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The central importance of information in studies of animal communication

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The concept of information plays a central role in studies of animal communication. Animals' responses to the calls of different individuals, to food calls, alarm calls, and to signals that predict behaviour, all suggest that recipients acquire information from signals and that this information affects their response. Some scientists, however, want to replace the concept of information with one based on the 'manipulation' of recipients by signallers through the induction of nervous-system responses. Here we review both theory and data that argue against hypotheses based exclusively on manipulation or on a fixed, obligatory link between a signal's physical features and the responses it elicits. Results from dozens of studies indicate that calls with 'arousing' or 'aversive' features may also contain information that affects receivers' responses; that acoustically similar calls can elicit different responses; acoustically different calls can elicit similar responses; and 'eavesdropping' animals respond to the relationship instantiated by signal sequences. Animal signals encode a surprisingly rich amount of information. The content of this information can be studied scientifically.
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The concept of information has played a long and productive role in the study of animal communication. Empirical research has attempted to specify the kinds and amount of information transferred in signalling systems as disparate as the dance language of honeybees (von Frisch 1967; Seeley 1997), the claw-waving displays of crustaceans (Dingle 1969), the songs of birds (Vehrencamp 2000), and the alarm calls of primates (Cheney & Seyfarth 1990). Theoretical analyses have relied heavily on the concept of information in contexts ranging from aggression to courtship to cooperation (Enquist 1985; Grafen 1990; Maynard Smith 1991).

Nevertheless, this approach has been criticized by a minority of researchers. Dawkins & Krebs (1978, page 309), for example, argued that animal signals should be viewed not in terms of information but in terms of the manipulation of receiver behaviour, arguing that 'it is probably better to abandon the concept of information transfer altogether'. The call to abandon information in favour of 'manipulation' or 'assessment/management' was later renewed by Owings & Morton (1997, 1998), who suggested that 'the informational perspective is not adequate as a concept or methodology to understand either the evolution or the process of vocal communication' (1998, page ix). Along with others, they advocate a view of communication as management by signallers of the behaviour of receivers (see also Owren & Rendall 1997, 2001; Owren 2000; Rendall et al. 2009). For example, following Morton (1977), Rendall et al. (2009) note that the squeaks, shrieks and screams of many animals have 'sharp onsets, dramatic frequency and amplitude fluctuations, and chaotic spectral structures, which are exactly the sorts of features that have direct impact on animals' nervous systems' (page 236). Similar generalizations hold for alarm calls which have evolved, they believe, to 'induce nervous-system responses' in receivers (Owren & Rendall 2001, page 61). Finally, the critics also argue that using terms like information implicitly commits scientists to the use of human communication, particularly language, as a model for communication in animals. It is therefore both anthropomorphic and inaccurate (Owings & Morton 1997, 1998).

These opposing views find parallels in studies of animal learning. For years, behaviourists argued that the mental activities of animals were not appropriate topics for research, either because they could not be studied scientifically (methodological behaviourism) or because they did not exist (radical behaviourism; Skinner 1974).

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Today, however, this view has largely been discarded. Modern theories of learning have a strong cognitive component, with many experiments designed to examine the content of animals' knowledge and the information that animals acquire as a result of experience (e.g. Colwell & Rescorla 1985; Kamil 1987; Rescorla 1988; Lieberman 2003).

CLARIFYING THE TERMINOLOGY

Current accounts of information are built on the theoretical advances made by Shannon (1948) and Wiener (1961). Shannon viewed information as a statistical measure of uncertainty, allowing for mathematical analyses of information processing. While information theory was initially developed to describe information transmission in technical systems, it quickly found its way into a range of other disciplines, including psychology and animal behaviour (e.g. Dingle 1969; Beecher 1989). For our purposes, treating information as a reduction of uncertainty in the recipient is useful because it connects communication to learning theory and to research on the mechanisms by which animals associate signals (or cues) with each other or with the outcomes of specific behaviours.

INFORMATION IN ANIMAL COMMUNICATION

Whenever there is a predictable relation between a particular signal and a specific social situation, the signal can be used by listeners to predict current states or upcoming events; that is, to provide information. A light that predicts shock, an alarm call that predicts the presence of an eagle, or a scream that predicts that a specific individual is involved in a fight all have the potential to provide a listener with information if they are reliably associated (Rescorla 1988) with a narrow range of events (Seyfarth & Cheney 2003). In each case we assume that the listener has acquired the contingent relation between two stimuli and thus reduced its uncertainty (or gained information) about events in the world: the light predicts shock, not food; the alarm call predicts an eagle, not a leopard; the screams predict that one individual, but not another, is involved in a dispute. We also assume that learning such associations (if learning is required) is adaptive because it allows the receiver to predict what is likely to happen next.

Empirical support for this use of information is widespread in studies of animal communication. It is now clear that individuals in many species consistently use specific signals in particular social or ecological contexts and that receivers have learned or otherwise acquired these contingent relations, gaining information as a result. For example, honeybees, *Apis mellifera*, acquire information about the location of food by observing the details of a worker bee's dance (e.g. Seeley 1997). In hermit crabs, *Pagurus bernhardus* (Laidre 2009), swamp sparrows, *Melospiza georgiana* (Ballentine et al. 2008), and banded wrens, *Pheugopedius pleurostictus* (Vehrencamp et al. 2007), certain visual or vocal displays are reliable predictors of an individual's subsequent aggressive behaviour, and recipients respond as if they know this relation. The begging calls of cliff swallows, *Hirundo pyrrhonota*, are individually distinctive and provide parents with information about individual identity; the begging calls of barn swallows, *H. rustica*, do not (Medvin et al. 1993). In black-capped chickadees, *Poecile atricapillus*, acoustic features of the 'seet' and 'chick-a-dee' alarm calls are correlated with both the type of predator present and the degree of danger. Playback experiments indicate that listeners acquire this information from the calls (Templeton et al. 2005). A similar generalization holds for the alarm calls of African suricates, *Suricata suricatta*. Suricates give acoustically different alarm calls to different predators (jackals, eagles and snakes), and within each call type produce calls with graded acoustic variation that is correlated with the urgency of the danger. The suricates' responses to call playbacks suggest that, upon hearing an alarm call, individuals acquire information about both predator type and urgency (Manser et al. 2001a, b). In California ground squirrels, *Spermophilus beecheyi*, acoustically different alarm calls encode information about urgency, but not predator type (Owings & Hennessy 1984); in primates, they encode information about different predators (vervet monkeys, *Chlorocebus aethiops*: Seyfarth et al. 1980; Diana monkeys, *Cercopithecus diana*: Zuberbühler et al. 1999). Macedonia & Evans (1993) discuss the evolution of alarm call systems that encode different types of information. Finally, in addition to their acoustically different alarm calls for ground and aerial predators (Evans et al. 1993), domestic chickens, *Gallus gallus domesticus*, produce food calls that signal the presence of food. Once again, playback experiments indicate that listeners acquire this information from the calls (Evans & Evans 1999, 2007).

Contrary to the critics' argument, investigators in these studies have not naïvely applied linguistic concepts to their subjects, nor have they claimed that their results demonstrate the same kind of information transfer found in language. Instead, they have simply tried to determine whether particular signals predict something about the world (e.g. the presence of food, the caller's identity, a particular kind of predator, or the urgency of danger) or about the signaller's next behaviour. In this respect, the critics have set up a straw man: although information plays a central role in studies of animal communication, ethology is in no danger of being taken over by linguistics.

The 'manipulative' approach also leaves many interesting questions unanswered. For example, some of the alarm calls mentioned above have acoustic features that are arousing and attention getting. Why, then, are the calls within each species acoustically so different? Why do individuals respond to them in such different ways? And why is there such wide variation across species in the acoustic properties of alarm calls? Rats' alarms have a whistle-like structure (Litvin et al. 2007), those of shifaks are low-frequency roar grunts (Fichtel & Kappeler 2002), while antelope produce snorts (Tilson & Norton 1981). An exclusive focus on the calls' arousing physical characteristics cannot answer these questions.

Nor does the presence of particular acoustic features preclude the acquisition of information by listeners. Primate screams, for example, may have 'aversive' acoustic qualities, but this does not preclude recipients from acquiring information from them. In fact, research on many primates has shown that screams are individually distinctive (e.g. Hammerschmidt & Fischer 1998). Their acoustic features can also be correlated with different types of aggression (Gouzoules et al. 1984), the caller's role in the interaction (Slocombe & Zuberbühler 2005), or the presence of a particular 'audience' (Slocombe & Zuberbühler 2007). As a result, screams used in playback experiments elicit different responses from different individuals, or from the same individual under different circumstances (Cheney & Seyfarth 1980; Gouzoules et al. 1984; Palombit et al. 1997; Fischer 2004; Fugate et al. 2008; Slocombe et al. 2009). Here again, an exclusive focus on the screams' aversive qualities cannot explain these results.

Theoretical Limitations

The critics argue that signals have evolved to manipulate listeners' behaviour, and that the acoustic properties of signals take the form that they do because they have a 'direct effect' on listeners' nervous systems, effects that are difficult for listeners to resist. This explanation assumes that listeners are automata that can be manipulated to respond in ways beneficial to the signaller as long as the right nervous-system buttons are pushed. However, as Searcy & Nowicki (2005, page 8) point out, 'The critical flaw with

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this reasoning is that it does not explain why the receiver would be selected to respond to the signal at all'. An analysis that allows the signaller's behaviour to evolve but does not permit any evolution in receiver response does not make sense. 'If there is, on average, no information of benefit to the receiver in a signal, then receivers should evolve to ignore that signal. If receivers ignore the signal, then signalling no longer has any benefit to the signaller, and the whole communication system should disappear' (Searcy & Nowicki 2005, page 8). In fact, receivers should evolve responses to signals only when it is advantageous to do so. And if it does not benefit receivers to respond in a particular way to a specific acoustic feature then selection will favour receivers that attend to some other cue.

Imagine, for example, a species of frog in which males compete with vocal displays and calls with a low dominant frequency induce a 'nervous-system response' that causes recipients to retreat. This response will be maintained by natural selection only if it benefits the recipient. This could happen if calls with a low dominant frequency accurately predict the caller's competitive ability, thereby providing recipients with information about their likely success if they compete with that opponent. If calls with a low dominant frequency do not allow accurate assessment, then selection will favour recipients who base their decision on some other cue, regardless of any impact that low dominant frequency might have on their nervous system.

Receivers are not, then, prisoners of the influence that specific acoustic properties have on their sensory systems. Instead, selection will favour receivers that act selfishly, adjusting their 'assessment rule' (Grafen 1990, page 521) so that it is most effective in reducing uncertainty, or in providing them with information.

Finally, Grafen (1990), Searcy & Nowicki (2005), and others have used the logic of information to explain the evolution of all animal signals, regardless of modality. This generality constitutes a strength of their approach. If the explanation based on manipulation is to be equally general, its advocates will need to show that, just as some auditory signals like screams manipulate listeners through 'loud bursts of jarring broadband noise' (Rendall et al. 2009), certain visual signals are equally aversive and manipulative by virtue of their physical properties. This seems unlikely.

Receiver Flexibility

Supporting the view that selection can act just as forcefully on receivers as it does on signallers, there is ample evidence that receivers can learn to respond in specific ways to signals regardless of the signals' acoustic properties (think, for example, of learning experiments using pure tones, white noise, or more naturalistic vocalizations as stimuli), and that receiver responses can evolve over time (cases of character displacement, for example, suggest that receiver response may be more malleable than signal form).

Other studies suggest that there is no obligatory relation between acoustic features and response. In songbirds that sing more than one song type, the rate of song type switching increases with increasing aggression in some species but decreases with increasing aggression in others (Vehrencamp 2000). Song type switching has no inherent, immutable effect on listeners' behaviour. Instead, listeners attend to song switching rate because it predicts the singer's behaviour and thus provides useful information.

Of course, there are also many cases in which acoustic features are closely linked to call function. Two examples are the relationship between call frequency and body size in frogs and toads (reviewed in Searcy & Nowicki 2005), and between formant spacing and body size in several mammals (reviewed in Fitch & Hauser 2003). In both of these cases, however, listeners attend to a crucial acoustic feature not just because it induces a 'nervous-system response' (although it may do this) but also because it reduces uncertainty (that is, provides information) about a competitor.

Finally, Rendall et al. (2009, page 236) argue that 'a frustrated primate weanling cannot force its mother to nurse, but can readily elicit such behaviour with sounds' that 'with repetition become very aversive'. But studies of primate mother–infant interactions show that aversive sounds do not always have this effect. Infants do get weaned, in part because mothers cease responding to their calls and reject their attempts to nurse (e.g. Hinde 1978; Altmann 1980, page 175–177; Maestripieri 2002; see also Hammerschmidt et al. 1994).

Calls with Similar Acoustic Features Can Elicit Different Responses

Animals often respond differently to acoustically similar calls. Chickens, for example, respond in very different ways to food calls and to ground predator alarm calls even though the calls have similar acoustic characteristics (Evans & Evans 1999). They also respond differently to the same food call depending on whether they already know about the presence of food (Evans & Evans 2007). Upon hearing a vervet monkey's eagle alarm call, nearby animals on the ground look up or run into a bush. Animals in a tree look up and/or run down out of the tree and into a bush, and animals already in bushes typically do nothing (Seyfarth et al. 1980; see also Fischer et al. 2000). Listeners' responses to baboon grunts depend on both the type of grunt given and details of the social and ecological context (Rendall et al. 1999; Rendall 2003), including the recipient's prior interaction with the caller (Cheney & Seyfarth 1997), and the relation between the caller and individuals with whom the recipient has recently interacted (Wittig et al. 2007). These differences in response to the same or acoustically similar calls cannot be attributed to acoustic features alone, but they are consistent with the hypothesis that responses depend upon the integration of information acquired from calls and other contextual cues.

Calls with Different Acoustic Features Are Judged To Be Similar

Diana monkeys that typically respond to the growl of a leopard by giving their own leopard alarm call will not give such calls in response to the growl if they have already heard a Diana's leopard alarm call coming from the same area. However, they respond in typical fashion to the leopard's growl if they previously heard a Diana's eagle alarm call coming from the same area. Although a leopard's growl and Diana monkey leopard alarm calls are very different acoustically, the monkeys respond as if they judge them to be similar (similar, at least, in the sense that responding to one call type produces habituation to the other; Zuberbühler et al. 1999). An exclusive focus on call acoustics cannot explain these results. They are, however, consistent with the hypothesis that listeners acquire information from a call, store it in memory, and respond to subsequent vocalizations depending on some combination of acoustic features, information provided by the current vocalization and context, and information stored in memory (for similar results see Fischer 1988; Cheney & Seyfarth 1988; Rendall et al. 1996; Hauser 1998).

Animals' Responses Depend on the Relationship Instantiated by Two Signals

Song sparrows, *Melospiza melodia*, sometimes match a neighbour's song by selecting from among their own repertoire the song type that most closely matches the song their neighbour just sang (Beecher et al. 1996). In studies using interactive playback experiments, subjects responded more strongly to a match than

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a nonmatch (Burt et al. 2001). It was not just the acoustic properties of the song that determined the neighbour's behaviour (although these were clearly important), but whether or not the two song types matched (see also Beecher & Campbell 2005).

Territorial songbirds learn to recognise their neighbours and associate them with specific areas by listening to their songs. They respond more strongly to a given song type when it comes from an unfamiliar area than when it comes from a familiar area (Brooks & Falls 1975; see also Herbinger et al. 2009). When a listener responds differently to the same vocalization played from different locations, it integrates information contained in the call itself with information stored in memory about the caller's typical location. The direct effects of acoustic features alone cannot explain this behaviour.

Songbirds also learn about the competitive abilities of potential intruders by listening to their singing bouts with the territory holders' neighbours (Peake et al. 2002). Such 'eavesdropping' is widespread among animals (McGregor 2005). When a bird or primate responds differently depending upon whether it has heard A dominate B or B dominate A (Peake et al. 2002; Bergman et al. 2003), its response depends not just on the calls' acoustic properties but also on the relationship between callers. As McGregor & Dabelsteen (1996, page 416) put it, the eavesdropper 'gains information from an interaction that could not be gained from a signal alone'. Once again, an exclusive focus on acoustic properties is insufficient to explain these results.

USING 'INFORMATION' IN ANIMAL COMMUNICATION

The experiments cited above, and many others, suggest that the manipulative hypothesis is insufficient to explain all that happens when one individual signals to another. Instead, results suggest that when recipients perceive a signal they acquire information, and the acquisition of this information (among other things) changes their behaviour. The information that receivers acquire has content, and this content can be studied scientifically.

Used in this way, 'information' helps to formulate hypotheses that guide research and sharpen our understanding of what we actually mean when we use the term. There is nothing wrong with this strategy, particularly if it leads to testable, falsifiable predictions. In fact, adopting such heuristic terms has a long and continuing history in the biological sciences. 'Gene', 'memory', 'mental map', 'auditory template' and 'neural representation' are other examples of words or phrases that scientists have used to label an entity whose physical properties they are only beginning to understand. The inability to specify precisely the information conveyed by a vocalization (that is, its meaning to a listener) does not prove that information is entirely absent.

The critics argue that we should abandon the concept of information, but what programme of research do they offer in its place? To reject the informational hypothesis entirely, we need evidence that recipients in studies like those reviewed here acquire *no information*. Although the 'manipulative' hypothesis has been around for many years, no such data are available. The influence that signallers have on receivers may help understand cases of sensory exploitation (e.g. Ryan 1990), but years of research on this topic do not compel us to abandon the concept of information. Indeed, if there exist cases of sensory exploitation without information transfer, the only way to make this distinction is to ask if a signal contains information, a question the critics see as 'ill-posed'. We agree that it is important to consider the form that signals take, and can imagine some useful experiments to test whether animals more readily learn pairings of certain types of signals with particular outcomes, but this work would be fully compatible with the informational perspective.

'Teleological' and 'Circular' Reasoning?

Both Owings & Morton (1998) and Rendall et al. (2009) object to the ways in which scientists studying animal communication have borrowed the term information from linguistics. Rendall et al. (2009) believe that this approach is 'both teleological and circular' because it 'virtually guarantees' that animal communication and language 'will be "found" to be similar' (page 238). In fact, however, quite the opposite is true. The informational approach has instead played a major role in uncovering differences between species, and between animal communication and language, in the kinds of information recipients acquire from signals.

For example, experiments on nonhuman primates have repeatedly shown that, whereas human listeners acquire information about a speaker's mental states (intentions, beliefs, desires) during conversation, nonhuman primate listeners appear to make no such attributions (reviewed in Tomasello & Call 1997; Cheney & Seyfarth 2007). Research on the information conveyed by vocalizations has thus led the way in revealing differences between human language and nonhuman primate communication.

Curiously, Rendall et al. (2009) support their argument against the 'informational' hypothesis by noting that recent studies have revealed 'an informational disconnection between signallers and perceivers [suggesting] that they do not share the same representational parity that characterizes human speech' (page 235). But this conclusion, first proposed by Premack (1972, 1975) and later elaborated (e.g. Cheney & Seyfarth 1990, 1996, 1998; Seyfarth & Cheney 2003), emerged not as a result of their 'manipulative' approach but instead as a consequence of the very informational perspective that they decry. Results demonstrate that, contrary to the critics' claims, the informational view is fully compatible with distinct roles for signallers and receivers.

Finally, the lack of language-like intentionality in animal communication does not mean that no continuities exist between human and animal communication, nor should it prompt us to abandon a research programme designed to search for precursors of language in animal communication and cognition. Marler (1982) was one of the first to examine similarities among birds, primates and humans in meaning and the categorization of signals (see also Cheney & Seyfarth 1990, 2007). Several recent studies have documented psychological skills in nonhuman primates, such as sensitivity to the presence of an audience or an awareness of the directedness of a vocalization, that may well have been precursors of intentional signalling during the course of human evolution (e.g. Engh et al. 2006; Wich & deVries 2006). It would be impossible to formulate hypotheses about the evolution of language if one started with the premise that testing for language-like attributes in animal communication is off-limits. Several recent studies in nonhuman primate neurophysiology, inspired by work on primate vocalizations, demonstrate the value of a research programme that tests for language-like processing in primates and other animals (e.g. Ghazanfar & Santos 2004; Gifford et al. 2005; Belin 2006; Ghazanfar et al. 2008; Petkov et al. 2008).

CONCLUSION

The critics have erected a straw man: most ethologists make no claim that the signals they study are like language. The critics' view is also inconsistent with evolutionary theory. Recipients are not powerless, unable to resist certain signals; instead, their responses will evolve to reflect their own interests, and will depend on both a signal's physical properties and the information they acquire from it.

Many studies argue against the critics' hypothesis. They show that calls with arousing or aversive features may also contain

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information that affects receivers' responses; receivers' responses can be highly flexible; acoustically similar calls can elicit different responses; acoustically different calls can elicit similar responses; and 'eavesdropping' animals respond to the relationship instantiated by signal sequences. All of these results support the view that animal signals encode a surprisingly rich amount of information, that the content of this information can be studied scientifically, and that recipients' responses depend at least in part on the information they acquire from signals.

Far from being 'teleological' and 'circular', research inspired by the informational perspective has clarified differences in the mechanisms that underlie the behaviour of signallers and recipients; revealed differences between species in the information that recipients acquire from signals; suggested fundamental differences between language and animal communication; and inspired a growing number of studies that examine the neurophysiological basis of call meaning. The informational hypothesis thus continues to prove its value in the most important way possible: by suggesting observations and experiments that drive our field forward.

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References

Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, Massachusetts: Harvard University Press.

Ballentine, B., Searcy, W. A. & Nowicki, S. 2008. Reliable aggressive signaling in swamp sparrows. *Animal Behaviour*, **75**, 693–703.

Beecher, M. D. 1989. Signaling systems for individual recognition: an information theory approach. *Animal Behaviour*, **38**, 248–261.

Beecher, M. D. & Campbell, E. 2005. The role of unshared songs in singing interactions between neighbouring song sparrows. *Animal Behaviour*, **70**, 1297–1304.

Beecher, M. D., Stoddard, P. K., Campbell, S. E. & Hornig, C. L. 1996. Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, **51**, 917–923.

Belin, P. 2006. Voice processing in human and nonhuman primates. *Philosophical Transactions of the Royal Society*, **361**, 2091–2107.

Bergman, T. J., Beehner, J. C., Cheney, D. L. & Seyfarth, R. M. 2003. Hierarchical classification by rank and kinship in baboons. *Science*, **302**, 1234–1236.

Brooks, R. J. & Falls, J. B. 1975. Individual recognition by song in white-throated sparrows. III. Song features used in individual recognition. *Canadian Journal of Zoology*, **53**, 1749–1761.

Burt, J. M., Campbell, E. & Beecher, M. D. 2001. Song type matching as threat: a test using interactive playbacks. *Animal Behaviour*, **62**, 1163–1170.

Cheney, D. L. & Seyfarth, R. M. 1980. Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour*, **28**, 362–367.

Cheney, D. L. & Seyfarth, R. M. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, **36**, 477–486.

Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World*. Chicago: University of Chicago Press.

Cheney, D. L. & Seyfarth, R. M. 1996. Function and intention in the calls of nonhuman primates. *Proceedings of the British Academy*, **88**, 59–76.

Cheney, D. L. & Seyfarth, R. M. 1997. Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour*, **54**, 409–415.

Cheney, D. L. & Seyfarth, R. M. 1998. Why monkeys don't have language. In: *The Tanner Lectures on Human Values Vol. 19* (Ed. by G. Petersen), pp. 175–219. Salt Lake City: University of Utah Press.

Cheney, D. L. & Seyfarth, R. M. 2007. *Baboon Metaphysics*. Chicago: University of Chicago Press.

Colwell, R. M. & Rescorla, R. A. 1985. Postconditioning devaluation of a reinforcer affects instrumental responding. *Journal of Experimental Psychology, Animal Behaviour Processes*, **11**, 120–132.

Dawkins, R. & Krebs, J. R. 1978. Animal signals: Information or manipulation? In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 282–309. Oxford: Blackwell.

Dingle, H. 1969. A statistical and informational analysis of aggressive communication in the mantis shrimp, *Gonodactylus bredini*. *Animal Behaviour*, **17**, 561–575.

Engh, A. L., Hoffmeier, R., Cheney, D. L. & Seyfarth, R. M. 2006. Who me? Can baboons infer the target of vocalizations? *Animal Behaviour*, **71**, 381–387.

Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour*, **33**, 1152–1161.

Evans, C. S. & Evans, L. 1999. Chicken food calls are functionally referential. *Animal Behaviour*, **58**, 307–319.

Evans, C. S. & Evans, L. 2007. Representational signaling in birds. *Biology Letters*, **3**, 8–11.

Evans, C. S., Evans, L. & Marler, P. 1993. On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, **46**, 23–38.

Fichtel, C. & Kappeler, P. 2002. Anti-predator behaviour of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology*, **51**, 262–275.

Fischer, J. 1988. Barbary macaques categorize shrill barks into two call types. *Animal Behaviour*, **55**, 799–807.

Fischer, J. 2004. Emergence of individual recognition in young macaques. *Animal Behaviour*, **67**, 655–661.

Fischer, J., Cheney, D. L. & Seyfarth, R. M. 2000. Development of infant baboons' responses to graded bark variants. *Proceedings of the Royal Society B*, **267**, 2317–2321.

Fitch, W. T. & Hauser, M. D. 2003. Unpacking honesty: vertebrate vocal production and the evolution of acoustic signals. In: *Animal Communication* (Ed. by A. M. Simmons, R. R. Fay & A. N. Popper), pp. 65–137. New York: Springer.

von Frisch, K. 1967. *The Dance Language and Orientation of Bees*. Cambridge, Massachusetts: Harvard University Press.

Fugate, J. M. B., Gouzoules, H. & Nygaard, L. C. 2008. Recognition of rhesus macaque (*Macaca mulatta*) noisy screams: evidence from conspecifics and human listeners. *American Journal of Primatology*, **70**, 594–604.

Ghazanfar, A. & Santos, L. R. 2004. Primate brains in the wild: the sensory basis for social interaction. *Nature Reviews Neuroscience*, **5**, 603–616.

Ghazanfar, A., Chandrasekaran, C. & Logothetis, N. K. 2008. Interactions between the superior temporal sulcus and auditory cortex mediate dynamic face/voice integration in rhesus monkeys. *Journal of Neuroscience*, **28**, 4457–4469.

Gifford, G. W., MacLean, K. A., Hauser, M. D. & Cohen, Y. E. 2005. The neurophysiology of functionally meaningful categories: macaque ventrolateral prefrontal cortex plays a critical role in spontaneous categorization of species-specific vocalizations. *Journal of Cognitive Neuroscience*, **17**, 1471–1482.

Gouzoules, S., Gouzoules, H. & Marler, P. 1984. Rhesus monkeys (*Macaca mulatta*) screams: representational signaling in the recruitment of agonistic aid. *Animal Behaviour*, **32**, 182–193.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.

Hammerschmidt, K. & Fischer, J. 1998. The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. *Ethology*, **104**, 203–216.

Hammerschmidt, K., Ansorge, V., Fischer, J. & Todt, D. 1994. Dusk calling in Barbary macaques (*Macaca sylvanus*): demand for social shelter. *American Journal of Primatology*, **32**, 277–289.

Hauser, M. D. 1998. Functional referents and acoustic similarity: field playback experiments with rhesus monkeys. *Animal Behaviour*, **55**, 1647–1658.

Herbinger, I., Papworth, S., Boesch, C. & Zuberbühler, K. 2009. Vocal, gestural, and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study. *Animal Behaviour*, **78**, 1389–1396.

Hinde, R. A. 1978. *Biological Bases of Human Social Behaviour*. New York: McGraw-Hill.

Kamil, A. C. 1987. A synthetic approach to the study of animal intelligence. *Nebraska Symposium on Motivation*, **7**, 257–308.

Laidre, M. E. 2009. How often do animals lie about their intentions: an experimental test. *American Naturalist*, **173**, 337–346.

Lieberman, D. A. 2003. *Learning and Memory: an Integrative Approach*. New York: Wadsworth.

Litvin, Y., Blanchard, C. & Blanchard, R. 2007. Rat 22 kHz ultrasonic vocalizations as alarm cries. *Behavioural Brain Research*, **182**, 166–172.

Macedonia, J. M. & Evans, C. S. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, **93**, 177–197.

McGregor, P. K. (Eds). 2005. *Animal Communication Networks*. Cambridge: Cambridge University Press.

McGregor, P. K. & Dabelsteen, P. 1996. Communication networks. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 409–425. Ithaca, New York: Cornell University Press.

Maestripieri, D. 2002. Parent–offspring conflict in primates. *International Journal of Primatology*, **23**, 923–951.

Manser, M. B., Seyfarth, R. M. & Cheney, D. L. 2001a. Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Science*, **6**, 55–57.

Manser, M. B., Bell, M. B. & Fletcher, L. 2001b. The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society B*, **268**, 2485–2491.

Marler, P. 1982. Avian and primate communication: the problem of natural categories. *Neuroscience & Biobehavioral Reviews*, **6**, 87–94.

Maynard Smith, J. 1991. Honest signaling: the Philip Sidney game. *Animal Behaviour*, **42**, 1034–1035.

Medvin, M. B., Stoddard, P. K. & Beecher, M. D. 1993. Signals for parent–offspring recognition: a comparative analysis of the begging calls of cliff swallows and barn swallows. *Animal Behaviour*, **45**, 841–850.

Morton, E. S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, **111**, 855–869.

Owings, D. & Hennessy, D. 1984. The importance of variation in sciurid visual and vocal communication. In: *Biology of Ground-dwelling Squirrels: Annual Cycles, Behavioral Ecology, and Sociality* (Ed. by J. O. Murie & G. R. Michener), pp. 322–347. Lincoln: University of Nebraska Press.

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Owings, D. H. & Morton, E. S. 1997. The role of information in communication: an assessment/management approach. In: *Perspectives in Ethology: Vol. 12, Communication* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 359–390. New York: Plenum.

Owings, D. H. & Morton, E. S. 1998. *Animal Vocal Communication: a New Approach*. Cambridge: Cambridge University Press.

Owren, M. J. 2000. Standing evolution on its head: the uneasy role of evolutionary theory in comparative cognition and communication. *Reviews in Anthropology*, **29**, 55–69.

Owren, M. J. & Rendall, D. 1997. An affect-conditioning model of nonhuman primate vocal signaling. In: *Perspectives in Ethology, Vol. 12, Communication* (Ed. by M. D. Beecher, D. H. Owings & N. S. Thompson), pp. 299–346. New York: Plenum.

Owren, M. J. & Rendall, D. 2001. Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology*, **10**, 58–71.

Palombit, R. A., Cheney, D. L. & Seyfarth, R. M. 1997. The adaptive value of 'friendships' to female baboons: experimental and observational evidence. *Animal Behaviour*, **54**, 599–614.

Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. 2002. Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proceedings of the Royal Society B*, **269**, 1925–1929.

Petkov, C. I., Kayser, C., Steudel, T., Wittingstall, K., Augath, M. & Logothetis, N. K. 2008. A voice region in the monkey brain. *Nature Neuroscience*, **11**, 367–374.

Premack, D. 1972. Concordant preferences as a precondition for affective but not for symbolic communication (or how to do experimental anthropology). *Cognition*, **1**, 251–264.

Premack, D. 1975. On the origins of language. In: *Handbook of Psychobiology* (Ed. by M. D. Gazzaniga & C. B. Blakemore), pp. 591–605. New York: Academic Press.

Rendall, D. 2003. Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. *Journal of the Acoustical Society of America*, **113**, 3390–3402.

Rendall, D., Rodman, P. S. & Emond, R. E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, **51**, 1007–1015.

Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J. 1999. The meaning and function of grunt variants in baboons. *Animal Behaviour*, **57**, 583–592.

Rendall, D., Owren, M. J. & Ryan, M. 2009. What do animal signals mean? *Animal Behaviour*, **78**, 233–240.

Rescorla, R. R. 1988. Pavlovian conditioning: it's not what you think it is. *American Psychologist*, **43**, 151–160.

Ryan, M. 1990. Sensory systems, sexual selection, and sensory exploitation. *Oxford Surveys in Evolutionary Biology*, **7**, 157–195.

Searcy, W. & Nowicki, S. 2005. *The Evolution of Animal Communication*. Princeton, New Jersey: Princeton University Press.

Seeley, T. D. 1997. Honey bee colonies are group-level adaptive units. *American Naturalist, Supplement*, **150**, S22–S41.

Seyfarth, R. M. & Cheney, D. L. 2003. Signalers and receivers in animal communication. *Annual Review of Psychology*, **54**, 145–173.

Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, **28**, 1070–1094.

Shannon, C. 1948. A mathematical theory of communication. *Bell Systems Technical Journal*, **27** 379–423, 623–656.

Skinner, B. F. 1974. *About Behaviourism*. New York: Knopf.

Slocombe, K. & Zuberbühler, K. 2005. Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology*, **119**, 67–77.

Slocombe, K. & Zuberbühler, K. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 17228–17233.

Slocombe, K., Townsend, S. & Zuberbühler, K. 2009. Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: evidence from a playback study. *Animal Cognition*, **12**, 441–449.

Templeton, C. N., Greene, E. & Davis, K. 2005. Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*, **308**, 1934–1937.

Tilson, R. & Norton, P. 1981. Alarm duetting and pursuit deterrence in an African antelope. *American Naturalist*, **188**, 455–462.

Tomasello, M. & Call, J. 1997. *Primate Cognition*. Oxford: Oxford University Press.

Vehrencamp, S. 2000. Handicap, index, and conventional signal elements of bird song. In: *Animal Signals: Signalling and Signal Design in Animal Communication* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 277–300. Trondheim: Tapir Academic Press.

Vehrencamp, S. L., Hall, M., Bohman, E., Depeine, C. & Dalziell, A. H. 2007. Song matching, overlapping, and switching in the banded wren: the sender's perspective. *Behavioral Ecology*, **18**, 849–859.

Wiener, N. 1961. *Cybernetics; or Control and Communication in the Animal and the Machine*. New York: MIT Press.

Wich, S. & deVries, H. 2006. Male monkeys remember which group members have given alarm calls. *Proceedings of the Royal Society B*, **273**, 735–740.

Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M. & Cheney, D. L. 2007. Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proceedings of the Royal Society B*, **274**, 1109–1115.

Zuberbühler, K., Cheney, D. L. & Seyfarth, R. M. 1999. Conceptual semantics in a nonhuman primate. *Journal of Comparative Psychology*, **113**, 33–42.

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