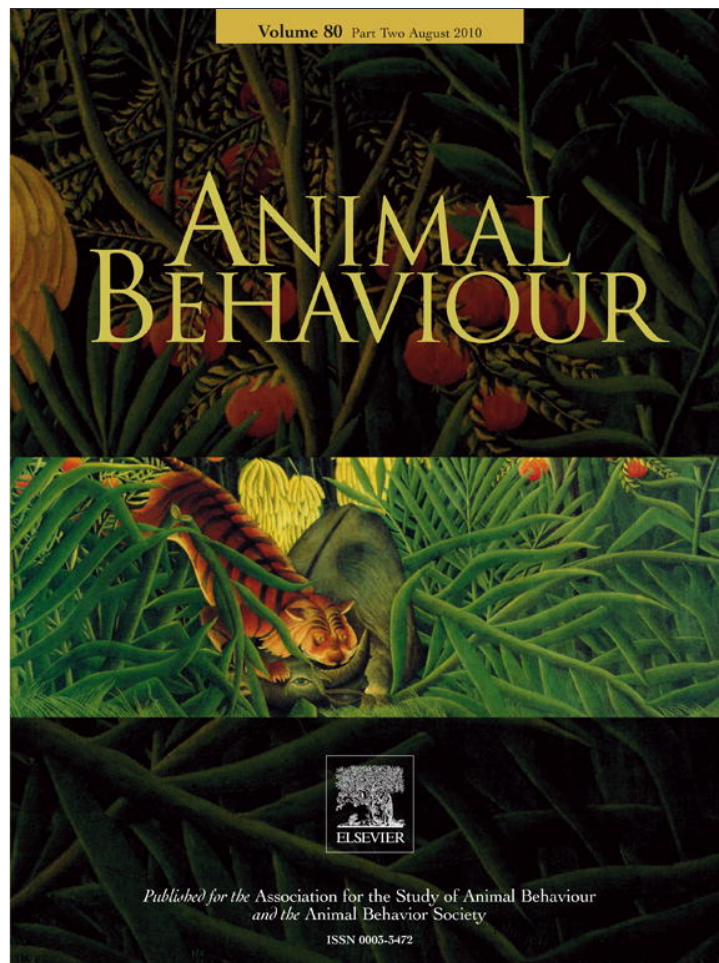


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Forum Article

Animals in translation: why there is meaning (but probably no message) in animal communication

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Despite decades of intensive research, the definitions of communication and signal remain controversial. Although the once influential view of communication as mutualistic 'information sharing' was seriously challenged during the 1970s, the concept of information is still deeply ingrained in our intuitive understanding of communication and remains an essential ingredient of many formal definitions of communication (Rendall et al. 2009). Recently, however, the so called 'informational approach' to animal communication has been criticized on several fronts. Scott-Phillips (2008, 2010) defends an adaptationist approach to communication built around the now familiar notion that signals are selected for their effects on receiver behaviour, pitting 'effects' against 'information' and concluding that only the former are necessary for a full definition of communication. Coming from a different perspective, Rendall et al. (2009) also point to shortcomings inherent in the informational approach, which they consider has 'core conceptual and empirical ambiguities' (page 236). According to Rendall et al. (2009), the linguistic metaphor that pervades the study of animal communication encourages the search for language-like meaning in animal signals, where none may actually exist. As an alternative to the informational approach, Rendall et al. (2009) advocate for an

approach that eschews language-based metaphors. While both of these proposals have merit, we feel that none of them offers a truly integrative framework for the study of communication. Elsewhere we have disputed the details of Scott-Phillips's (2008) argument, particularly the claim that information should explicitly be excluded from a definition of communication (Carazo & Font 2010). Here we argue that adaptationist definitions and nonlinguistic metaphors are fully compatible with the idea that information, albeit in a qualified form, plays a fundamental role in animal communication.

The recurring question in recent attacks on the informational approach is 'Do animal signals have meaning?' Smith (1977, 1997) first proposed a distinction between the *message* and the *meaning* of animal signals. He defined the message as the information that the sender encodes in the signal, and the meaning as the significance/information that the receiver derives from the signal and from other sources contextual to it. We agree with Scott-Phillips (2008) and Rendall et al. (2009) that the question of whether animal signals have meaning is ill posed and misconstrued, but for a different reason. As we will argue below, we think that all animal signals must, by design, have meaning. Therefore, in our view the right question to ask is not whether signals have meaning, which they do, but whether it makes sense to think of them as carriers of messages encoded by senders.

Figure 1 in Rendall et al. (2009) illustrates core features of the linguistic metaphor as applied to the study of animal

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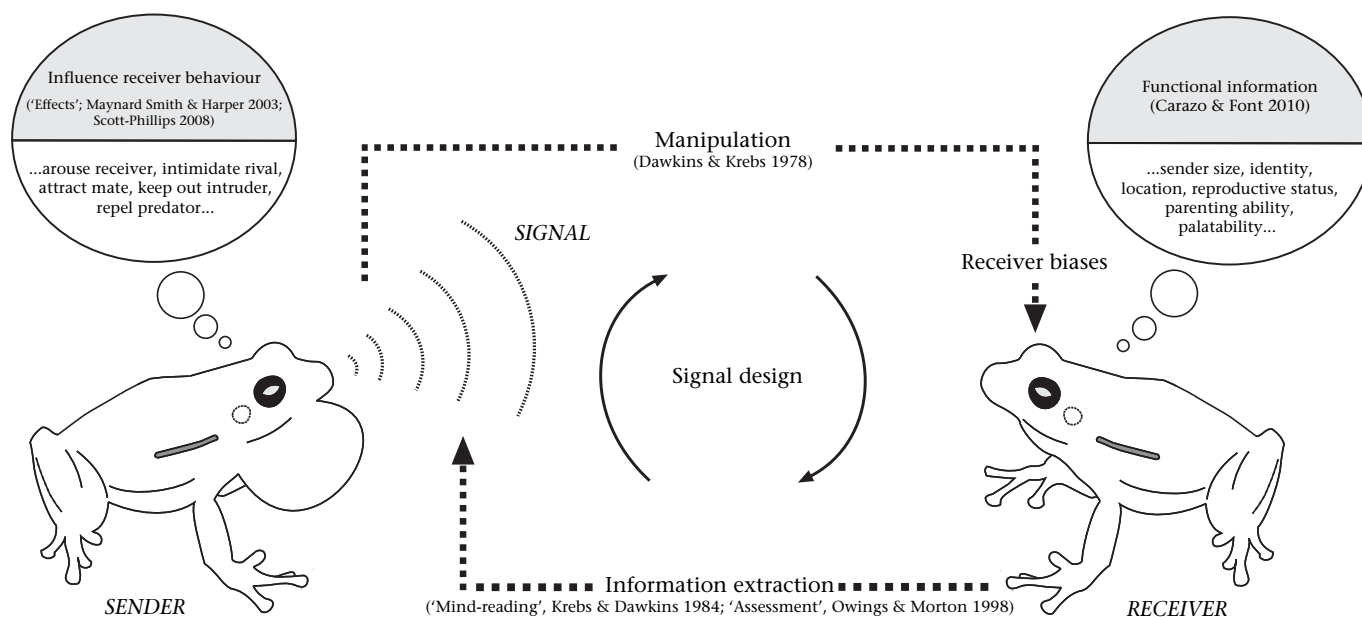


Figure 1. Schematic illustration of core features of the adaptationist approach to communication incorporating 'functional information'. Here, information is not something transmitted by senders but actively extracted by receivers, and it is precisely this 'functional information' being extracted that makes receiver response adaptive. The evolution of a given signal may be driven by senders or receivers. It may begin, for example, with senders producing certain stimuli that manipulate receiver behaviour to their own advantage (e.g. through sensory exploitation), or with receivers tapping on certain aspects of sender behaviour to extract information that is valuable to them. Irrespective of what happens first, manipulation places receivers in a position to extract functional information from senders, while information extraction opens the opportunity for senders to use those behaviours that are being 'read' to their own advantage. Thus, both 'manipulation' and 'information extraction' will feed back into each other, driving a coevolutionary dynamic that will either end with the disappearance of the signal, or with its stabilization into a signal whose design features will reflect this 'arms race' between senders and receivers. Information extraction is the ultimate aim of receivers to the same extent that influencing receiver behaviour is the ultimate aim of senders. Signal evolution and signal design cannot be understood without acknowledging both strategies, and thus the concept of information is not only useful, but absolutely central to animal communication. Although we have arbitrarily chosen two anurans to stand in as sender and receiver, the effects and functional information included in the example encompass a wide diversity of signalling contexts.

communication. The figure shows two monkeys engaged in some sort of 'conversation'. A cognitive (internal) representation in the mind of the sender is translated into a message whose content is encoded in a signal and transmitted to the receiver. The receiver receives the signal, decodes it, and recovers the message, which then produces a corresponding representation in the receiver's mind. By analogy with human language, animal signals are endowed with word-like properties, and communication is seen as a deliberate attempt to invoke and manipulate conceptual representations in the minds of others (Rendall & Owren 2002).

Although Rendall et al.'s figure portrays rather well the way communication is conceptualized by many students and nonspecialists, it is clearly a straw man. The linguistic metaphor has intuitive appeal but the processes that govern information acquisition in most of human language and animal communication are fundamentally different (Seyfarth & Cheney 2003). Many and possibly all animal signals have meaning in the sense that they make information available to receivers, but there are good reasons to doubt whether signals ever encode messages in the sense outlined above. The current model of animal communication considers that senders and receivers have different roles in communication and, more importantly, are under different selection pressures. Although both participate in the communicative act, the interaction is adaptive for them for different reasons: senders obtain 'effects', whereas receivers obtain 'information' (Carazo & Font 2010). Scott-Phillips (2008) and Rendall et al. (2009) acknowledge the asymmetry between senders and receivers, but their proposals fail to incorporate the essence of the communicative act: the trading of information (about the sender or the environment) for effects (receiver responses). As Seyfarth & Cheney (2003) and many others before them have noted (e.g. Hennessy et al. 1981; Wiley 1983;

Krebs & Dawkins 1984; Harper 1991; Endler 1993; Hasson 1994, 2000; Johnstone 1997; Bradbury & Vehrencamp 1998; Owings & Morton 1998; Maynard Smith & Harper 2003), selection favours senders whose signals affect the behaviour of receivers to the sender's advantage, and selection favours receivers that are capable of extracting useful information from the senders' signals (Fig. 1). In short, senders signal because they benefit from the effects accrued by the signals' influence on receivers (not because they want to share information with them), whereas receivers respond to signals because they benefit from the information they obtain about the sender. Information sharing is not part of the senders' aims, proximately or ultimately, and therefore receivers acquire information from senders that do not intend to provide it (Owren & Rendall 1997, 2001; Seyfarth & Cheney 2003). There is meaning in animal signals, but there probably is no message.

Inspired by the linguistic metaphor, it is easy to think of communication as a transaction that involves the passing and receiving of information. In Rendall et al.'s illustration, information is seen as a commodity that flows from sender to receiver, the signal being the vehicle for the transmission. The receiver in this view is basically passive, 'like a telephone waiting to be rung' (Morton & Page 1992). Information is essential for communication but its role differs from that suggested by the linguistic metaphor so ably caricatured by Rendall et al. (2009). The old view that selection should act on senders to increase the efficiency of transmitting information for the benefit of senders and receivers has been superseded by a framework centred on the coevolution of selfish senders that signal strategically and equally selfish receivers that extract whatever information they can from the communicative interaction. Many misunderstandings in the study of animal communication may have been caused by the expression

'information transfer/transmission', which figures prominently in several current definitions of communication. Communication involves the transmission of signals, not information. It is simply not correct to think of communication as information flowing from sender to receiver (Owren & Rendall 2001). Most of the time, if not always, information is not transferred or transmitted, but rather *extracted* by receivers (often against the senders' best interests), whose role in the communicative dynamics is still underappreciated (Morton & Page 1992; Owings & Morton 1998).

If senders do not intend to inform receivers, why do they signal in the first place? The answer has been around for several decades, since Dawkins & Krebs (1978) introduced the idea of manipulation to the study of animal communication. In this view, the function of signalling is to influence receiver behaviour in a way that promotes the fitness of the sender. Signals are thus traits whose specific evolutionary benefit to senders stems from their potential to affect the behaviour of others (Maynard Smith & Harper 1995; Hasson 2000). Using the logic of evolutionary game theory, Dawkins & Krebs (1978) proposed that, in contrast to the 'traditional ethological view' (another straw man, see Smith 1986), selection should act against senders that convey accurate information. Many have taken this to imply that information has no place in communication. However, Dawkins & Krebs (1978) were not criticizing information itself, but rather the idea that information is transmitted from senders to receivers in the way the coding–decoding scheme suggests. In fact, in a later paper Krebs & Dawkins (1984) gave receivers centre stage and contended that communication is the result of a coevolutionary arms race between senders playing the role of manipulators and receivers playing the role of mind-readers. Krebs & Dawkins (1984) stressed the receiver's ability to deduce and anticipate the sender's future behaviour (hence the expression 'mind-reading') but the argument has more generality and later work has revealed that receivers can and indeed do obtain other types of information about the sender, not just its intentions. Again, it is expressions like 'information transmission' or 'information sharing', not the concept of information, that are to be blamed for generating confusion.

It has been argued that manipulation provides a plausible scenario for the evolution of communication, but that it is not an adequate explanation of communication at the proximate level (Blumberg & Alberts 1997; Owings & Morton 1998). According to this view, manipulative and information transmission accounts would be complementary rather than alternative, with the former addressing the evolutionary trade-offs involved and the latter dealing with proximate mechanisms. After all, manipulation could be accomplished by releasing information that is either false (deceitful) or incomplete. However, recent research has revealed that information transmission is not an adequate explanation of the proximate mechanisms that underlie senders' behaviour, and that senders in general seem oblivious to the informational value of their own signals as well as to the informational needs of their potential receivers (Cheney & Seyfarth 1996; Rendall et al. 2000, 2009; Seyfarth & Cheney 2003). As Rendall et al. (2009, page 235) put it, these findings 'highlight an informational disconnection between signallers and perceivers and suggest they do not share the same representational parity that characterizes human speech'. This is possibly one of the reasons why, compared to words, most animal signals have rudimentary referential properties. Often, the information obtained by the receiver refers to some property of the sender or the sender's behaviour (e.g. its needs, intentions, or quality as a mate or as a competitor), but signals tend not to be very informative about other potential referents that could be relevant for receivers (Smith 1977; Hasson 1997).

Rendall et al. (2009) suggest replacing the traditional emphasis on information for an emphasis on the influence exerted by senders

on receivers (i.e. senders affect/influence/manipulate the behaviour of receivers rather than inform them). This proposal rests on the assumption that manipulation and information are mutually exclusive alternatives. In fact, the two are fully compatible as long as we keep in mind that information is not intentionally made available by the sender, as in the linguistic metaphor, but rather extracted by the receiver (see also Wiley 1983; Smith 1986). There is abundant evidence that unintended receivers can and do extract information from a communicative interaction, a phenomenon known as eavesdropping. Eavesdropping comes at a significant cost to senders and has been described in many taxa (McGregor 1993, 2005). Similarly, several studies have shown that bystanders acquire information by being present at but not involved in aggressive interactions (Dugatkin 2001). As Seyfarth & Cheney (2003) point out, it does not seem a logical position to grant the acquisition of information to bystanders and deny it to the signaler's intended receivers.

If not by deliberately coding information valuable to receivers, how can senders influence the behaviour of receivers? How do signals achieve their effects? Rendall et al. (2009) point out that many signals appear to be designed to achieve their effects directly by tapping into basic perceptual, neuroendocrine and psychological processes of receivers (see also Guilford & Dawkins 1991; Arak & Enquist 1993, 1995; Christy 1995). The design features of many signals make them ideally suited to attract the receiver's attention, induce arousal, and/or evoke conditioned or unconditioned reflexive affective responses. In other words, signals are designed so that receivers cannot simply choose to ignore them. For example, vocalizations such as an infant's cry may be effective simply because their acoustic properties make them aversive to receivers and difficult to habituate to (Owings & Zeifman 2004). That the alarm calls of many birds and mammals have similar acoustic properties and elicit similar orienting and flight preparation behaviours in receivers, also points to shared, perhaps ancestral mechanisms whereby sounds of certain characteristics trigger specific responses in receivers. Most of the examples provided by Rendall et al. (2009) have to do with vocalizations, but the same principles apply to signals in other sensory modalities. Many visual signals, for example, are designed to maximally stimulate the visual system of receivers (Stevens 2005, 2007; Stevens et al. 2008).

Scott-Phillips (2008) and Rendall et al. (2009) are not alone in their plea to ban information from the study of communication. Since its introduction to the study of animal communication in the 1950s, the concept of information has been an endless source of confusion and misunderstanding, and there have been several proposals to do away with it (Owings & Morton 1997, 1998; Owren 2000). This may be due at least in part to the uneasy coexistence of two meanings of information: technical and semantic (e.g. Krebs & Dawkins 1984; Markl 1985; Owings & Morton 1998). The two address different aspects of the communicative process. Information in the technical sense is reduction in the uncertainty (to an external observer) caused by the sending of a signal. Wiley (1983) further distinguishes between 'broadcast' and 'transmitted' technical information. Broadcast information is an observer's reduction in uncertainty about the sender's behaviour caused by a signal, whereas transmitted information is reduction in uncertainty about the receiver's behaviour. Semantic or 'colloquial' sense information (Dawkins 1995; Maynard Smith & Harper 1995), on the other hand, attempts to characterize the content or 'aboutness' of animal signals (i.e. that property of the sender or its environment that signals are about). Technical and semantic information are concerned with different levels of semiotic analysis: technical information is concerned with the syntactic level of analysis, whereas semantic information, as the name implies, corresponds to the semantic level.

Technical information had its origin in the field of electrical engineering as a quantitative measure of the amount of information (measured in *bits*) that can be encoded and transmitted efficiently through a given channel. Technical information has the appeal of a rigorous mathematical theory. However, its application to animal communication is beset with difficulties. First, there is the problem of specifying the behavioural options available to senders and receivers (and their associated probabilities). Unless our partitioning of the behaviour stream into discrete units agrees with the way the animals themselves partition behaviour, we are bound to come up with meaningless estimates of uncertainty reduction. If, for example, the animals divide up behaviour into more units than the observer, the amount of uncertainty reduced by the signal may be underestimated (Krebs & Dawkins 1984). A second problem with the technical meaning of information is receiver relativity: in order to determine how much uncertainty is reduced by the reception of a signal, we need to know what the receiver (not the external observer) already knew about the sender or its environment before the signal was produced. Thus, the amount of technical information transmitted is determined at least in part by the receiver (Scott-Phillips 2008). Finally, there is the problem of referential indeterminacy (Quine 1960). Technical information focuses on one of the consequences of information transmission (i.e. uncertainty is reduced), but it does not give an explicit account of what specific signals are about. Technical information is content-neutral (Dennett 1987) or content-free (Di Paolo 1997), and therefore indifferent to the kinds of information (in the semantic sense) provided by a given signal.

This last point has generated the most misunderstanding. Several authors have attempted to reconcile the two meanings of information by pointing out how one can easily go from technical to semantic information and vice versa (Wiley 1983; Krebs & Dawkins 1984; Hasson 1994; Smith 1997). A signal that reduces the receiver's uncertainty about some feature of the sender or the environment (technical information) can be viewed as a source of semantic information about that particular feature. As Allen & Hauser (1992) explain, 'this may seem to provide a notion of [semantic] content since it helps to characterize what a given signal is about' (page 84). The equivalence/correspondence, however, is illusory: technical information provides a measure of the amount of information, but it does not specify the type of information (in the semantic sense) transmitted.

By definition, all signals transmit technical information (i.e. reduce uncertainty), but some signals may reduce the receiver's uncertainty about trivial and uninteresting aspects of the sender or the environment (Scott-Phillips 2008). Imagine a male uttering a string of territorial calls. The n th call may convey as much semantic information ('I'm a territorial male in full reproductive mode') as the first, but it will not further reduce the uncertainty of a receiver that has already listened to the $n - 1$ previous calls. The information (in the semantic sense) that the sender is a territorial male is not news to the receiver and therefore her uncertainty in that respect is not reduced by the male's call. Thus, signalling will have resulted in a reduction in the receiver's uncertainty (e.g. about the fact that the receiver is still alive and has not changed sex), but not about those features that actually drove the evolution of the signal because the latter were already known to the receiver.

This is not to say that the concept of technical information has no use in the study of animal communication (see, for example: Rand & Williams 1970; McCowan et al. 2002), but most authors consider it inadequate for understanding the selective pressures acting on senders and receivers. Information as uncertainty reduction 'rarely encapsulates all of the important qualities of information from a whole-organism perspective' (Dall et al. 2005, pp. 187–188). It is telling that many papers and book chapters on

communication devote considerable space to the definition and measurement of technical information, only to conclude that the concept of information implied in most discussions of communication is semantic, not technical information (Wiley 1983; Krebs & Dawkins 1984; Dawkins 1995; Maynard Smith & Harper 1995; Barnard 2004). However, semantic information is not free from criticisms. In fact, both meanings of information, technical and semantic, are considered too broad for a rigorous analysis of communication (Carazo & Font 2010), which is the main reason why information as currently construed cannot be a central defining property of communication. For example, animals often obtain information from sources other than signals, including direct assessment, cues, prior probabilities (Bradbury & Vehrencamp 1998), and even signalling components of non-signalling behaviours (Lotem et al. 1999).

In an effort to accommodate information within the adaptationist framework of communication, we have proposed yet another meaning of information. *Functional information* is the attribute or attributes of the sender and/or the environment that correlate with one or several characteristics in the design of a signal and are responsible for the evolution (or maintenance) of the response to that signal (Carazo & Font 2010). Functional information is whatever information (in the semantic sense) can be extracted from the communicative exchange that makes it adaptive for the receiver to respond to a given signal. Functional information is thus the subset of semantic information that encompasses those features of the sender or the environment that allow the receiver to make informed decisions that improve its fitness. Note that here we are using the term 'functional' in the strictly Tinbergian sense of adaptive value. Recently, 'functional' has also been used as a device to avoid potentially awkward implications of intentionality in discussions of nonhuman animal behaviour (e.g. functional referentiality, functional deception, functional altruism). Functional deception, for example, is behaviour that 'has the effects of deception without necessarily having the cognitive underpinnings that we would require of deception in humans' (Searcy & Nowicki 2005, page 5). This meaning of functional is different from the one we use here.

If a signal is to be effective in eliciting the appropriate response, it must make functional information available to receivers. For example, a female that hears a male's call will know that a conspecific male is nearby, and may also be able to learn something about the male's size, age, physical condition or quality as a potential mate. If the information acquired by the receiver more than outweighs the costs involved in sensing, processing and responding to the signal, then we have a potentially stable communication system. If no functional information is available, receivers will evolve counterstrategies and coevolution between sender and receiver will proceed until signals disappear or an equilibrium that benefits both parties is reached (Moynihan 1970; Bradbury & Vehrencamp 1998). The concept of functional information allows us to formulate a definition of a communicative signal that nicely synthesizes adaptationist and informational approaches as 'any act or structure that (1) affects the behaviour of other organisms; (2) evolved (or is maintained) because of those effects; (3) is effective because it makes functional information available to receivers (i.e. it allows receivers to extract functional information)' (Carazo & Font 2010). This definition deliberately leaves out deceptive signals (i.e. cases in which signals do not make functional information available to receivers; e.g. aggressive mimicry, false alarm calls). However, this does not mean that deceptive signals should be excluded from the study of communication (Carazo & Font 2010). From the receiver's perspective, honest and deceptive signals are one and the same, both proximally (because their structure is sufficiently similar that discriminating

between them is beyond the receiver's perceptual abilities) and at the ultimate level (because honest and deceptive instances of the signal are part of a signalling system that favours receiver responses to signals that are 'honest on average'; [Johnstone & Grafen 1993](#); [Kokko 1997](#)). For example, male armyworm moths respond to the chemical released by bolas spiders because they cannot differentiate between it and the pheromone emitted by female moths and because, on average, they benefit more from approaching the source of the chemical than from ignoring it ([Maynard Smith & Harper 1995](#)). Honest and deceptive signals are key elements of the same signalling system, but the concept of 'functional information' allows us to distinguish between two types of signals that are the result of different underlying evolutionary processes ([Carazo & Font 2010](#)). From the sender's perspective, honest signals work because they make functional information available to receivers (otherwise, receivers would not respond); deceptive signals, on the other hand, are effective because others (i.e. the honest senders) make functional information available to receivers.

An example may help clarify some of the conceptual issues discussed above. Lateral or broadside displays are common in agonistic encounters between rival males in many taxa ([Chiszar 1978](#); see examples in [Bradbury & Vehrencamp 1998](#), page 509). An animal performing a lateral display orients itself in such a way that it presents its lateral aspect to its opponent. Two explanations are available to account for the evolutionary origins of such a display. According to classical ethological lore, displays evolve from nonsignalling behaviours that give away information of use to receivers. Not surprisingly, among such protosignals are intention movements such as those preceding the execution of specific actions ([Tinbergen 1952](#)). Lateral displays in particular are believed to have evolved from the blending of antithetical intention movements of escape and attack. Given such evolutionary origins, early ethologists reasonably interpreted lateral displays as signals that allow receivers to assess the sender's current motivational state ([Baerends 1975](#)). An alternative explanation focuses instead on the sender and its ability to manipulate receivers by exploiting latent sensory or neural biases. Big things are potentially more dangerous than small things, and many animals seem to follow the rule of thumb 'bigger is meaner' in their interactions with members of their own or a different species. As animals engaged in a lateral display project a larger image onto the retinas of others with which they interact than animals that adopt alternative body orientations, lateral displays should be more intimidating to rivals and thus selection should favour senders that perform lateral rather than other types of displays. Of course, the evidence to choose among these alternative scenarios will be lacking in most cases, but the important point is that the two explanations are not mutually exclusive. Even if the signal initially arose from sender manipulation of receiver biases, selection should favour receivers that benefit from the interaction. One obvious way that receivers can benefit is to obtain information (functional information) about the sender. This can be information about the sender's motivational state or probability of attack, as surmised by classical ethologists, or about its body size or any other attribute that may relate to its competitive ability as proposed by modern adaptationists.

Often two opponents face each other laterally in a reciprocal lateral display, adopting either a parallel (head to head) or anti-parallel (head to tail) orientation. Examples include the lateral displays of many fish and lizard species, and the parallel walk in red deer stags. The standard line holds that the function of reciprocal lateral displays is to allow opponents to assess their relative body size and reveal possible size asymmetries between them. Even such an apparently harmless statement can be misleading if care is not taken to distinguish the roles of sender and receiver. The statement is potentially misleading because it suggests that, as senders, the

participants in an aggressive interaction intentionally release information regarding their body size. It suggests that each animal in the interaction benefits, as a sender, from making information available to receivers. In fact, information about a rival's size is the benefit each participating animal derives, as receiver, from the interaction. The display works because it intimidates rivals, and the mechanisms whereby that effect is achieved probably have little to do with the voluntary provision of information. Of course, the distinction between the benefits accruing to senders and receivers may seem artificial because both animals participating in the interaction are at the same time senders and receivers. But the distinction is important for a correct understanding of the evolutionary dynamics involved.

During lateral displays it is fairly common for animals to enlarge their lateral profile by some sort of body compression in the sagittal plane. Sagittal compression has been interpreted as a result of the animal 'trying to make itself look bigger'. In fact, from the sender's perspective sagittal compression works not because it misrepresents the animal's true size but because it projects a larger image onto the receiver's retina and is thus more intimidating to receivers that abide by the 'bigger is meaner' rule. It is easy to imagine how such a trait could evolve: in a population in which every individual is performing lateral displays, a mutant that increased its apparent size through sagittal compression would enjoy an immediate fitness advantage. The signal then becomes deceptive to receivers because sagittal compression distorts the relationship between the sender's lateral profile and its actual body size. The term 'exaggerator' was proposed by [Maynard Smith & Harper \(2003\)](#) for those features, like sagittal compression, that increase the apparent size of a structure. Once they arise, exaggerators will rapidly be adopted by all the members of a population. If sagittal compression really works, in the sense of making the displaying individual a more intimidating adversary, selection will soon result in all individuals doing the new trick. When this happens, the exaggerator becomes an index, a signal that is unfakeable due to physical constraints ([Maynard Smith & Harper 2003](#)). The first individuals to perform sagittal compression were exaggerating their apparent size; now, however, every individual in the population is doing it and, as long as there is a close relationship between the sender's maximum attainable profile and its true size, the signal will again be reliable ([Hasson 1997](#)). At this point, receivers may be able to extract other types of information about the sender, in addition to its motivational state or body size. In iguanian lizards, for example, sagittal compression is thought to hinder breathing, thereby handicapping the performing lizard ([Brandt 2003](#)). Thus, the time that an individual spends in sagittal compression could act as a quality handicap ([Hasson 1997](#)) reflecting endurance capacity, which in turn is related to fighting ability.

Once everybody is using sagittal compression as part of their lateral displays, the stage is set for a new round of coevolutionary arms race, one involving additional acts or structures that increase the apparent size of the displaying animal even further, such as raised hackles, fluffed up feathers, erected crests and extended fins. Some of these traits will initially be exaggerators of body size, but as selection tends to fix them in the population they will also turn into indices, perhaps providing other types of functional information to receivers. Although the specific details may be speculative, the bottom line is that information is important at every stage in the evolution of this signalling system, even though we risk missing it by an exclusive focus on signal effects and on the benefits reaped by senders ([Scott-Phillips 2008](#)). On a proximate level, information allows receivers to make informed decisions; on an ultimate level, it is the reason why receivers respond to signals. Manipulation and information are fully compatible as long as we take account of the two-pronged nature of communication and the different selection

pressures acting on senders and receivers. The integration of these two evolutionary mechanisms provides a general theory that explains the evolution of animal communicative signals, and the concept of functional information is fundamental to this aim.

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References

- Allen, C. & Hauser, M. 1992. Communication and cognition: is information the connection? *Yearbook of the Philosophy of Science*, **2**, 81–91.
- Arak, A. & Enquist, M. 1993. Hidden preferences and the evolution of signals. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 207–213.
- Arak, A. & Enquist, M. 1995. Conflict, receiver bias and the evolution of signal form. *Philosophical Transactions of the Royal Society of London, Series B*, **349**, 337–344.
- Baerends, G. P. 1975. An evaluation of the conflict hypothesis as an explanatory principle for the evolution of displays. In: *Function and Evolution of Behaviour* (Ed. by G. Baerends, C. Beer & A. Manning), pp. 187–228. Oxford: Clarendon Press.
- Barnard, C. 2004. *Animal Behaviour: Mechanism, Development, Ecology and Evolution*. Harlow, Essex: Pearson & Prentice Hall.
- Blumberg, M. S. & Alberts, J. R. 1997. Incidental emissions, fortuitous effects, and the origin of communication. In: *Perspectives in Ethology. Vol. 12: Communication* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 225–249. New York: Plenum.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Brandt, Y. 2003. Lizard threat display handicaps endurance. *Proceedings of the Royal Society B*, **270**, 1061–1068.
- Carazo, P. & Font, E. 2010. Putting information back into biological communication. *Journal of Evolutionary Biology*, **23**, 661–669.
- Cheney, D. L. & Seyfarth, R. M. 1996. Function and intention in the calls of nonhuman primates. *Proceedings of the British Academy*, **88**, 59–76.
- Chiszar, D. 1978. Lateral displays in the lower vertebrates: forms, functions, and origins. In: *Contrasts in Behavior: Adaptations in the Aquatic and Terrestrial Environments* (Ed. by S. Reese & F. J. Lighter), pp. 105–135. New York: J. Wiley.
- Christy, J. H. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *American Naturalist*, **146**, 171–181.
- Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M. & Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, **20**, 187–193.
- Dawkins, M. S. 1995. *Unravelling Animal Behaviour*, 2nd edn. Harlow, Essex: Longman.
- Dawkins, R. & Krebs, J. R. 1978. Animal signals: information or manipulation. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 282–309. Oxford: Blackwell.
- Dennett, D. C. 1987. *The Intentional Stance*. Cambridge, Massachusetts: MIT Press.
- Di Paolo, E. A. 1997. An investigation into the evolution of communication. *Adaptive Behavior*, **6**, 285–324.
- Dugatkin, L. A. 2001. Bystander effects and the structure of dominance hierarchies. *Behavioral Ecology*, **12**, 348–352.
- Endler, J. A. 1993. Some general comments of the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 215–225.
- Guilford, T. & Dawkins, M. S. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour*, **42**, 1–14.
- Harper, D. G. C. 1991. Communication. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), 3rd edn. Oxford: Blackwell.
- Hasson, O. 1994. Cheating signals. *Journal of Theoretical Biology*, **167**, 223–238.
- Hasson, O. 1997. Towards a general theory of biological signaling. *Journal of Theoretical Biology*, **185**, 139–156.
- Hasson, O. 2000. Knowledge, information, biases and signal assemblages. In: *Animal Signals: Signalling and Signal Design in Animal Communication* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 445–463. Trondheim, Norway: Tapir Academic Press.
- Hennessy, D. F., Owings, D. H., Rowe, M. P., Coss, R. G. & Leger, D. W. 1981. The information afforded by a variable signal: constraints on snake-elicited tail flagging by California ground squirrels. *Behaviour*, **78**, 188–226.
- Johnstone, R. A. 1997. The evolution of animal signals. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 155–178, 4th edn. Oxford: Blackwell.
- Johnstone, R. A. & Grafen, A. 1993. Dishonesty and the handicap principle. *Animal Behaviour*, **46**, 759–764.
- Kokko, H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology*, **41**, 99–107.
- Krebs, J. R. & Dawkins, R. 1984. Animal signals: mind-reading and manipulation. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 380–402, 2nd edn. Oxford: Blackwell.
- Lotem, A., Wagner, R. H. & Balshine-Earn, S. 1999. The overlooked signaling component of nonsignaling behavior. *Behavioral Ecology*, **10**, 209–212.
- McCowan, B., Doyle, L. R. & Hanser, S. F. 2002. Using information theory to assess the diversity, complexity, and development of communicative repertoires. *Journal of Comparative Psychology*, **116**, 166–172.
- McGregor, P. K. 1993. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 237–244.
- McGregor, P. K. 2005. *Animal Communication Networks*. Cambridge: Cambridge University Press.
- Markl, H. 1985. Manipulation, modulation, information, cognition: some of the riddles of communication. In: *Experimental Behavioral Ecology and Sociobiology* (Ed. by B. Holldobler & M. Lindauer), pp. 163–194. Stuttgart: Gustav Fischer Verlag.
- Maynard Smith, J. & Harper, D. G. C. 1995. Animal signals: models and terminology. *Journal of Theoretical Biology*, **177**, 305–311.
- Maynard Smith, J. & Harper, D. G. C. 2003. *Animal Signals*. Oxford: Oxford University Press.
- Morton, E. S. & Page, J. 1992. *Animal Talk: Science and the Voices of Nature*. New York: Random House.
- Moynihán, M. 1970. Control, suppression, decay, disappearance and replacement of displays. *Journal of Theoretical Biology*, **29**, 85–112.
- Owings, D. H. & Morton, E. S. 1997. The role of information in communication: an assessment/management approach. In: *Perspectives in Ethology. Vol. 12: Communication* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 359–390. New York: Plenum.
- Owings, D. H. & Morton, E. S. 1998. *Animal Vocal Communication: a New Approach*. Cambridge: Cambridge University Press.
- Owings, D. H. & Zeifman, D. M. 2004. Human infant crying as an animal communication system: insights from an assessment/management approach. In: *Evolution of Communication Systems: a Comparative Approach* (Ed. by D. K. Oller & U. Griebel), pp. 151–170. Cambridge, Massachusetts: MIT Press.
- Owren, M. J. 2000. Standing evolution on its head: the uneasy role of evolutionary theory in comparative cognition and communication. *Reviews in Anthropology*, **29**, 55–69.
- Owren, M. J. & Rendall, D. 1997. An affect-conditioning model of nonhuman primate vocalizations. In: *Perspectives in Ethology. Vol. 12: Communication* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 299–346. New York: Plenum.
- Owren, M. J. & Rendall, D. 2001. Sound on the rebound: returning form and function to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology*, **10**, 58–71.
- Quine, W. V. O. 1960. *Word and Object*. Cambridge, Massachusetts: MIT Press.
- Rand, A. S. & Williams, E. E. 1970. An estimation of redundancy and information content of anole dewlaps. *American Naturalist*, **104**, 99–103.
- Rendall, D. & Owren, M. J. 2002. Animal vocal communication: say what? In: *The Cognitive Animal* (Ed. by M. Bekoff, C. Allen & G. Burghardt), pp. 307–314. Cambridge, Massachusetts: MIT Press.
- Rendall, D., Cheney, D. L. & Seyfarth, R. M. 2000. Proximate factors mediating 'contact' calls in adult female baboons and their infants. *Journal of Comparative Psychology*, **114**, 36–46.
- Rendall, D., Owren, M. J. & Ryan, M. J. 2009. What do animal signals mean? *Animal Behaviour*, **78**, 233–240.
- Scott-Phillips, T. C. 2008. Defining biological communication. *Journal of Evolutionary Biology*, **21**, 387–395.
- Scott-Phillips, T. C. 2010. Animal communication: insights from linguistic pragmatics. *Animal Behaviour*, **79** (1), e1–e4.
- Searcy, W. A. & Nowicki, S. 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton, New Jersey: Princeton University Press.
- Seyfarth, R. M. & Cheney, D. L. 2003. Signallers and receivers in animal communication. *Annual Review of Psychology*, **54**, 145–173.
- Smith, W. J. 1977. *The Behavior of Communicating: an Ethological Approach*. Cambridge, Massachusetts: Harvard University Press.
- Smith, W. J. 1986. An 'informational' perspective on manipulation. In: *Deception, Perspectives on Human and Nonhuman Deceit* (Ed. by R. W. Mitchell & N. S. Thompson), pp. 71–86. New York: State University of New York Press.
- Smith, W. J. 1997. The behavior of communicating, after twenty years. In: *Perspectives in Ethology. Vol. 12: Communication* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 7–53. New York: Plenum.
- Stevens, M. 2005. The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. *Biological Reviews*, **80**, 573–588.
- Stevens, M. 2007. Predator perception and the interrelation between different forms of protective coloration. *Proceedings of the Royal Society B*, **274**, 1457–1464.
- Stevens, M., Hardman, C. J. & Stubbins, C. L. 2008. Conspicuousness, not eye mimicry, makes 'eyespot' effective antipredator signals. *Behavioral Ecology*, **19**, 525–531.
- Tinbergen, N. 1952. 'Derived' activities; their causation, biological significance, origin, and emancipation during evolution. *Quarterly Review of Biology*, **27**, 1–32.
- Wiley, R. H. 1983. The evolution of communication: information and manipulation. In: *Animal Behaviour. Vol. 2: Communication* (Ed. by T. R. Halliday & P. J. B. Slater), pp. 156–189. Oxford: Blackwell.