Animal Behaviour 78 (2009) 233–240

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

Essay

What do animal signals mean?

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ARTICLE INFO

Article history:
Received 18 May 2009
Final acceptance 25 May 2009
Published online 9 July 2009
MS. number: 09-00322

Keywords:
animal communication
animal signals
information
information transmission
language
manipulation
meaning
sensory exploitation
sexual selection

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.

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 charaterizing 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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doi:10.1016/j.anbehav.2009.06.007

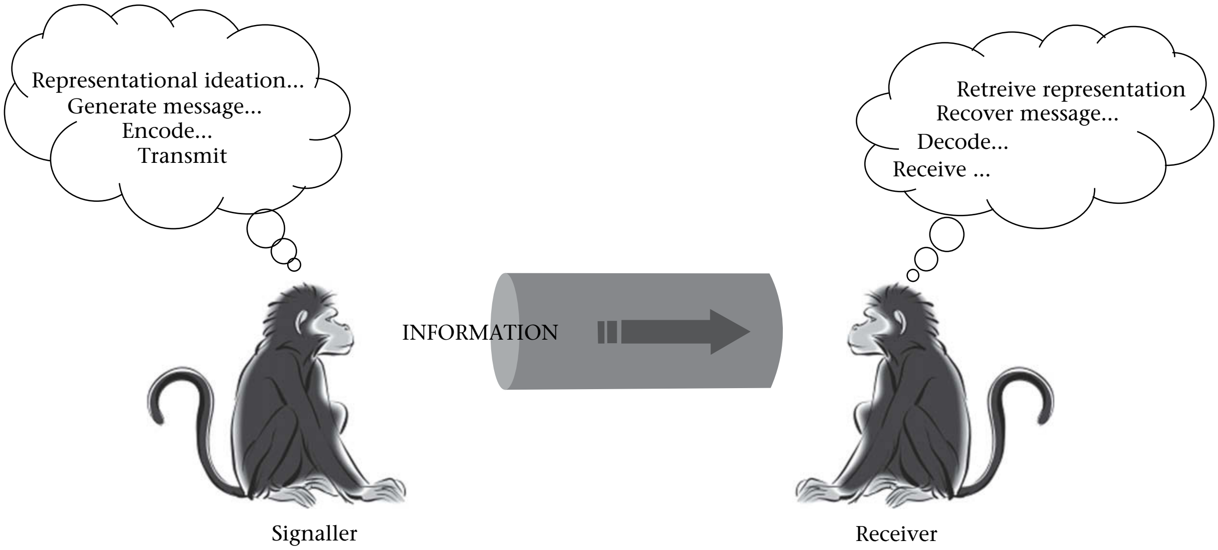

Figure 1. Schematic illustrating core features of classic information transmission approaches to animal communication. According to such frameworks, signalling events involve some kind of representational ideation on the part of the signaller that is translated into a message whose content is then encoded 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.' 'the signal must *carry information*,—about the state or future actions of the signaler, or about the external world—that is of interest to the receiver'	None
Searcy & Nowicki 2005, page 2	Endorse Otte's (1974) definition	None
Fitch 2008, page 385	'Honest signals are those which accurately (but not necessarily perfectly) *convey information* about some relevant quality of the signaler (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

Table 2
Some examples of informal use of informational and linguistic constructs in recent characterizations of animal communication (emphases added)

Source	Explanations of signals, signalling or communication
Cheney & Seyfarth 1996, page 59	'The alarm and contact calls of monkeys *provide information* about the signaller's current physical and mental states, but they are not deliberately given to inform or instruct others. Instead, listeners appear to *extract relevant information* about a call's function based on behavioral contingencies and their own experiences.'
Zuberbühler 2000b, page 717	'From the perspective of the call recipient, however, the differences between primate alarm calls and human linguistic utterances are less explicit. In this and other studies, it was the *meaning* of the stimuli, but not the acoustic features that explained the subjects' response patterns. These results extend this finding … by showing that *semantic understanding can be based on arbitrary signals, as it is [sic] the case for word meaning.*'
Bugnyar et al. 2001, page 949	'*Signals may encode information* about attributes of the sender … and about stimuli or events in the environment … If such *signals provide receivers with sufficient information* to determine the context underlying signal production … the signals are regarded as functionally referential.'
Manser et al. 2002, page 55	'Recent work on suricates, an African mongoose, shows that animal alarm calls simultaneously *encode information* about both predator type and the signaler's perception of urgency.'
Cheney & Seyfarth 2005, page 135	'Here we review research on the vocal communication and cognition of nonhuman primates … we conclude, first, that nonhuman primates' inability to represent the mental states of others makes their communication fundamentally different from human language. Second, while nonhuman primates' production of vocalizations is highly constrained, their ability to *extract complex information* from sounds is not. Upon hearing vocalizations, *listeners acquire information* about their social companions that is *referential, discretely coded, hierarchically structured, rule-governed, and propositional.*'
Templeton et al. 2005, page 1934	'If a species is preyed upon by different predators that use different hunting strategies or vary in the degree of danger they present, selection can favor variation in alarm signals that *encode this information.* Such variation in alarm signals can be used to *transfer information* about the type of predator, the degree of threat that a predator represents, or both.'
Slocombe & Zuberbühler 2007, page 17228	'Our first goal was to examine to what degree chimpanzee victim screams *conveyed information* about the nature of the conflict, thus *providing valuable information* for nearby receivers *deciding* whether or not to interfere. Previous research on macaques has revealed that callers produce acoustically distinct scream types that are *meaningful to listeners.*'

occurs when the speaker and the listener have similar representational processes that ensure corresponding coding and decoding of signal meaning. The details of signal design are not critical. Indeed the design, or form, of most words is thought to be largely arbitrary with respect to the things they represent. What is more critical is that speakers and listeners make implicit attributions about each other's mental states, such as their thoughts, beliefs or states of knowledge, because these are what motivate and sustain reciprocal semantic exchange.

This view of language-like meaning and communication has also been used to organize studies of primates and some other taxa because our own experience with language makes it a natural metaphor for studying communication in other species. The practice was also further encouraged by seminal studies of primate communication which highlighted some provocative parallels to language. For example, some vocalizations were found to be produced in specific contexts, such as when encountering predators or food, and listeners responded to such vocalizations in equally specific and appropriate ways as if semantic information had been exchanged (Seyfarth et al. 1980). Such outcomes suggested that some animals might use vocalizations in a representational fashion, similar to the way humans use words (Gyger et al. 1987; Zuberbühler 2000a).

Subsequent research, however, has complicated this picture. Representational modes of signalling have been reported in only a few species, and then only in a small fraction of the vocal repertoire. Even in cases of representational signalling in primate species closely related to humans, subsequent studies demonstrate a surprising absence of the intention to inform by calling animals (Cheney & Seyfarth 1990; Cheney et al. 1996; Rendall et al. 2000). Thus, although listeners sometimes respond to vocalizations '*as if*' they contained semantic information, callers prove to be fundamentally unaware of the informational value of their own signals.

These more recent findings highlight an informational disconnection between signallers and perceivers and suggest they do not share the same representational parity that characterizes human speech (Cheney & Seyfarth 1996, 1998, 2005). In fact, the failure of calling animals to take account of the informational needs of listeners corroborates a growing literature showing that nonhuman primates show little of the perspective taking and mental state attribution abilities considered to be foundational to the referential quality of human language (reviewed in Penn & Povinelli 2007).

These differences are paralleled by data on the neural control of vocal production. For example, in squirrel monkeys, *Saimiri sciureus* (Jürgens 1998), dogs, *Canis familiaris* (Solomon et al. 1995) and cats, *Felis catus* (de Lanarolle & Lang 1988), vocal behaviour is modulated primarily by involuntary processes involving subcortical brain structures such as the limbic system, midbrain and brainstem. In contrast, language production in humans also involves a variety of subcortical circuits but relies importantly on volitionally controlled processes in temporal- and frontal-lobe cortical regions (Lieberman 2002).

Hence, both in details of neuroanatomical involvement and in broader representational and intentional processes, there are important qualitative differences in the communication systems of humans and animals, including even the primate species most closely related to humans. Summarizing such findings, Cheney & Seyfarth (1996, page 59) concluded very definitively that 'the mental mechanisms underlying the vocalizations of nonhuman primates…appear to be fundamentally different from those that underlie human speech'.

Nevertheless, efforts to establish the meaning and referential quality of primate signals continue apace (Hauser 1998; Zuberbühler 2000a, 2003; Di Bitetti 2003; Slocombe & Zuberbühler 2005; Arnold & Zuberbühler 2006a, b) and, in fact, have spread to include a variety of more distantly related mammals and birds (e.g. meerkats, *Suricata suricatta*: Manser et al. 2001, 2002; red squirrels, *Tamiasciurus hudsonicus*: Greene & Meagher 1998; chickens, *Gallus gallus domesticus*: Evans et al. 1993; Evans & Evans 1999, 2007; Smith & Evans 2009; chickadees, *Poecile atricapillus*: Templeton et al. 2005; ravens, *Corvus corax*: Bugnyar et al. 2001) and additional organizational properties of language (e.g. syntax: Zuberbühler 2002; Clarke et al. 2006). The difference is that more recent work on signal meaning is now conducted under the banner of a modified theoretical construct: 'functional reference' (Marler et al. 1992; Macedonia & Evans 1993; Evans 1997; Furer & Manser 2009). As Hauser (1996, page 509) explained, 'the motivation for this terminological change was to make clear that nonhuman animal calls are not exactly like human words, but rather appear to function in the same way'. The apparent rationale for adopting this qualified view of reference is that it is important to be able to continue to rely on the notion that signals have independent meaning and are, like human words, 'about' things, even when signallers do not intend to transmit the information they are encoding (Cheney & Seyfarth 1996). At the same time, though, the idea of functional reference represents a conceptual retreat in acknowledging that animal signals may never meet the semantic sine qua non of human language. As a result, the term itself must be seen as an oxymoron. Designed to preserve some conceptual connection to language, the construct instead represents an admission that the central, linguistically based concept of meaning simply does not apply.

The logical incoherence is readily illustrated in a concurrent conceptual development, specifically that the meaning of animal signals is typically neither purely motivational in nature nor purely referential, but instead can be seen to lie somewhere along a continuum between these hypothetical endpoints (Marler et al. 1992). Whereas formally intentional communication has signallers encoding and transmitting information about their own cognitive representations that have the effect of activating similar mental states in receivers, the concept of functional reference implies that the information conveyed simply allows receivers to *infer* the contexts of signal production. Hauser (1996, page 509) noted here that 'the acoustic structure of functionally referential signals provides listeners with sufficient information to determine the context underlying signal production' (see also Marler et al. 1992; Evans 1997). The motivational end of the continuum must therefore concern the information signallers make available about internal states, while the functionally referential end represents the extent to which receivers can make inferences about external events from hearing the signal. If so, however, the continuum evaporates.

As Premack (1972, 1975) and many others have noted (Marler 1977; Marler et al. 1992; Snowdon 1992; Owings 1994), inferences can also be drawn from motivational signals. One can, for instance, imagine a set of acoustically discriminable calls that reflect only the motivational state of a signaller, but that are usually produced in different circumstances. Receivers who know something about an individual's typical affective response to each situation can then infer which circumstance the signaller has encountered even though its communicative behaviour is purely motivational. Classically motivational signals can therefore also be functionally referential even though no linguistic-like representations are involved. Placement of a signal on the continuum thus comes to depend less on its purported information content and more on whether one adopts the signaller's or perceiver's perspective. Because the continuum is necessarily based on motivational or referential encoding processes in the signaller, bringing the inferential capacities of the receiver into the picture makes nonsense of it. Either the distinction between the endpoints evaporates, or any given signal must be said to exist at multiple locations on the continuum at the same time depending on whose perspective is being considered.

Ultimately, then, there are core conceptual and empirical ambiguities with informational approaches to communication in primates and other animals. Attempts to persevere with them in the face of these ambiguities risk shoe-horning an increasing array of fundamentally incompatible signalling phenomena into a narrow, linguistically inspired informational frame. To address this problem, a number of researchers have called for alternative approaches to central research questions in this field. In general, these proposals have advocated staying closer to basic evolutionary principles, for instance by granting signallers and perceivers more distinct roles in the communication process, including often divergent interests. In this view, the function of signalling is to influence the behaviour of perceivers rather than to metaphorically transmit meaningful, language-like information (Dawkins & Krebs 1978; Ryan 1990; Guilford & Dawkins 1991; Blumberg & Alberts 1997; Dawkins & Guilford 1997; Owings & Morton 1997, 1998; Owren & Rendall 1997, 2001). Corollaries include emphasizing the role of signal structure in effecting such influence, and expanding the conception of communication well beyond just representational-like exchanges.

In primates, for example, alarm vocalizations produced upon encountering dangerous predators are found not to be arbitrarily structured at all, instead typically being short with abrupt onsets and broadband noisy spectra. These widely shared acoustic features are ideally suited for capturing and manipulating listener attention and arousal through short, direct links from the auditory periphery to brainstem regions regulating whole-body arousal and activation. As a result, alarm calls elicit in listeners immediate orienting responses and movements preparatory to flight which are obviously highly functional to them in the context of predator encounters. In fact, the same basic alarm call structure and response is seen in a range of other mammals and birds (Marler 1955; Owings & Morton 1998; Owren & Rendall 2001), suggesting a highly conserved response system that is likely to be traceable to detection and localization functions related to predator avoidance and prey capture in early vertebrates (Grothe 2003).

Developmental studies in primates have shown further that generalized startle responses to species-typical alarm calls are induced even in naïve infants with limited experience and who have not yet developed adult-like escape responses (Herzog & Hopf 1984; Seyfarth & Cheney 1986). It is likely that these reflexive responses provide critical scaffolding for learning about predators, because the same circuits that connect the auditory periphery to brainstem regions regulating overall arousal also link directly to the amygdala and hippocampus (LeDoux 2000; McGaugh 2003). Hence, strong, call-elicited autonomic responses probably serve to help the infant learn and remember details of predator encounters and associated behavioural sequelae. Thus, while the informational account of primate alarm calls appeals to underspecified language-like representational constructs (do vervet alarm calls *mean* 'leopard', 'large cat', 'run into a tree'?), noninformational accounts look to more concrete explanations grounded in the influence that specific acoustic properties of the calls have on broadly conserved neural, sensory, affective and learning systems in listeners that together help to support adaptive behavioural responding (Owings & Hennessy 1984; Owren & Rendall 1997, 2001; Owings & Morton 1998).

The potential importance of general auditory mechanisms in understanding antipredator vocalizations can also be applied to how signallers exert influence in other contexts where signaller and perceiver interests are not so clearly aligned. For example, one class of vocalizations produced by many primates but also many other mammals, birds and crocodilians are labelled 'squeaks, shrieks and screams'. These sounds have sharp onsets, dramatic frequency and amplitude fluctuations, and chaotic spectral structures, which are exactly the sorts of features that have direct impact on animal nervous systems (Rendall et al. 2009). Such sounds are common in infants and juveniles who otherwise have little influence on the behaviour of older and larger individuals. For example, a frustrated primate weanling cannot force its mother to nurse, but can readily elicit such behaviour with sounds whose acoustic features trigger the mother's attentional mechanisms, increase her arousal state, and with repetition become very aversive. Adults can be similarly impotent when interacting with more dominant individuals. Lower-ranking victims of aggression seldom offer much serious physical resistance, but they can make themselves unappealing targets by screaming vociferously, producing loud, jarring bursts of broadband noise and piercing, high-frequency, tonal sounds in variable streams whose aversive qualities are difficult for listeners to resist or habituate to (Hammerschmidt et al. 1994; Owren & Rendall 2001; Rendall et al. 2009).

These latter signalling phenomena are not uncommon in primates and other species, nor are they easily characterized in informational terms. The contexts they mediate do not lend themselves to mutualistic information exchange and the chaotically structured signals involved are poorly suited as information carriers. Instead, the behavioural contexts epitomize the push-and-pull of social conflict and the signals themselves bear the mark of design for influence and manipulation, with features well suited to access and exploit listeners' basic perceptual sensitivities and central nervous system reflexes.

SEXUAL SELECTION AND ACOUSTIC COMMUNICATION

These same themes of information versus influence emerge in a completely different domain, namely sexual selection and communication. Much of this work is conducted with taxa (e.g. birds, frogs, fish, insects) for which the language metaphor has far less intrinsic appeal. Nevertheless, similar informational constructs have been central in this research area as well (Zahavi & Zahavi 1997; Bradbury & Vehrencamp 2000). Here, the emphasis is on the information males provide to females in terms of health, vigour or genetic make-up. Hence, courtship signals are *about* male quality, and the communication process is modelled in terms of how males *encode quality information* in their signals, and how females in turn *extract this information* to make mating decisions. The assumption is that male-quality signals are fundamentally honest, and that such honesty is enforced by females who can discount all but honest signals (Maynard Smith & Harper 2003).

While this informational approach has been the basis for much productive research, it is also metaphorical and abstract. It offers little consideration of signal design and, as a result, actually overcomplicates the information-processing requirements proposed to be involved. For example, in many species, the most basic requirement for any signal is that it be detectable against background noise, and it is here that the results of selection on the design of many courtship signals are, in fact, most obvious. Thus, males are often under strong selection to produce repeatedly signals of high amplitude that also have spectral and temporal characteristics that minimize transmission degradation and attenuation, and that do not overlap other sounds in the temporal or spectral domain. Included in the 'background noise' that a male must combat are the calls of other conspecifics. This factor alone can lead to an arms race that contributes to elaborate, sexually selected displays (Ryan & Cummings 2005). Furthermore, once detected, signals must be localized in order to be functional in mate attraction. This additional requirement shapes yet other features of signal design that yield the cues used by many vertebrate brains to resolve spatial location (Grothe 2003).

Importantly, the processes of simply detecting and localizing signals can by themselves play an important role in modulating female mating behaviour. For example, as discussed above for primates, the auditory systems of both birds (Cheng & Peng 1997) and frogs (Wilczynski & Chu 2001) are directly linked to the neuroendocrine processes that regulate affect and motivation, in this case female proceptivity. Females must hear male courtship calls in order even to enter a physiological state of sexual receptivity (reviewed in Wilczynski et al. 2005; Cheng 2008).

Direct effects of courtship signals on female receptivity and mating behaviour are well known in birds, which produce some of the most structurally complex and variable sounds in the animal world. Indeed, the number and diversity of songs produced could be taken as an indication of extensive and detailed information content. And, yet, one important function of structurally complex song appears simply to be precluding receiver boredom or habituation (Hartshorne 1973; Searcy 1992). Analogous 'antihabituation' effects have been shown at the molecular, cellular and neural levels as well (Dong & Clayton 2009). The relatively narrow focus of informational frameworks on what signals indicate about male quality ignores many of these basic sensory and psychological factors that shape courtship signals and how they might relate to signal detectability, localizability and antihabituation.

A second important shortcoming of informational approaches to courtship signals is the proposal that they must be 'honest' to be functional (Zahavi & Zahavi 1997; Maynard Smith & Harper 2003). This assumption overlooks two fundamental and inter-related points noted above: that perceivers have evolved sensory systems to detect, localize and discriminate important features of the environment; and that they must perform these functions in many contexts, not just in the service of mate choice. Hence, sensory abilities in perceivers that are functional across a range of domains might not be perfect, or optimal, in any one of them, and greater functional sensitivity in one domain can influence sensitivity in another, leaving perceivers inherently susceptible to signaller influence. For example, in some fish, the sensitivity of photoreceptors evolved to allow detection of prey items in the local photic environment, but males have subsequently evolved colours to match the photoreceptor sensitivity (Cummings 2007; Seehausen et al. 2008).

Similarly, certain spectral characteristics of the courtship signals of túngara frogs, *Physalaemus pustulosus*, evolved to match preexisting auditory sensitivity (Ryan 1990). In this classic example, male túngara frogs have developed a mating call with two signal components: a 'whine' that is produced by males of several closely related species and is necessary and sufficient to attract females for mating; and a 'chuck' that male túngara frogs sometimes append to the whine and that makes the signal more attractive to females. Female attraction to both call components is explained mechanistically by the tuning of the two amphibian inner-ear organs. One of these organs, the amphibian papilla, is most sensitive in the region matching the dominant frequency of the whine component, while the second inner-organ, the basilar papilla, is most sensitive in the region matching the dominant frequency of the chuck. Thus, the regions of greatest signal energy in the mating calls of male túngara frogs match the regions of greatest sensitivity in the auditory periphery of females (reviewed in Ryan & Rand 2003).

This kind of auditory filter matching to mating calls has been shown more broadly in anurans (Gerhardt & Schwartz 2001). In the case of the túngara frog, it is best explained evolutionarily by a process of sensory exploitation in which males' production of the chuck component tapped latent sensitivity in a deeply conserved neural feature of the female auditory system (Ryan & Rand 1993).

There are numerous other examples of this pattern of sensory exploitation in which males evolve courtship signals that exploit pre-existing sensory biases that females cannot simply choose to ignore (e.g. Endler & Basolo 1998; Ryan 1998; Bradbury & Vehrencamp 2000). As a result, many aspects of the general biology of communication do not fall under the purview of the information approach. A broader view of courtship signals might be that they have evolved not necessarily to provide females with specific information about male quality per se, but rather to influence females in ways that promote mating (Dawkins & Krebs 1978). Such a view requires consideration of the species' history and the sensory, neurophysiological and psychological processes that characterize the perceiver during the course of signal–perceiver evolution. To the extent that the influence exerted on females is not ultimately in females' interests, there will, of course, be counterselection on females to resist such influence. However, it cannot simply be assumed a priori that selection on female resistance always trumps selection on male influence and thereby guarantees signal honesty. Also, in any given situation, the signalling dynamic might be in flux rather than at a stable equilibrium. How the courtship signalling dynamic plays out and where it is at any point in evolutionary time will depend on inevitable asymmetries in the reproductive interests of males and females coupled to constraints placed on signal production and perception by morphological and neurological limitations.

CONCLUDING REMARKS

We conclude by returning to the overarching questions that framed this essay. 'What do animal signals mean?' 'What information do they convey?' These are the common and core questions that structure a great many research programmes in animal communication, if sometimes only implicitly. Our argument is that, explicit or otherwise, the questions are ill-posed. They reflect a natural but loose casting of animal communication systems in linguistic or informational terms. Although the loosely defined linguistic and informational constructs make convenient explanatory shorthand, they are problematic when elevated beyond metaphor and pressed into service as substantive explanation for the broad sweep of animal-signalling phenomena (Owren & Rendall 2001). The implicit commitment such approaches make to information as a communicative commodity to be transferred, shared or exchanged often either overlooks many important factors that shape functional signal design in different species, or it blurs more than it illuminates the proximate factors that it does attempt to address by invoking abstract, metaphorical constructs very foreign to ethological inquiry and explanation.

We therefore suggest replacing the traditional emphasis on *information* with an emphasis on *influence* that stays closer to basic evolutionary principles in ascribing signallers and perceivers distinct roles and potentially divergent interests in communication processes (Dawkins & Krebs 1978). The corollary is that we must also accept that signalling phenomena will often entail asymmetries not generally observed or modelled in formal systems like language. These will include asymmetries in the mechanisms that support signal production in senders versus reception in perceivers, and functional asymmetries that leave signallers and perceivers at different points in the evolutionary dynamic. With this emphasis, the details of signal design are not arbitrary, or somehow secondary to the process of communicating, as they are thought to be in language, but rather they are absolutely central to it.

We also want to stress that our critique of the use of linguistic and informational constructs in studies of animal communication is not a declaration of evolutionary discontinuity. On the contrary, understanding animal signalling is likely to be key to working out the evolution of human communication behaviour as well. However, we seriously bias our 'discovery' of potential commonalities by borrowing and applying to animal communication systems from the start the very linguistic or informational constructs we are ultimately trying to understand and explain in language. That approach unduly narrows the possibilities from the outset and, in fact, virtually guarantees that signalling phenomena in the two groups will be 'found' to be similar. It is also both teleological and circular in using constructs developed for one recently evolved and possibly highly derived system of communication (language) to model processes involved in scores of other simpler and phylogenetically older systems in other species. That approach gets the evolutionary and epistemological logic completely backwards. Instead, and as in other areas of ethology and biological inquiry, it is by comparing phenomena across a wide range of animal taxa that we discover the general principles with which to understand the characteristics of any single one. As ethologists, then, we can and probably should be striving to contribute to the eventual understanding of language (Hauser et al. 2002). However, we should do so by applying established evolutionary and ethological principles to the phenomena of animal communication and human language alike, rather than confusing matters from the outset by importing notoriously slippery linguistic and informational constructs.

Finally, we do not expect that all readers will endorse the concerns we raise in this essay or the alternatives we recommend to address them. In fact, we expect that some readers will object strenuously. We therefore explicitly invite commentary and feedback on our arguments with the goal of converging on more agreeable and biologically realistic accounts of animal communication.

Acknowledgments

For generous grant support over the years, we thank the Natural Sciences and Engineering Research Council (NSERC) of Canada and the NIH and the NSF of the United States. We are grateful to several referees for their valuable comments on the manuscript.

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APPENDIX: THE CONDUIT METAPHOR AND SHANNON–WEAVER INFORMATION

The field of animal communication has been strongly influenced, although often unknowingly, by a view that linguist Michael Reddy (1979) famously referred to as the conduit metaphor. In this approach, information is treated as if it were a concrete entity that signallers encode and send, and that listeners can receive and decode (see Fig. 1). Encoded information is afforded a material form that exists independently of the individuals that are communicating. Signals are, for instance, considered to 'contain' and 'convey' encoded information, whose subsequent existence depends neither on the signaller (once the information is sent) nor on the perceiver (who might or might not perceive, attend to or even understand the information).

While intuitively appealing, this metaphorical approach also carries with it a definitional sleight-of-hand that undermines its scientific integrity. Specifically, although information is given a central role in explaining terms like communication and signal, the term information, as well as the related concepts of encoding and decoding, are left undefined (see Beecher 1989 for an exception). This failure to account for the constructs placed at the centre of animal communication necessarily creates a conceptual vacuum at the heart of the field. To get around this difficulty, researchers have fallen back on listing important 'characteristics' of information (e.g. Smith 1997), or referencing Shannon and Weaver's formal quantitative approach to information as tacit validation for conduit-based thinking (cf. Owings & Morton 1997). However, neither tactic is adequate. On the contrary, grounding the idea of communication in undefined informational constructs renders both those constructs and others that flow from them untenable.

Furthermore, Shannon and Weaver's more rigorous and specific definition of information is actually wholly incompatible with the conduit view it is sometimes cited to justify. In the Shannon–Weaver approach, information is an inherently statistical construct defined in terms of uncertainty reduction which can be quantified only in the context of known properties of signallers and receivers. These properties include the range of signal production options available to signallers and the range of response options available to receivers. However, these are also the very properties of signallers and receivers that are unknown in animal-signalling systems and that research is designed to uncover. As a result, the various processes that informational frameworks appeal to as hypotheticals are precisely the components that the Shannon–Weaver approach requires a priori in order to create a quantifiable information construct.

At the same time, in Shannon–Weaver's statistical characterization of information, the notions of encoding and decoding have no role. Thus, whereas the conduit approach leads to viewing signals as having encoded 'meaning' or 'symbolic-', 'semantic-' or 'reference-like' value, such ideas are anathema in Shannon and Weaver's formulation. As they themselves emphasize (Shannon & Weaver 1949, page 8): 'The word information, in this theory, is used in a special sense that must not be confused with its ordinary usage. In particular, information must not be confused with meaning. In fact, two messages, one of which is heavily loaded with meaning and the other of which is pure nonsense, can be exactly equivalent as regards information'.