Redefining animal signaling: influence versus information in communication

Michael J. Owren · Drew Rendall · Michael J. Ryan

Abstract Researchers typically define animal signaling as morphology or behavior specialized for transmitting *encoded information* from a signaler to a perceiver. Although intuitively appealing, this conception is inherently metaphorical and leaves concepts of both information and encoding undefined. To justify relying on the information construct, theorists often appeal to Shannon and Weaver's quantitative definition. The two approaches are, however, fundamentally at odds. The predominant definition of animal signaling is thus untenable, which has a number of undesirable consequences for both theory and practice in the field. Theoretical problems include conceptual circularity and running afoul of fundamental evolutionary principles. Problems in empirical work include that research is often grounded in abstractions such as signal honesty and semanticity, and thereby distracted from more basic and concrete factors shaping communication. A revised definition is therefore proposed, making *influence* rather than transmission of encoded information the central function of animal signaling. This definition is conceptually sound, empirically testable, and inclusive, yet bounded. Implications are considered in both theoretical and empirical domains.

M. J. Owren (✉)
Department of Psychology, Georgia State University, P.O. Box 5010, Atlanta, GA 30302-5010, USA
e-mail: owren@gsu.edu

D. Rendall
Department of Psychology, University of Lethbridge, Lethbridge, AB, Canada

M. J. Ryan
Section of Integrative Biology, University of Texas, Austin, TX, USA

Animal signaling[1] is a rich field of study, with social communication found to occur in virtually every animal species and over a range of modalities. However, while much is known about the behavior, morphology, and neural underpinnings of signaling in many taxa, critical aspects of theory remain surprisingly underdeveloped. In particular, animal signaling is typically defined using constructs that are themselves left undefined and that may even be undefinable. One example is the concept of *information*, which is grounded in intuition and metaphor, and routinely conflated with meaning. Another is *encoding*, which is often invoked in the context of viewing communication as information transmission, yet is left unsubstantiated. The current work argues that relying on these constructs creates confusion, pushes the field away from basic principles of evolutionary biology, and impedes continued progress. A variety of examples are presented in support of these arguments, drawing most heavily on two particular, but prominent research areas, namely sexually selected calling in frogs and vocal behavior in primates. Finally, a potential remedy is presented, namely to revise the definition of animal signaling by replacing the problematic notions of information and encoding with the broader, yet better bounded and testable idea of communication as *influence*.[2]

Historical notes

The field of animal signaling has important roots in twentieth-century classical ethology, which viewed signals as innately specified, *sign stimuli* that triggered rigidly organized, hard-wired responses in conspecifics (Tinbergen 1951; Gould 1982). Many of the signaling phenomena studied were in birds, in which, for example, aggressive gestures were suggested to have originated from preparatory movements preceding flight and head-bowing associated with attack. While signals were believed to become ritualized and emancipated from such origins over evolutionary time, the overall approach nonetheless emphasized a mechanistic and mutually beneficial "lock-and-key" process in which signalers "released" innately determined, stereotyped responses in perceivers.[3]

---

[1] The terms "signaling" and "communication" are used interchangeably in this article, as they typically are in the animal-signaling literature. The focus throughout is on non-humans, as human communication processes such as language can be fundamentally different. A requisite goal is to emphasize that animal signaling should be defined and studied in its own right, and not by reference to human behavior.

[2] This article is primarily grounded in the ethological literature and does not explicitly integrate related work by philosophers such as Millikan (1995, 2004), Stegmann (2005, 2009), and others. However, some points arguably also apply to this other work as well, including relying on an undefined notion of information, viewing animal communication as inherently representational, and implicitly or explicitly using human language to understand signaling in other species.

[3] "Signaler" and "perceiver" are being used in place of the more common terms "sender" and "receiver" because the latter derive from the Shannon–Weaver theory of communication that we argue has been misapplied in animal studies. The commodity being "sent" and "received" is information, thus implying a particular view of the communication process. The terms "signaler" and "perceiver" are more agnostic.

Prevailing conceptions changed dramatically, however, as the information-processing perspective of electronic computing took hold in biology and psychology in the second half of the century. Contrary to the then predominant classical-ethology approach, for instance, Smith (1977) argued that there were too few unique signals in a given species' repertoire to be triggering corresponding, hard-wired responses. He instead argued for perceivers as active information processors rather than passive responders, for instance evaluating communication events based on a combination of signal information, the communicative context involved, and prior experience (see also Leger 1993). Signals were characterized as carrying *motivational* messages, meaning that the information being transmitted concerned signaler *arousal*, *emotion*, and/or *likely upcoming behavior*. Although not explicitly described as such, communication was coming to be considered representational, with signals "standing for" or being "about" the signaler's internal state or imminent behavior rather than merely acting as a triggering stimulus. Seminal work by Dawkins and Krebs (1978) subsequently did take issue with viewing communication as an inherently cooperative event, arguing instead that signalers were more likely to be manipulating than informing perceivers. Their view of signaling as a predominantly selfish act nonetheless also embraced a view of signaling as information transmission, as will be further discussed below.

Much greater changes were afoot, however, with both the pace and emphasis of subsequent work being significantly altered by studies showing that non-human signals can have language-like properties. One key event was Seyfarth et al.'s (1980) demonstration that acoustically distinct alarm vocalizations produced by vervet monkeys threatened by various kinds of predators allowed listening animals to respond with specific, differentiated escape responses. Seyfarth and colleagues tested for symbolic-like value in these alarm calls by playing the sounds to wild vervets in the absence of predators, finding that vocalizations alone could precipitate appropriate responses. They concluded that animal signals can do more than "merely" reflect caller motivation or arousal, with these alarm calls instead referring to external objects or events. The researchers further proposed that the vocalizations have an additional, language-like property of *arbitrariness*, meaning having no inherent relationship between call acoustics and the particular predator being referred to. This work and its interpretation was a watershed event for the field, inspiring many other investigators to focus on possible language-like communication in non-humans (reviewed by Seyfarth and Cheney 2003; although see Owings 1994), including various primates, non-primate mammals (ground squirrels, prairie dogs, meerkats), and some birds (e.g., domestic fowl).

Language-like, symbolic communication was not the only focus of research during this period, of course, with topics such as signal production (Greenewalt 1968), energy propagation in signaling environments (Morton 1975), and perceiver sensory responses (Capranica 1977) also being of central interest. Such aspects are particularly important for sexually selected mating signals, which have been extensively studied in insects, fish, amphibians, birds, as well as mammals. While there is less impetus to compare this kind of communication to language, the constructs of information and encoding play a significant role nonetheless. Both are, for instance, fundamental to the concept of signal *honesty*, which is central in both

theoretical and empirical work (Zahavi 1975; Bradbury and Vehrencamp 2000; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). A common example is that a signal is considered honest to the extent that transmitted information accurately reflects signaler characteristics or intentions. Thus, larger-bodied frogs tend to have larger larynges, which vibrate at lower rates than the smaller larynges of smaller-bodied individuals of the same species. When that relationship holds, vocal pitch becomes inversely correlated with body size, providing an "honest indicator" of how large the caller is.

Defining animal signaling

As the classical ethology era waned, the intertwined constructs of information and encoding quickly permeated virtually every subdiscipline of animal signaling, being used both to describe particular instances of communication and in defining the phenomenon itself. Otte's (1974, 385) widely cited definition of animal signals as "behavioural, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms" was arguably a tipping point, with the rigid "signal-releaser" approach thereafter giving way to new, informational perspectives. Many researchers subsequently followed in Otte's definitional footsteps, including the authors of some of the most influential texts in the field (reviewed by Rendall et al. 2009). Animal signaling is thus currently described in terms such as "sharing of information" (Smith 1997, 1), "informational content" (Hauser 1996, 6), and "provision of information" (Bradbury and Vehrencamp 1998, 2).

The term "encoding" appears less frequently in formal definitions of signaling, but also emerged as a fundamental component of communication early in the informational era. As Green and Marler (1979, 3) wrote, "Information is encoded into a signal by one individual. When received by another animal, the information undergoes decoding while still retaining a specifiable relationship to the encoded information." Contemporary empirical work also relies on this concept, such as when investigators say that "signals may encode information about attributes of the sender… and about stimuli and events in the environment" (Bugnyar et al. 2001, 949), that "if a species is preyed upon by different predators that use different hunting strategies… selection can favor variation in alarm signals that encode this information" (Templeton et al. 2005, 1934), and that "animal alarm calls simultaneously encode information about both predator type and the signaler's perception of urgency" (Manser et al. 2002, 55). The prototypical, contemporary characterization might thus define animal signaling as *a process in which evolutionarily specialized morphology or behavior in a signaler is used to encode and convey information to a perceiver, who in turn relies on evolved neural and perceptual processes to decode and recover the information.* As argued in the next sections, however, using the concepts of information and encoding in this fashion makes them so vague, elastic, and insubstantial as to lose their scientific value.

Information

While relying heavily on the notion of information, Otte (1974) and later authors have uniformly failed to define this construct.[4] Nor is it explained what is meant by saying that information is conveyed from one individual to another. Instead of tackling the definition directly, work on animal signals routinely invokes Shannon and Weaver's (1949) theory of information, at least implicitly. Developed by Claude Shannon at Bell Labs, this probability-based approach was initially applied to understanding the transmission capacity of telephone lines, quantified in the logic of bits. However, the associated concept of *Shannon information* refers strictly and solely to observable correlations between events in the world. In other words, if the occurrence of one event is predictive of some other discernible circumstance, the former is said to "carry" information about the latter. While taken from everyday language, the idea that signals carry information is meant as shorthand for a purely statistical relationship between a given event and any and all possible sequelae associated with it. The number and conditional probabilities of such sequelae then provide the basis for defining information in quantitative terms, namely as a reduction in *uncertainty* about one state of the world based upon observing another. Signals can thus be said to be informative in the sense that they allow perceivers to draw inferences about their environment, other individuals, and the like.

Authorities such as Hauser (1996), Bradbury and Vehrencamp (1998), and Greenfield (2002) reference Shannon and Weaver's approach explicitly to support their respective views of communication, but then do not explain how their quantitative metric applies to viewing information as encoded content that signalers provide to perceivers. Rather than referring to a statistical relationship, "carrying" information here reflects the well-known *conduit* or *containment* metaphor of human language, as described by Reddy (1979).[5] Information no longer refers correlations among events, but rather becomes an entity unto itself. For example, whereas Shannon information allows an observer with the necessary cognitive wherewithal to form a representation of the circumstances that gave rise to the signal, information in animal communication is considered representational in its own right. While familiar and comfortable, this metaphorical view of information is primarily based on intuition and everyday conceptions. It has no connection to Shannon and Weaver's definition, and is not a scientifically grounded construct.

Encoding

A corollary of the information-as-representation approach taken in animal communication is that signaling must involve some form of code. This requirement

---

[4] Bradbury and Vehrencamp (1998) discuss information extensively, yet never offer a specific definition of this term. They do provide a specific, unequivocal definition of communication—with information given a central role.

[5] Shannon and Weaver's approach is arguably metaphorical as well, in this case a "transmission" metaphor. However, their usage "is a radical departure from the container and conduit metaphors, [including] that meanings reside in human understanding, not in the signals transmitted" (Krippendorff 1993: 10).

holds regardless of the nature of the representation, for instance whether pertaining to some internal state or likely behavior, some external object or event, or some aspect of signaler fitness. The key point is that a "standing for" relationship is being invoked, which in turn implies a corresponding coding scheme. But again, prevailing theory says little about the nature of such coding. Taken literally, the word "encoding" means systematic assignment of arbitrary or iconic values to a set of items in such a way that the originals can be recovered from associated coded versions. In everyday usage then, a code is inherently symbolic. In contrast, animal-communication researchers have been careful to distinguish explicitly symbolic encoding as it occurs in human language from language-like signaling in non-humans that might not be equivalently symbolic. The rationale is that non-humans cannot be assumed to have fully human-like cognitive abilities and that their signals should be interpreted with requisite caution. Rather than claim language-like symbolism per se for animal signals, it is therefore common to use the more qualified term "functional referentiality" (Evans 1997).

Adding a qualifier does not solve the problem, however, as the implied distinctions between possible "non-symbolic," "symbolic-like," and "fully symbolic" coding systems have not been explained. The most relevant proposal has arguably been Marler et al.'s (1992) conception that "motivational" versus "referential" signals lie at opposite ends of a representation continuum. These authors argue that a signal should at least be considered functionally referential if it can be interpreted without specific knowledge of the immediate signaling context involved. Vervet alarm calls and other predator-related signals are thus considered particularly good examples of functional reference. In contrast, motivational signals are considered to be rather imprecise (Smith 1977), with perceivers being unable to interpret the significance of such events without taking other circumstances into account. While therefore not typically considered functionally referential, Marler et al. (1992) propose that motivational communication can become referential if the internal state and associated signal occur only under a restricted range of circumstances. For example, if a particular captive chimpanzee produces "high-" versus "low-arousal" food grunts only when a preferred food such as bread is available, its cage-mates will be able to infer solely from hearing this individual's calls that bread must be available (Slocombe and Zuberbühler 2005).

However, the deeper issue of how to understand encoding itself is never addressed. For instance, signals are said to encode information regardless of whether they are motivational or referential, but with no explanation of what "unencoded information" or "non-referential encoding" might be. As with "information," the term "encoding" is routinely stretched to fit whatever communicative circumstance is at hand. If a motivational signal is conveying a desire to engage in mutual grooming, encoding is taken to involve an inherent link between the signal and some need- or emotion-related physiological process. For a referential signal such as an alarm call, however, encoding is considered to reflect a fundamentally cognitive kind of process. Finally, when the information concerns an individual's traits, including age, size, or competitive ability, encoding refers only to a correlation between that characteristic and the signal being produced. While it is not obvious what these diverse versions of the construct have in common, theorists have kept mum on this point.

Conflating information and meaning

The discrepancy between information in the Shannon and Weaver versus animal-signaling senses is even more profound than described above. As noted, Shannon information concerns statistical relationships between the occurrence of particular events (including signals) and possible states of the world. Information encoding, on the other hand, reflects a representational relationship between a signal and the meaning or significance of that event. However, meaning and significance are quite different from Shannon information, as Weaver takes care to point out in the famous treatise.

> 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, from the present viewpoint, as regards information…the semantic aspects of communication are irrelevant to the engineering aspects. (Shannon and Weaver 1949, 99)

Shannon and Weaver's information construct has nonetheless been applied in many contexts for which it was not intended (Piccinini and Scarantino in press; Pierce 1980), with animal signaling being just such an instance. Contra the originators' admonition to separate information from meaning (see also Dretske 1981), animal-communication researchers routinely conflate the two.

Summary

Definitions of animal signaling are problematic in putting information and encoding in central roles while failing to provide definitions for either. Instead, both theoretical and empirical work in this field relies on intuitive, metaphorical, and highly elastic versions of these constructs. While sometimes purported to find support in Shannon and Weaver's quantitative-information theory, the information concept invoked for animal signals is actually incommensurate with their approach. As outlined in the next sections, the lack of credible definitions for its central constructs is a hindrance for the discipline, both in theory and in practice. Problems include that signaling is an untestable concept, that the field of animal communication operates at cross-purposes with central tenets of evolutionary biology, and that contemporary empirical work is often subject to unhealthy conceptual constraints in design and interpretation.

Consequences for theory

Begging the communicative question

A basic problem with the prevailing information-based definition of animal communication is that because information and encoding are left undefined, it

becomes impossible to actually show that a given bit of morphology or behavior is or is not a signal. Instead, purported instances of communication are simply asserted, with no provision made for testing whether "encoded information" is present or absent. The argument plays out more or less as follows. "This morphology or behavior is obviously a signal. Signaling has the property of transmitting encoded information. Therefore, this morphology or behavior is transmitting encoded information." Such reasoning constitutes the logical fallacy of "begging the question" (petitio principii), meaning that a proposition is being used to prove itself. In this case, the assertion that communication is occurring is taken as evidence that information is being transmitted, rather than information transmission being required as evidence for asserting communication. The objection is not so much that every possible instance of signaling must be shown empirically to meet some fixed set of criteria, but rather that the definition of signaling itself rules out the possibility of such demonstrations.

Turning evolution on its head

Animal signaling is a biologically grounded discipline, one that routinely puts evolution through natural selection at the heart of the inquiry. Each and every communicative phenomenon is thus assumed to have emerged and to be maintained in accordance with established principles of evolutionary theory. One of the most basic of these principles is that evolution works through modification of existing characteristics, meaning that understanding the form and function of traits in extant organisms importantly includes investigating their origins among ancestral species. In order to understand human bipedality, for instance, anthropologists examine the morphology and energetics involved in quadrupedal locomotion as a model of likely ancestral characteristics. In contrast, the language-inspired conduit metaphor used in animal signaling encourages just the opposite approach. As further discussed below, characteristics of signaling in an array of species are routinely tested for possible language-like properties—thereby turning the normal evolutionary approach on its head. The equivalent for locomotion would be to take the mechanisms, functions, and energetics of human bipedality as a model for understanding the quadrupedal condition from which it evolved. This rationale is no more compelling when applied to language and animal signaling, where the most complex, naturally occurring communication system known is used to model simpler, less-derived systems.

Confusing metaphor with mechanism

The eagerness to compare animal-signaling to human language has also led to instances of ignoring fundamental differences in the mechanistic underpinnings of the communication systems involved. Aside from vervet alarm calls, for example, such comparisons have probably most often been made for the honeybee dance "language" described by von Frisch (1967). Here, decades of work on foraging bees dancing in the hive after encountering a particularly good food source has led researchers to conclude that the dance encodes information about the direction and distance to that food (Seeley 1995; although see Wenner 2002). Even though there

is virtually no chance that the mechanisms involved in honeybee dancing and human language are substantively similar, comparisons continue—just as they do for vervet calling. But if the mechanisms in each of these three species are fundamentally different, the parallels that are so often drawn exist primarily in a metaphorical rather than a real-world domain. We suggest that they are therefore more a distraction than a boon to serious scientific inquiry.

Conflating signaler and perceiver fitness

Another bedrock principle of evolutionary biology is that new traits rarely become established in a population unless they provide a net fitness benefit to the individuals that possess them. There are of course multiple ways that a socially related trait in particular can be beneficial, including by increasing an individual's own fitness directly, by increasing the fitness of the individual's genetic kin, or by providing benefits to unrelated conspecifics who later reciprocate. In every instance, understanding the evolutionary history and current function of the trait requires that costs and benefits are tallied separately by individual. In social behavior, fitness interests for any two parties can routinely coincide in some contexts but conflict in others. Even individuals whose fitness interests are as importantly intertwined as mammalian mothers and their infants routinely exhibit divergent interests, including during gestation (e.g., Haig 1993), at weaning (e.g., Trivers 1974), and in allocation of maternal resources among offspring (e.g., Voland 1998; Bereczkei 2001).

The principle that the interests of different individuals should always be considered separately is effectively lost by defining signaling based on encoded information. While it is generally agreed that animal signaling ultimately benefits signalers, the informational approach demands that perceivers also benefit, or at least that they have in the evolutionary past. Specifically, if a communicative event requires perceivers to recover signaler-encoded information, a corresponding and reciprocal decoding process is necessarily involved. However, this kind of coordination must then reflect a history of cooperative co-evolution if the parties are to have converged on a common informational code. Some theorists go so far as to propose that "true communication" is limited to instances in which signaler and perceiver enjoy mutual benefit (Bradbury and Vehrencamp 1998; Maynard Smith and Harper 2003).

Selfish communication and honest signaling

Selfish signalers

This problem of conflating signaler and perceiver fitness was the motivation for Dawkins and Krebs's (1978; Krebs and Dawkins 1984) attempt to recast signaling in inherently selfish terms, with signal evolution more often reflecting competition than cooperative information-sharing. In this view, divergent fitness interests typically make the evolution of communication an arms race in which signalers are selected to manipulate and perceivers to resist. For example, the threatening, bared-teeth display of dogs is widely understood to have evolved from small, incipient lip

movements that reliably preceded biting. Classical ethologists proposed that these movements then became exaggerated and stereotyped through an evolutionary process of ritualization that enhanced the informational value of this display. Dawkins and Krebs argued just the opposite, namely that a dog's original, nuanced and subtle lip movements were actually disadvantageous, as they betrayed its internal state to the perceiver. Once perceivers were attending and responding to the subtle movements, subsequent ritualization served to mask rather than enhance that information (Krebs and Dawkins 1984), with exaggeration and stereotyped movements becoming a form of "salesmanship" that increased the impact of the signal while decreasing its informational value.

Dawkins and Krebs's compelling logic represented a sea-change in the understanding of ritualization, a concept that remains central in the field. However, the authors continued to embrace an information-based definition of communication (Krebs and Dawkins 1984, 401), even as their new argument contradicted that approach. Specifically, if natural selection creates ritualized signals that are less informative than the incidental cuing from which they arise, information cannot be the driving force behind the evolution of ritualized signaling—just the opposite. In proposing that signals can manipulate and persuade via means such as increased amplitude and repetition, Dawkins and Krebs were thus adopting an unacknowledged, non-informational view of communication.

Selfish perceivers

Dawkins and Krebs's (1978) proposals were met with a great deal of criticism, particularly because they seemed to be casting perceivers as passive dupes rather than active participants with their own selfish fitness interests. The ensuing discussion highlighted the issue of signal honesty, for example with Zahavi (1975; Zahavi and Zahavi 1997) arguing that perceivers are active, skeptical consumers of signal information and thereby exert considerable selection pressure on signalers. In this view, perceivers are necessarily selected to discount or outright ignore inherently manipulative signals, thereby trumping the selfish interests of signalers and ultimately forcing communication toward honesty and informativeness. Signal honesty has become ever more important in animal signaling, with some considering it to be the central, defining issue in the field (Maynard Smith and Harper 2003; Searcy and Nowicki 2005).

The logic of honest signaling is compelling, yet also cannot be easily squared with the information and encoding constructs being invoked. As noted earlier, for example, defining signals based on encoded information implies an initial, cooperative stage of signal evolution during which signalers and perceivers converge on a common code. Signaling must therefore always begin honestly and cooperatively, with the possibility of dishonesty arising only later. Given that the notion of honest signaling is itself inspired by the selfish and frequently conflicting interests of signalers and perceivers, there is some irony in also implicitly ascribing a primal role to cooperative co-evolution. Alternatively, if coding is not invoked, signals can emerge due primarily to perceiver-driven selection. Sexually selected signals could, for example, occur when incidental colors, sounds, or other traits of

the signaler are exaggerated because they are correlated with overall fitness. However, in both cases, *perceivers* become the dominant force in signal evolution. In Zahavi's (1975) encoded-information conception, perceivers inevitably force signalers into costly, self-handicapping communication. Even when eschewing encoding by proposing that signaling arises from incidental correlations between signals and traits, the process remains a one-sided affair in which perceivers are the ultimate arbiters of the evolutionary dynamic.

Thus, whereas Dawkins and Krebs (1978) argue that the inherent conflicts of interest between signaler and perceiver put the former in the driver's seat, grounding the argument in honesty produces the converse outcome. However, even in extremely asymmetrical cases such as the mother-infant conflicts mentioned earlier, the resulting dynamic is never as one-sided as these views imply for signaling (e.g., Trivers 1974; Haig 1993). As Krebs and Dawkins (1984) noted, an advantage gained by either of the parties necessarily drives selection for countermeasures by the other, making it doubtful that conflicting interests in signalers and perceivers can consistently produce unilateral benefit to either side. This later work was requisitely careful to grant signalers and perceivers equal roles in driving signal evolution, although the authors did not acknowledge then needing to account for the common coding systems implied by arguing that signaler "salesmanship" can be "persuasive" to perceivers.

Consequences for empirical work

The problems identified in animal-signaling theory have had implications for empirical work as well. Specifically, empirical investigations typically begin by assuming that the purported communicative phenomenon of interest is based on transmission of encoded information, and seek to understand the significance of that information. Examples of resulting problems are drawn from two different areas, namely studies of sexual selection and courtship signaling in frogs, and of hypothesized, language-like properties in primate vocal communication. These are both active and diverse fields of research and will not be comprehensively reviewed. Instead, the examples presented will help illustrate that problems created by relying on information and encoding affect research across disparate taxa and communicative systems.

Sexually selected courtship vocalizations

Courtship signaling is a form of communication that is common throughout the animal kingdom, recruits all known sensory modalities, and often leads to the evolution of costly traits through sexual selection. While researchers rarely attribute language-like properties per se to such signals, the information and encoding constructs are nevertheless much in evidence (e.g., Zahavi and Zahavi 1997; Bradbury and Vehrencamp 2000). Here, the emphasis is on information that signalers provide about their attributes to perceivers, for instance concerning health, vigor, or genetic makeup. Male courtship signals in particular are often assumed to

encode fitness-related information, which females extract and decode in deciding with whom to mate.

A basic assumption is that these courtship signals are consistently honest, due to strong selection pressure on females to discount or ignore less-than-accurate versions (Maynard Smith and Harper 2003). While this informational approach has inspired much productive research, it is nonetheless metaphorical, abstract, and misleading. For instance, focusing on information distracts from more basic considerations such as signal design, while encouraging over-complicated accounts of perceiver processing. One case in point is that, in many species, the most basic requirement is simply that a courtship display is detectable against background noise. That demand has obvious implications for signal design. Male mating calls are, for example, frequently found to be high-amplitude events that are produced repeatedly. The acoustic properties of such signals are often demonstrably resistant to transmission degradation, while avoiding overlap with other sounds. Calls of conspecifics are of course also a kind of "background noise" that a male must combat, which can create an arms-race effect and highly elaborated displays (Ryan and Cummings 2005). Acoustic design of courtship vocalizations must also take into account perceiver processing, for instance to ensure that females can readily localize the signals. Spatial localization of conspecific sounds is required across a wide variety of species, creating commonalities both in signal form and in associated brain mechanisms (Grothe 2003). Overall, the fundamental nature of "mere" detection and localization can make these central considerations for both males and females.

Consistent with this perspective, audition in both birds (Cheng and Peng 1997) and frogs (Wilczynski and Chu 2001) has been found to be directly linked to the neuroendocrine processes that regulate affect and motivation, in this case female proceptivity. For example, females may have to hear male courtship calls in order to physiologically become sexually receptive (Cheng 2008; Wilczynski et al. 2005). The direct impact that courtship signals can have on females is well-known in birds, which produce some of the most structurally complex and variable sounds of any animal. Although the number and diversity of songs produced in some species could be taken to reflect extensive and detailed information content, one important function of this complexity appears simply to be avoiding perceiver habituation, or "boredom" (Hartshorne 1973; Searcy 1992). Analogous anti-habituation effects have also been found to occur at molecular, cellular, and neural levels (Dong and Clayton 2009). Work focusing narrowly on male-quality information has tended to ignore these basic sensory and psychological factors, as aspects such as detectability, localizability, and perceiver habituation fall outside this framework.

While downplaying the importance of basic signal functions, starting from encoded information also ignores that perceiver sensory systems are central in non-communicative contexts as well, such as in acquiring food and evading predators. These functions place critical demands on detection, localization, and discrimination capabilities, and are performed across disparate circumstances. If perceiver senses are to perform well across a range of situations, optimal performance in any one of them becomes unlikely. Rather, trade-offs must be expected, with selection for greater sensitivity and accuracy in one domain likely blunting effectiveness in

others. One consequence for courtship communication is that perceivers become susceptible to influence through signalers playing on whatever sensitivities happen to be present. In some fish, for example, the presence of photoreceptors that facilitate detection of prey has secondarily produced selection for corresponding coloration in males. The latter thereby become more visually salient to females, but not as a signal of mate quality (Cummings 2007; Seehausen et al. 2008). The change is neither "honest" nor "dishonest," instead occurring because photoreceptor characteristics in these species have diverse functional effects. Changes driven by one kind of selection pressure will therefore affect fitness in complex ways across multiple domains.

Similarly, acoustic characteristics of the sexually selected vocalizations of túngara frogs (*Physalaemus pustulosus*) evidently evolved to match this species' pre-existing auditory sensitivities (Ryan 1990). In this taxon, male mating calls can include both "whine" and "chuck" components. The whine is produced by several closely related frog species and is both necessary and sufficient to attract females. The chuck occurs only sometimes and only in male túngara frogs and their closest relatives (*P. petersi* and *P. freibergi*). However, this added component makes the call significantly more attractive to females—not only in túngara frogs, but also in species whose males do not produce it. This effect likely reflects basic inner-ear design in these animals, with one organ (the amphibian papilla) being most sensitive in the region matching the strongest frequency of the whine. A second organ (the basilar papilla) is most sensitive in the region of the strongest chuck frequency. Thus, the regions of greatest energy in túngara male mating calls match the regions of greatest auditory sensitivity in females (Ryan and Rand 2003). This kind of matching between auditory sensitivity and call energy occurs in many anurans (Gerhardt and Schwartz 2001), but in this particular case is best explained as a process of *sensory exploitation* in which a central feature of the female's auditory system showed a latent sensitivity that males began to tap for their own purposes (Ryan and Rand 1993).

Across species, there are numerous other cases in which males have evolved courtship signals that exploit preexisting sensory biases in females (e.g., Endler and Basolo 1998; Ryan 1998; Bradbury and Vehrencamp 2000). Here again, critical aspects of communication have little to do with encoding and decoding of representational information. Instead, the broader view is that courtship signals do not evolve to carry information about signaler quality, but rather to influence perceiver mating behavior by any and all available means (Dawkins and Krebs 1978; Owings and Morton 1998). Seen from this perspective, signal honesty may not even be relevant to the most basic constraints and selection pressures involved.

To the extent that signaler influence is detrimental to perceivers, counter-selection is certainly to be expected. Nonetheless, there is little to justify an a priori assumption that perceiver resistance will routinely override selection for signaler influence and thereby guarantee honesty. Instead, a process of competitive co-evolution is expected, because if perceivers are successful in thwarting signaler effects in one domain, selection will trigger "assaults" in other domains. While, a signaling system in which perceivers are strongly exploited is unlikely to persist, selection will continue until signalers come to tap a vulnerability that perceivers

cannot readily close off due to mechanistic or functional constraints. An equilibrium point at which perceivers are somewhat disadvantaged is therefore probably common. Thus, understanding sexually selected signaling necessarily requires taking into account not only the respective fitness interests of signalers and perceivers, but also proximate factors such as the constraints created by species-typical sensory processing and other nervous-system functions.

Semantic-like primate vocalizations

Studies of primate vocal behavior are typically deeply grounded in the perspective of encoded information, in fact often being specifically geared toward demonstrating human-like complexities in representation and meaning. Although the latter are slippery concepts even in human language (e.g., Goethals 2003), they are nonetheless frequently applied to signaling in primates, other mammals, and some birds, and even honeybees (Seyfarth et al. 1980; Gyger et al. 1987; Macedonia 1990; Seeley 1995; Zuberbühler 2003; Templeton et al. 2005). A guiding principle here is that a signal produced in a specific, narrow range of circumstances that also evokes a similarly specific, narrow range of responses can and should be considered symbolic- or semantic-like—at least in the qualified, functional-reference sense discussed earlier. In other words, if signalers and perceivers behave *as if* representational information is being encoded, transmitted, and decoded, then a language-inspired interpretation is both appropriate and helpful. Disregarding for present purposes any issues about methods or evidence in particular studies, the question of interest becomes whether beginning from encoded information and language is in fact useful in understanding primate calls.

It can be argued that, even more than with sexually selected signals, focus is again deflected from more basic considerations. For example, while the possibility of word-like, representational signaling has received much empirical attention, only a few clear instances have been reported for non-humans, and then only for a fraction of these species' respective vocalizations. In fact, even after decades of work, Seyfarth et al.'s (1980) seminal study with vervets remains the most compelling example of semantic-like vocalization for any non-human. In contrast, every well-documented mammalian repertoire appears to have calls that are produced across a range of contexts. These non-specific sounds are often the most-used vocalizations in the repertoire, yet are not easily linked to a specific motivation or circumstance (Owren and Rendall 2001). Examined in more detail, however, even word-like calling by nonhumans has been found to be quite different from using language. Important discrepancies include that callers show an evident lack of intention to inform, that call production is grounded in emotion-related neural systems, that call development is not dependent on first hearing the vocalizations from others, and that calls show non-arbitrary acoustic features.

Intention to inform

One of the givens for humans using language is that their communication shows intentionality. In other words, humans routinely taking the beliefs, motivations, and

knowledge of listeners into account when speaking to them, thereby communicating more effectively and efficiently. In contrast, primates routinely show little intention to inform others through their calls (Cheney and Seyfarth 1990; Cheney et al. 1996; Rendall et al. 2000). Even when non-human listeners are able to respond as if vocalizations are referential, the vocalizers themselves appear unaware of any informational content. The representational parity that characterizes human speech is thus not evident for primate signalers and perceivers (Cheney and Seyfarth 1996, 1998, 2005). Summarizing such findings, Cheney and Seyfarth (1996, 59) conclude that "the mental mechanisms underlying the vocalizations of non-human primates… appear to be fundamentally different from those that underlie human speech." While initially surprising, this evidence is consistent with other demonstrations that non-human primates have limited understanding of the mental states of others—an ability considered fundamental in using language (reviewed in Penn and Povinelli 2007).

Vocal production

This interpretation is compatible with finding that calls in primates and other non-human mammals are importantly emotion-triggered signals that have more in common with human vocalizations such as spontaneous laughter and crying than with language. For instance, emotion-related, subcortical brain structures that include the limbic system, midbrain, and brainstem have been found to be primary for vocal production in monkeys (Jürgens 1998), dogs (Solomon et al. 1995), and cats (de Lanarolle and Lang 1988). This outcome is quite different from human speech production, where volitionally controlled processes in temporal and frontal regions of the cerebral cortex play a central role. While speech production is known to include subcortical circuitry, output occurs specifically through cortical pathways (Lieberman 2002).

Call development

The developmental processes underlying primate calling and speech are also fundamentally different. For instance, Seyfarth and Cheney (1980, 1986) found that infant vervets produce recognizable alarm calls in largely appropriate circumstances without evident need for practice in either call acoustics or usage. They did find one kind of production learning, namely that infants sometimes called to non-predator events such as falling leaves and passing warthogs, and then stopped doing so over time. However, even these false alarms occurred in the correct categories, with falling leaves eliciting "eagle" calls, and warthogs provoking "leopard" vocalizations. Equally striking was that infants were vocalizing appropriately upon seeing a given predator in spite of not knowing how to respond to the same call when heard from others. Instead, these youngsters would freeze, run to their mothers, or even act in ways that increased their risk of being taken. Adult-like responses emerged gradually over the first year, likely based on experience with predator attacks, hearing alarm calls, and reactions shown by conspecifics. This "production-precedes-comprehension" pattern of development is exactly the opposite of the

"comprehension-precedes-production" pattern that typifies human language-learning. The stronger parallel appears to be with spontaneous laughter, which occurs in recognizable form even in deaf and blind humans (reviewed by Makagon et al. 2008).

Non-arbitrary acoustics

Basic acoustics-related questions have also received relatively little attention from researchers focusing on possible word-like properties of calls. In fact, a typical approach has been to argue that the acoustics of vocalizations such as vervet alarm calls are arbitrary, in the sense that the various versions bear little or no discernible relationship to their respective referents. Yet vocalizations such as predator alarms appear to be anything but arbitrary. As is the case with frogs, the acoustics of these calls are well-designed for detection and localization, and likely also prime listeners by engaging low-level attention and arousal mechanisms. Regardless of whether the calls are used narrowly or broadly, alarm vocalizations in many primates are short with abrupt onsets, noisy or with strong pitch modulation. These widely shared acoustic features are ideally suited for capturing and manipulating listener attention and arousal via short, direct links from the auditory periphery to brainstem regions regulating whole-body activation. As a result, alarm-call acoustics alone tend to elicit orienting responses and preparatory movements—reflexive listener reactions that are clearly beneficial in the context of predator attack. The same basic alarm-call structure and response is also seen other mammals and birds (Marler 1955; Owings and Morton 1998; Owren and Rendall 2001), suggesting a conserved system that may date back to early vertebrates (Grothe 2003).

Generalized startle responses to species-typical alarm calls are thus observable even in naïve infants with limited experience (Herzog and Hopf 1984; Seyfarth and Cheney 1986), and are likely to provide critical scaffolding for learning about predators. Here, the same circuits that connect the auditory periphery to arousal-regulating brainstem regions also have direct links to the amygdala and hippocampus (LeDoux 2000; McGaugh 2003). Strong, call-elicited autonomic responses thereby likely help the infant learn and remember details of predator encounters and associated behavioral sequelae. These kinds of effects appear pervasive and fundamental, providing a more powerful and concrete foundation for understanding the evolution and acoustics of calls than appealing to vaguely specified, language-like representations.

Rethinking animal signaling

We have argued that defining animal signaling based on encoded information creates problems in both theoretical and empirical domains. Appeals to Shannon and Weaver's approach notwithstanding, researchers relying on these concepts are conflating information with meaning. The definition of signaling is furthermore undermined by relying on constructs that themselves are neither defined nor testable. Researchers are thereby led away from fundamental precepts of evolutionary theory,

for instance in using language as a model for simpler systems and conflating signaler and perceiver interests. There are practical consequences as well, with derived constructs such as honesty and semanticity distracting from more fundamental aspects of communication, such as structure–function relationships in acoustics and usage, the importance of perceiver processing, and evolutionary constraints on both signalers and perceivers. It is difficult to escape the conclusion that the prevailing definition of animal signaling should be modified so as to avoid these problems, and this issue is examined in the next sections.

Communication as influence

Over the years, at least some researchers have expressed dissatisfaction with the dominant theoretical roles played by encoded information and information-sharing in animal signaling, as well as suggesting alternative perspectives. While differently phrased and presented, a recurring theme in these proposals has been that from the signaler's side, communication is fundamentally an attempt to *influence* others. As discussed earlier, Dawkins and Krebs (1978) argue that signalers first and foremost *manipulate* perceivers, who in turn are selected to *mind-read* those individuals (Krebs and Dawkins 1984). Owings (1994) and Owings and Morton (1997, 1998) importantly view communication as a reciprocal process in which signalers are selected to *manage* the behavior of perceivers, who in turn must *assess* the implications of signals vis-à-vis their own interests in a given circumstance. Owren and Rendall (1997, 2001) and Ryan (1990, 1998) have gone on to suggest specific ways in which auditory signals can be used to influence perceivers without appealing to encoded content.

In spite of these kinds of arguments, the ideas of encoded information and cooperative signaling remain prominent in the literature. We propose that a revised definition of animal signaling may therefore be helpful, for instance by giving formal expression to a broader, influence-based conception. Animal signaling is therefore here defined as the use of *specialized, species-typical morphology or behavior to influence the current or future behavior of another individual*. This definition is quite inclusive and can accommodate all key phenomena currently considered to involve transmission of encoded information. That inclusiveness derives in part from the definition being signaler-centered, with the only requirements for perceivers being that they are demonstrably influenced by the signaling events. However, as outlined below, the definition is also bounded. In fact, by being grounded in observable changes in perceiver behavior, it is necessarily narrower than if based on elastic, undefined notions of information and encoding. There is thus no contradiction in noting that some signal characteristics can become closely correlated with signaler characteristics, *as if* transmitting honest information. Signals can also become context-specific, with perceivers responding *as if* encoded information has been transmitted. However, those strategies are proposed to be only a few of a larger number of possible evolutionary outcomes, likely including many that remain to be discovered. If these kinds of examples are to be understood based on information and encoding, the revised approach puts the onus on those proposing to use the constructs both to provide meaningful definitions and to reconcile them with demonstrated, non-informational aspects of communication.

Wilson ([1975](#)) presents a similar definition to ours, while requiring that benefit need only accrue to either signaler or perceiver (or both). As discussed in the next sections, we believe that perceiver benefit should be excluded from consideration. Maynard Smith and Harper's ([2003](#), 3) formal definition is also similar, but the authors then immediately qualify it to include that signals convey information that perceivers benefit from receiving. Their approach is thus very similar to the archetypal definition paraphrased earlier. The closest formulation is likely Dawkins and Krebs's ([1978](#)) view that signaling is information-transmission that functions to manipulate perceivers. We, of course, eschew the informational component, and also prefer the more generic word "influence" as a term that is equally applicable to both competitive and cooperative co-evolutionary circumstances. Whereas "manipulation" implies that signals have a consistently detrimental effect on perceivers, we stress that signaler influences may be either detrimental or beneficial, and that both outcomes are likely common.

Perceivers need not benefit

The proposed definition retains specialization through natural selection as a critical component (Scott-Phillips [2008](#)), but only for signalers. No specialization is required for perceivers, nor is there any implicit or explicit expectation of a history of cooperative co-evolution. While specialized perceiver responses are known to have evolved in many instances, sensory channels typically first arise for perception of more basic aspects of the external environment. Communication-related responses emerge secondarily and therefore likely always co-exist with, and are constrained by, very basic perceptual functions such as predator avoidance and prey detection. Seen from this perspective, the evolutionary history and multi-functionality of perceptual systems probably makes sensory bias a routine and important component of the evolution of communication. Not only do perceiver sensitivities in a given modality shape both signaler behavior and signal form, they inherently create susceptibility to being influenced through that channel. Perceivers may also benefit from signalers tapping their sensory biases, however, as resulting signals are easier to detect, localize, and potentially respond to. In that sense, sensory "exploitation" need not be detrimental, and when it is, selection on perceivers will naturally tend to produce countermeasures. Nonetheless, constraints imposed by selection in other contexts remain a limiting factor, which can produce some net advantage for signalers.

Honesty in courtship displays

Applied to sexually selected displays, an influence-based interpretation views courtship first and foremost as signalers attempting to sway the decisions of prospective partners, with a caveat that selection pressure through competition with other signalers may be just as strong as from perceivers. On the one hand, then, pressure from perceivers can and likely often does select for courtship displays whose features are correlated with signaler fitness. Rather than requiring attribution of encoded information, however, these kinds of correlations are straightforward instances of Shannon information. Measuring the relative strength of such relationships thus constitutes a generic and defensible way to approach the question of signal

"honesty." On the other hand, mate-quality signaling is just one component of the display, with signalers being selected to influence perceivers by any and all possible means. This pressure brings species history and non-courtship-related selection pressures into play, constraints that can decrease the observed correlation between signal and mate-quality, but is nonetheless not equivalent to the signals "conveying dishonest information." Finally, to the extent that the influence exerted by a signal is detrimental to perceivers, selection will favor resistance to such effects. However, a variety of constraints can come into play there as well, with no guarantee that the net outcome will consistently favor perceivers.

Semantic-like signaling

The neural and developmental evidence described above for vervet monkey alarm calling neatly illustrates that describing these calls in metaphorical terms explains very little about them. While relying on notions of encoded information creates the appearance of similarity to human language, the two phenomena are fundamentally dissimilar. As noted, vervet alarm-call production is a biologically grounded event, emerging early in development without evident practice. Infants thus produce recognizable calls prior to learning how to respond to them—in other words, without the signaler-perceiver representational parity that is the hallmark of language. Furthermore, neural evidence from primates and other mammals indicates that call production is controlled through the limbic system, rather than showing direct cortical involvement, as in humans.

Thinking in influence-related terms produces a much more substantive understanding of how word-like function can nonetheless emerge from emotion-triggered vocalizations. The limitations of emotion-triggered production do not apply to the other side of the equation, as hearing calls engages cortical and sub-cortical systems alike in perceivers. In other words, the notable cognitive sophistication of primates is fully in play for listeners learning about the significance of vocalizations heard from others. A plausible evolutionary scenario for vervets becomes that their various alarm calls originally derived from a single, general vocalization whose salient acoustic features were attention-getting and even startling to listeners. With predation being a case in which signalers and perceivers can readily have coincident fitness interests, differentiation in the limbically controlled motor behavior underlying vocalization would then be enough to create a functioning, semantic-like alarm call system. Specifically, if hearing acoustically distinct vocalizations is correlated with the distinctive features of various predators, perceivers would be easily capable of acquiring call-specific responses by learning from the reactions of others. Here again, the concept of Shannon information has a key role to play, while describing the calls as conveying encoded information adds nothing of substance.

Communication is a large, but bounded domain

The proposed definition of animal communication is inclusive by design, while also having clear boundaries. In contrast, the current, information-based definition is unbounded, with investigators deciding through intuition and preference rather than

principle what should or should not be considered a signal. Revising the definition to put influence at the center will thus necessarily be odds with some of these judgments, as would likely be true for any attempt at formalization. To illustrate a few of the salient properties of the proposed reformulation, the next sections briefly illustrate both its inherent inclusiveness and some conceptual boundaries created.

Direct impact is communication

The influence-based definition essentially states that *any* behavior with an evolved function of influencing another individual qualifies as signaling. This aspect will likely be difficult for many to accept, for instance because it flies in the face of the common intuition that communication is a kind of "action at a distance." Signaling is deemed to occur, for example, if a monkey gestures threateningly, a bird actively displays its brightly colored feathers, or a frog makes a mating call. In contrast, if that monkey hits another, the bird pecks a rival, or the frog grapples with a rival over a territory, the events are typically not considered communicative. Although widely recognized and applied (Maynard Smith and Harper 2003), this distinction is not grounded in principle. For example, physical contact is not the key element, as tactile communication is recognized in virtually every animal group (see Sebeok 1977; in primates reviewed by Hertenstein et al. 2006). Pleasantness is also not key, as unpleasant physical contact that is nonetheless considered communication includes interactions such as nipping, biting, and pushing (Harrington and Asa 2003; Kam and Hui 2002; O'Donnell 2006; Shakti et al. 2008). If there is a principled distinction to make between unpleasant tactile signaling and physical aggression, it is thus unclear how to make it. Finally, overt ritualization is not required, although ritualization can occur in such displays.

A principled approach would have to be able to distinguish communication from non-communication based on the presence or absence of encoded information in a possible signal. As noted earlier, however, the concepts of encoding and information are not subject to empirical testing. From an influence-based perspective, each of the aforementioned events does constitute signaling, so long as specialization and influence are demonstrably involved. The larger argument is that communication is not inherently different from other evolved functions in non-human animals, and is granted no special status or ineffable, unmeasurable properties. In this view, signaling simply comprises the very large set of morphological traits and behavioral actions through which one individual can influence the behavior of another.

Incidental cuing is not communication

In spite of this inclusiveness, the influence-based definition is also bounded. For example, if a monkey mother sees her infant disappear into a bush and then sees part of the bush itself moving, she can likely infer the infant's location much as if the youngster had vocalized. While there is little functional difference from the mother's perspective, from the infant's side the moving bush is an incidental cue while vocalization is communication. On the one hand, both are examples of Shannon information, with animals moving within bushes being correlated with

movement of the vegetation, and caller identity and caller location being associated with particular kinds and patterns of acoustic features in vocalizations. On the other hand, the definition precludes incidental bush movement as a signal, because the infant is not showing specialized behavior with an adapted function of influencing another. Conflating the two cases would destroy the conceptual boundaries of the influence-based definition, although the bush movement could readily become communication, for instance through selection on infants to produce exaggerated movements.

The same distinction can be drawn from an information-encoding perspective, but problems arise in other cases of incidental cuing, such as *eavesdropping*. This term refers to third parties detecting and responding to signaling events that they themselves are not directly involved in. Examples include eavesdropping conspecifics that modify their behavior toward a signaler or perceiver as a result of a communicative event (Johnstone 2001), as well as predators whose eavesdropping helps them detect and home in on prey (Page and Ryan 2008). Adopting an influence-based perspective, eavesdropping is easy to distinguish from communication. On the one hand, if the responses of eavesdroppers are on average beneficial to signalers, these parties become perceivers and communication is occurring. If the responses are detrimental to signalers, however, selection will favor signals that have *less* rather than *more* impact on the eavesdroppers. This pressure will tend to make signaling more cryptic rather than more salient, making eavesdropping the converse of communication.

In contrast, adopting the encoded-information perspective makes eavesdropping nearly impossible to interpret, as when a transient bird uses vocal interactions between neighboring territory-holders to discretely assess their fitness and fighting capacity. In Bradbury and Vehrencamp's (1998) informational account, this scenario qualifies as communication so long as both signaler and eavesdropper benefit. But if so, the communicative status of the signaler's behavior depends on the eavesdropper's response. For instance, if the intruder evaluates and moves on, both parties have potentially benefited and "true communication" has occurred. But if the eavesdropper's evaluation leads it to challenge the resident, the outcome would be considered exploitation rather than communication (Bradbury and Vehrencamp 1998, p 380). The same signaler behavior thereby becomes communication for listeners that choose to move on, but not for those who move in. Yet these kinds of intruder assessments are influenced by other factors as well, such as overall territory availability and the bird's own physical condition. The upshot is that one and the same singing bird may or may not be deemed to be communicating with the eavesdropper, depending on factors entirely extraneous to the singer.

Conclusions

As noted earlier, the kinds of phenomena currently considered to represent core instances of animal communication all fit comfortably within the proposed definition, including mutually beneficial signaling, signals whose characteristics closely reflect mate-quality, and semantic-like signaling. In each of these cases,

communication is ultimately grounded in Shannon information, meaning that selection has acted to create a reliable association between signal properties and some aspect of signaler traits, states, behavior, or salient aspects of the external environment. However, the phenomenon of communication encompasses a broad range of other possible evolutionary outcomes as well. These include signals (or aspects of signals) that manipulate, capitalize on sensory vulnerabilities, influence others by being inherently attractive or noxious, include forceful physical contact, and bear little relationship to either internal state or external circumstances. Adopting this broader perspective thus emphasizes that many different kinds of signaling phenomena can occur, with the task being to understand both the variety involved and the conditions under which each kind evolves. As outlined next, metaphorical approaches do not have an important role to play in this endeavor.

Can information metaphors be useful?

Metaphor is intrinsic to language, both in science and in everyday life. In each case, for instance, metaphor can provide a convenient, simplified way to refer to complex ideas. A related role is that metaphor can be, as Lakoff and Johnson (1980, 193) elegantly put it, "one of our most important tools for trying to comprehend partially what cannot be comprehended totally." Unfortunately, the information metaphors discussed here do not play either of these roles in animal communication. On the one hand, for a metaphor to be useful as a simple stand-in or placeholder, there has to be general agreement as to how to "cash in" that term for the more complex principles actually being referred to. In animal signaling, there is no such agreement. In fact, terms such as information and encoding have little or no meaning outside the metaphorical domain. On the other hand, there is little reason to believe that animal communication is somehow currently beyond scientific comprehension. The problem instead appears to be that relying on metaphor is deflecting attention away from the actual goal, which is to understand signaling in concrete mechanistic terms.

The upshot is that terms such as information and encoding are not being used as shorthand, but as explanation. In other words, instead of characterizing species such as bees, frogs, vervets, and even humans as responding *as if* signals transmit encoded information, they are argued to respond *because* signals transmit encoded information. This confusion of metaphor with scientific understanding bears out Rosenblueth and Wiener's prescient warning that "the price of metaphor is eternal vigilance" (cited in Lewontin and Carroll 2001). Rather than being vigilant concerning the inherent dangers of the information metaphor, the field of animal communication appears to have adopted it wholesale. The same may be happening in other disciplines as well, with informational metaphors being particularly popular in fields such as developmental biology, genetics, and cognitive science (see Brooks 1999; Oyama 2000; Stegmann 2005 for recent reviews). Commenting on the prevalence of "information talk" in genetics, Griffiths and Neumann-Held (1999, 657) succinctly express what we have tried to describe for animal signaling, namely that "…the possibility of translating the information metaphor into substantive theory is an illusion."

Looking forward

While metaphorical notions of information and encoding have little value in understanding animal signaling, there is a clear difference between these kinds of undefined characterizations and information as a well-defined, scientific construct. Shannon and Weaver's (1949) approach to information represents the latter, offering conceptual and quantitative tools that continue to play central roles in applications such as digital signal processing and computing. Although the quantitative methodologies associated with this formal information theory have been little used in animal communication, they may nonetheless be applicable to a number of topics (McCowan et al. 1999). The concept of Shannon information itself can also be useful, for example as illustrated here in the discussion of signals that are clearly correlated with signaler characteristics or environmental circumstances. This version of information provides a concrete way of thinking about such relationships, and while currently more or less ignored in animal signaling, may also have significant, untapped potential for work in this field.

In concluding, we would like to point out that virtually all the criticisms made in this article could be summarily dismissed if someone were simply to provide specific, testable, and demonstrably useful definitions of information and encoding in animal communication. Our position is that such definitions are impossible. Any and all attempts along such lines could nonetheless be valuable, if only through serving as a catalyst for meaningful discussion of the underlying issues. Other aspects aside, the most important take-home message of this article is that there is something seriously amiss in the conceptual foundations of animal communication. While there is no immediate and easy remedy, acknowledging that a problem does in fact exist would be a good start. To that end, we hope to have provided some of the impetus needed to move the field from an apparent state of widespread denial to one of widespread effort.

References

Bereczkei T (2001) Maternal trade-off in treating high-risk children. Evol Hum Behav 22:197–212

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer, Sunderland

Bradbury JW, Vehrencamp SL (2000) Economic models of animal communication. Anim Behav 59:259–268

Brooks RA (1999) Cambrian intelligence. MIT, Cambridge

Bugnyar T, Kijne M, Kotrschal K (2001) Food calling in ravens: are yells referential signals? Anim Behav 61:949–958

Capranica RR (1977) Auditory processing in anurans. Fed Proc 37:2324–2328

Cheney DL, Seyfarth RM (1990) How monkeys see the world. University of Chicago, Chicago

Cheney DL, Seyfarth RM (1996) Function and intention in the calls of non-human primates. Proc Br Acad 88:59–76

Cheney DL, Seyfarth RM (1998) Why animals don't have language. In: Pearson GB (ed) The Tanner lectures on human values. University of Utah, Salt Lake City, pp 173–209

Cheney DL, Seyfarth RM (2005) Constraints and preadaptations in the earliest stages of language evolution. Linguist Rev 22:135–159

Cheney DL, Seyfarth RM, Palombit R (1996) The function and mechanisms underlying baboon 'contact' barks. Anim Behav 52:507–518

Cheng M-F (2008) The role of vocal self-stimulation in female responses to males: implications for state-reading. Horm Behav 53:1–10

Cheng M-F, Peng JP (1997) Reciprocal talk between the auditory thalamus and hypothalamus: an antidromic study. NeuroReport 8:653–658

Cummings ME (2007) Sensory trade-offs predict signal divergence in surfperch. Evolution 61:530–545

Dawkins R, Krebs JR (1978) Animal signals: information or manipulation? In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 282–309

de Lanarolle NC, Lang FF (1988) Functional neural pathways for vocalization in the domestic cat. In: Newman JD (ed) The physiological control of mammalian vocalization. Plenum, New York, pp 21–42

Dong S, Clayton DF (2009) Habituation in songbirds. Neurobiol Learn Mem 92:183–188

Dretske FI (1981) Knowledge and the flow of information. MIT, Cambridge

Endler JA, Basolo AL (1998) Sensory ecology, receiver biases and sexual selection. Trends Ecol Evol 13:415–420

Evans CS (1997) Referential signals. In: Owings DH, Beecher MD, Thompson NS (eds) Perspectives in ethology: vol 12 communication. Plenum, New York, pp 99–143

Gerhardt HC, Schwartz JJ (2001) Auditory tunings and frequency preferences in anurans. In: Ryan MJ (ed) Anuran communication. Smithsonian Institution, Washington DC, pp 73–85

Goethals P (2003) The conduit metaphor and the analysis of meaning. In: Simon-Vandenbergen AM, Taverniers M, Ravelli L (eds) Grammatical metaphor. John Benjamins, Amsterdam, pp 369–390

Gould JL (1982) Ethology. WW Norton, New York

Green S, Marler P (1979) The analysis of animal communication. In: Marler P, Vandenbergh JG (eds) Handbook of behavioral neurobiology, vol 3: social behavior and communication. Plenum, New York, pp 73–158

Greenewalt C (1968) Bird song: acoustics and physiology. Smithsonian Institution, Washington, DC

Greenfield MD (2002) Signalers and receivers: mechanisms and evolution in arthropod communication. Oxford University, Oxford

Griffiths PE, Neumann-Held EM (1999) The many faces of the gene. Bioscience 49:656–660

Grothe B (2003) New roles for synaptic inhibition in sound localization. Nat Rev Neurosci 4:540–550

Gyger M, Marler P, Pickert R (1987) Semantics of an avian alarm call system: the male domestic fowl, Gallus domesticus. Behaviour 102:15–40

Haig D (1993) Genetic conflicts in human pregnancy. Q Rev Biol 68:495–532

Harrington F, Asa CS (2003) Wolf communication. In: Mech LD, Boitani L (eds) Wolves: behavior, ecology, and conservation. University of Chicago, Chicago, pp 66–103

Hartshorne C (1973) Born to sing. Indiana University, Bloomington

Hauser MD (1996) The evolution of communication. MIT, Cambridge

Hertenstein MJ, Verkamp JM, Kerestes AM, Holmes RM (2006) The communicative functions of touch in humans, nonhuman primates, and rats: a review and synthesis of the empirical research. Genet Soc Gen Psychol Monogr 132:5–94

Herzog M, Hopf S (1984) Behavioral responses to species-specific warning calls in infant squirrel monkeys reared in social isolation. Am J Primatol 7:99–106

Johnstone RA (2001) Eavesdropping and animal conflict. Proc Nat Acad Sci 98:9177–9180

Jürgens U (1998) Neuronal control of mammalian vocalization with special reference to the squirrel monkey. Naturwissen 85:376–388

Kam Y-C, Hui WA (2002) Female–offspring communication in a Taiwanese tree frog, Chirixalus eiffingeri (Anura: Rhacophoridae). Anim Behav 64:881–886

Krebs J, Dawkins R (1984) Animal signals: mind-reading and manipulation. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 2nd edn. Blackwell, Oxford, pp 380–402

Krippendorff K (1993) Major metaphors of communication and some constructivist reflections on their use. Cybern Hum Knowing 1:3–25

Lakoff G, Johnson M (1980) Metaphors we live by. University of Chicago, Chicago

LeDoux J (2000) Emotion circuits in the brain. Annu Rev Neurosci 23:155–184

Leger DW (1993) Contextual sources of information and responses to animal communication signals. Psychol Bull 113:295–304

Lewontin RC, Carroll SB (2001) In the beginning was the word. Science 291:1293–1295

Lieberman P (2002) On the nature and evolution of the neural bases of human language. Yearb Phys Anthropol 45:36–62

Macedonia JM (1990) What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ringtailed and ruffed lemurs. Ethology 86:177–190

Makagon MM, Funayama ES, Owren MJ (2008) An acoustic analysis of laughter produced by congenitally and normally hearing college students. J Acoust Soc Am 124:472–483

Manser MB, Seyfarth RM, Cheney DL (2002) Suricate alarm calls signal predator class and urgency. Trends Cogn Sci 6:55–57

Marler P (1955) Characteristics of some animal calls. Nature 176:6–8

Marler P, Evans CS, Hauser MD (1992) Animal signals: motivational, referential, or both? In: Papousek H, Jürgens U, Papousek M (eds) Nonverbal vocal communication: comparative and developmental approaches. Cambridge University, New York, pp 66–86

Maynard Smith J, Harper D (2003) Animal signals. Oxford University, Oxford

McCowan B, Hanser SF, Doyle LR (1999) Quantitative tools for comparing animal communication systems: information theory applied to bottlenose dolphin whistles. Anim Behav 57:409–419

McGaugh JL (2003) Memory and emotion: the making of lasting memory. Columbia University, New York

Millikan RG (1995) A bet with peacock. In: Macdonald C, Macdonald G (eds) Philosophy of psychology: debates on psychological explanation. Oxford University, Oxford, pp 285–292

Millikan RG (2004) The varieties of meaning. MIT, Cambridge

Morton ES (1975) Ecological sources of selection on avian sounds. Am Nat 109:17–34

O'Donnell S (2006) Polybia wasp biting interactions recruit foragers following experimental worker removals. Anim Behav 71:709–715

Otte D (1974) Effects and function in the evolution of signaling systems. Annu Rev Ecol Syst 5:385–417

Owings DH (1994) How monkeys feel about the world: a review of "How monkeys see the world". Lang Commun 14:15–30

Owings DH, Morton E (1997) The role of information in communication: an assessment/management approach. In: Owings DH, Beecher MD, Thompson NS (eds) Perspectives in ethology: vol 12 communication. Plenum, New York, pp 359–390

Owings DH, Morton E (1998) Animal vocal communication: a new approach. Cambridge University, New York

Owren MJ, Rendall D (1997) An affect-conditioning model of nonhuman primate vocal signaling. In: Owings DH, Beecher MD, Thompson NS (eds) Perspectives in ethology: vol 12 communication. Plenum, New York, pp 299–346

Owren MJ, Rendall D (2001) Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocalization. Evol Anthropol 10:58–71

Oyama S (2000) Ontogeny of information: developmental systems and evolution, 2nd edn. Duke University, Durham

Page R, Ryan MJ (2008) The effect of signal complexity on localization performance in bats that localize frog calls. Anim Behav 76:761–769

Penn DC, Povinelli DJ (2007) On the lack of evidence that chimpanzees possess anything remotely resembling a 'theory of mind'. Philos Trans R Soc B 362:731–744

Piccinini G, Scarantino A (in press) Computation vs. information processing: why their difference matters to cognitive science. Stud Hist Philos Sci

Pierce JR (1980) An introduction to information theory, symbols, signals and noise, 2nd edn. Dover, New York

Reddy MJ (1979) The conduit metaphor—a case of frame conflict in our language about language. In: Ortony A (ed) Metaphor and thought. Cambridge University, New York, pp 284–324

Rendall D, Seyfarth RM, Cheney DL (2000) Proximate factors mediating "contact" calls in adult female baboons (Papio cynocephalus). J Comp Psychol 114:36–46

Rendall D, Owren MJ, Ryan MJ (2009) What do animal signals mean? Anim Behav 78:233–240

Ryan MJ (1990) Sensory systems, sexual selection, and sensory exploitation. Oxf Surv Evol Biol 7:157–195

Ryan MJ (1998) Receiver biases, sexual selection and the evolution of sex differences. Science 281:1999–2003

Ryan MJ, Cummings M (2005) Animal signals and the overlooked costs of efficacy. Evolution 59:1160–1161

Ryan MJ, Rand AS (1993) Sexual selection and signal evolution: the ghost of biases past. Phil Trans R Soc Lond B, Biol Sci 340:187–195

Ryan MJ, Rand AS (2003) Mate recognition in túngara frogs: a review of some studies of brain, behavior, and evolution. Acta Zool Sinica 49:713–726

Scott-Phillips TC (2008) Defining biological communication. J Evol Biol 21:387–395

Searcy WA (1992) Song repertoire and mate choice in birds. Am Zool 32:71–80

Searcy WA, Nowicki S (2005) The evolution of communication: reliability and deception in animal signaling systems. Princeton University, Princeton

Sebeok TA (1977) How animals communicate. Indiana University, Bloomington

Seehausen O, Terai Y, Magalhaes I, Carleton K, Mrosso H, Miyagi R, van der Sluijs I, Schneider M, Maan M, Tachida H (2008) Speciation through sensory drive in cichlid fish. Nature 455:620–626

Seeley TD (1995) The wisdom of the hive. Harvard University, Cambridge

Seyfarth RM, Cheney DL (1980) The ontogeny of vervet monkey alarm calling behavior. Z Tierpsychol 54:37–56

Seyfarth RM, Cheney DL (1986) Vocal development in vervet monkeys. Anim Behav 34:1640–1658

Seyfarth RM, Cheney DL (2003) Signalers and receivers in animal communication. Ann Rev Psych 54:145–173

Seyfarth RM, Cheney DL, Marler P (1980) Vervet monkey alarm calls: semantic communication in a free-ranging primate. Anim Behav 28:1070–1094

Shakti L, Chandrasekhar K, Gadagkar R (2008) Signaling hunger through aggression—the regulation of foraging in a primitively eusocial wasp. Naturwissen 95:677–680

Shannon CE, Weaver W (1949) A mathematical model of communication. University of Illinois, Urbana

Slocombe KE, Zuberbühler K (2005) Functionally referential communication in a chimpanzee. Curr Biol 15:1779–1784

Smith WJ (1977) The behavior of communicating. Harvard University, Cambridge

Smith WJ (1997) The behavior of communicating, after twenty years. In: Owings DH, Beecher MD, Thompson NS (eds) Perspectives in ethology: vol 12 communication. Plenum, New York, pp 7–51

Solomon NP, Luschei ES, Liu K (1995) Fundamental frequency and tracheal pressure during three types of vocalizations elicited from anesthetized dogs. J Voice 9:403–412

Stegmann U (2005) John Maynard Smith's notion of animal signals. Biol Philos 20:1011–1025

Stegmann U (2009) A consumer-based teleosemantics for animal signals. Philos Sci 76:864–875

Templeton CN, Greene E, Davis K (2005) Allometry of alarm calls: black-capped chickadees encode information about predator size. Science 308:1934–1937

Tinbergen N (1951) The study of instinct. Oxford University, Oxford

Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249–264

Voland E (1998) Evolutionary ecology of human reproduction. Annu Rev Anthropol 27:347–374

von Frisch K (1967) The dance language and orientation of bees. Harvard University, Cambridge

Wenner A (2002) The elusive honey bee dance "language" hypothesis. J Insect Behav 15:859–878

Wilczynski W, Chu J (2001) Acoustic communication, endocrine control, and the neurochemical systems of the brain. In: Ryan MJ (ed) Anuran communication. Smithsonian Institution, Washington, DC, pp 23–35

Wilczynski W, Lynch KS, O'Bryant EL (2005) Current research in amphibians: studies integrating endocrinology, behavior, and neurobiology. Horm Behav 48:440–450

Wilson EO (1975) Sociobiology. Harvard University, Cambridge

Zahavi A (1975) Mate selection—a selection for a handicap. J Theor Biol 53:205–214

Zahavi A, Zahavi A (1997) The handicap principle, a missing piece of Darwin's puzzle. Oxford University, Oxford

Zuberbühler K (2003) Referential signalling in non-human primates: cognitive precursors and limitations for the evolution of language. Adv Study Behav 33:265–307