mean?

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Animal communication studies often use analogies to human language and related constructs such as information encoding and transfer. This commonality is evident even when research goals are very different, for example when primate vocalizations are proposed to have word-like *meaning*, or sexually selected signals are proposed to *convey information* about a signaller's underlying quality. We consider some of the ambiguities and limitations inherent in such informational approaches to animal communication as background to advocating alternatives. The alternatives eschew language-based metaphors and broader informational constructs and focus instead on concrete details of signal design as they reflect and interact with established sensory, physiological and psychological processes that support signalling and responding in listeners. The alternatives we advocate also explicitly acknowledge the different roles and often divergent interests of signallers and perceivers that can yield fundamental asymmetries in signalling interactions, and they therefore shift the focus of interpretations of animal communication from *informing* others to *influencing* others.

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## THE ROLE OF INFORMATION IN COMMUNICATION THEORY

The concept of information features prominently in most sciences, but how it is invoked and applied as an explanatory construct varies greatly. For example, Dall et al. (2005, page 192) recently observed that 'evolutionary and behavioural ecologists do not adopt consistent, rigorous concepts of information... [instead] informal use of the term information is the norm'. Dall et al. go on to consider how such traditionally loose and informal concepts of information are now inadequate for many of the emerging problems in behavioural ecology. We echo this concern and in this essay consider how the concept of information has been used specifically in studies of animal communication. In the end, we draw very different conclusions from Dall et al. concerning the most productive remedies in our respective fields. However, our

arguments are prompted by the same problem because research in animal communication similarly suffers from the lack of clear and rigorous definitions of information, yet none the less affords the construct a central explanatory role.

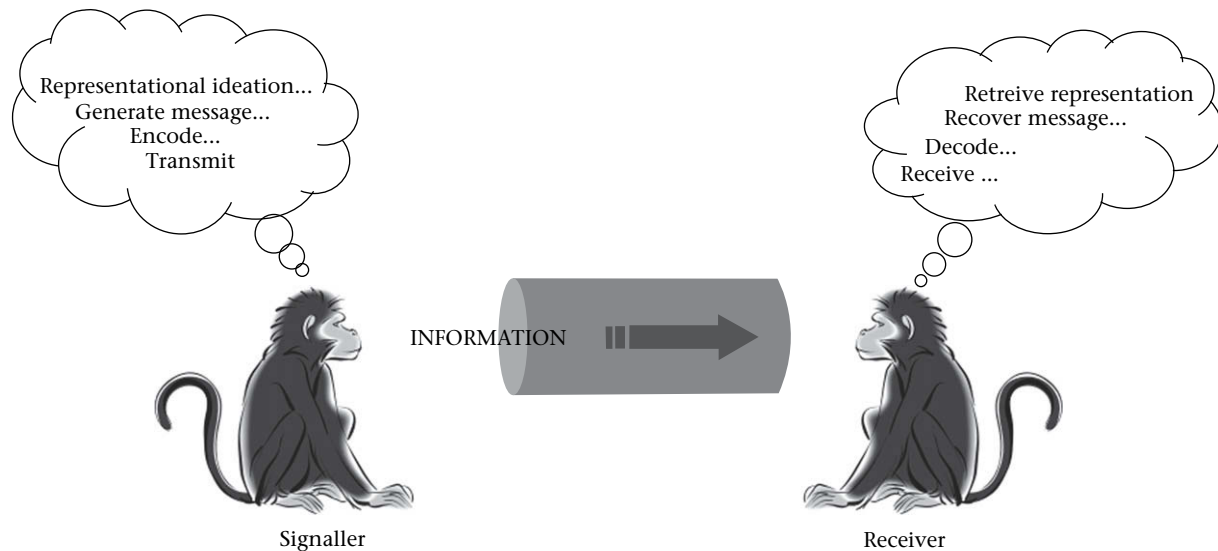
Taking two influential textbooks in animal communication as examples, Hauser (1996, page 6) defined signals as '[carrying...] informational content, which can be manipulated by the sender and differentially acted on by the perceiver', while Bradbury & Vehrencamp (1998, page 2) characterized communication as 'provision of information from a sender to a receiver', going on (page 3) to say that 'true communication' is 'information exchange' from which both sender and receiver benefit. These authors modelled animal communication systems in explicitly informational terms (see Fig. 1), and they are not alone. Tables 1 and 2 provide additional examples of the frequent use of informational and linguistic constructs in animal communication research. In characterizing animal signalling in this way, researchers are adopting what Reddy (1979) has called the 'conduit metaphor' of communication. In an Appendix, we explain this metaphor, which may be unfamiliar to many communication researchers even if they implicitly ascribe to it, and we compare its information constructs to those articulated in the formal theoretical treatment of information outlined originally by Claude Shannon and Warren Weaver (Shannon 1948; Shannon & Weaver 1949).

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**Figure 1.** Schematic illustrating core features of classic information transmission approaches to animal communication. According to such frameworks, signalling events involve some kind of representational ideation on the part of the signaller that is translated into a message whose content is then encoded in a signal and transmitted to the receiver. The receiver then receives the signal, decodes it, recovers the message and retrieves the relevant representational content. The burden of communication falls squarely on the disembodied 'packet of information' encoded in the signal flowing from signaller to receiver.

The upshot is that, although informational approaches have tremendous intuitive appeal, they are at one and the same time both too loose and too restrictive to cover the broad range of animal-signalling phenomena. They are too loose because their core explanatory construct, information, is either only ever vaguely defined and operationalized, or, more often than not, left entirely tacit. They are too restrictive because their informational focus, whether explicitly articulated or only unknowingly adopted, unduly narrows the focus of study and limits the range of questions asked and problems investigated. As a result, informational approaches often either overlook, obscure or underspecify many of the fundamental properties of signal phenomena.

In what follows, we elaborate these points using specific examples drawn from two diverse areas of animal communication, namely studies of the language-like properties of vocal

communication in primates and studies of sexual selection and courtship signalling in frogs. Our examples do not constitute a comprehensive review of animal communication research, nor are they meant to. Rather they are intended only to illustrate that the problems we identify are very broad such that they cover research on taxa as diverse as primates and frogs and on signalling phenomena as diverse as predator alarm calls and mating displays.

### PRIMATE COMMUNICATION AND THE METAPHOR OF LANGUAGE

Studies of primate communication are often couched in the metaphor of language where *meaning* is the central explanatory construct and arises from the common representational states of speakers and listeners. This representational parity in language

**Table 1**  
Some classic and contemporary definitions of animal communication from textbooks and articles (emphases added)

Source	Definition of signals, signalling or communication	Definition of information
Otte 1974, page 385	'[signals are] behavioural, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms'	None
Green & Marler 1979, page 73	'[communication] consists of the transmission of information from one animal to another. Information is encoded by one individual into a signal. When received by another animal, this information undergoes decoding, while still retaining a specifiable relationship to the encoded information.'	None
Smith 1997, page 11	'[communication is] any sharing of information between entities—in social communication, between individual animals'	None
Hauser 1996, page 6	'[carrying...] informational content, which can be manipulated by the sender and differentially acted on by the perceiver'	None
Bradbury & Vehrencamp 1998, page 2	'provision of information from a sender to a receiver'	None
Maynard Smith & Harper 2003, page 3	'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.'	None
Searcy & Nowicki 2005, page 2	'the signal must carry information,—about the state or future actions of the signaller, or about the external world—that is of interest to the receiver'	None
Fitch 2008, page 385	Endorse Otte's (1974) definition 'Honest signals are those which accurately (but not necessarily perfectly) convey information about some relevant quality of the signaller (e.g. its species, sex, size, condition, etc.) or environment.'	None
Shannon & Weaver 1949, page 3	'all of the procedures by which one mind might affect another'	Uncertainty reduction in the receiver

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