

- 33 Lloyd, J.E. (1984) in *Oxford Surveys in Evolutionary Biology* (Vol. 1) (Dawkins, R. and Ridley, M., eds), pp. 48–84, Oxford University Press
 34 Trail, P.W. (1987) *Auk* 104, 496–507
 35 Sih, A. (1988) *Anim. Behav.* 36, 1846–1848

- 36 Magnhagen, C. (1990) *Behav. Ecol. Sociobiol.* 26, 331–335
 37 Montgomerie, R.D. and Weatherhead, P.J. (1988) *Q. Rev. Biol.* 63, 167–187
 38 Lima, S.L. and Dill, L.M. (1990) *Can. J. Zool.* 68, 619–640

- 39 Clark, C.W. and Ydenberg, R.C. (1990) *Evol. Ecol.* 4, 21–34
 40 Zahavi, A. (1987) in *Proceedings of the International Symposium on Biological Evolution* (Delfino, V.P., ed.), pp. 305–327, Adriatica Editrice Bari

'Intentional' Signaling in Animal Communication

Marc D. Hauser and Douglas A. Nelson

The problem of 'intentional' signaling is of interest to evolutionary biologists concerned with animal conflicts and to cognitive ethologists attempting to determine whether nonhuman animals exhibit evidence of complex mental states. Recent theoretical and empirical advances in this area have led to a number of important insights concerning the nature of competitive social interactions. Specifically, and in contrast to earlier claims, individuals involved in social conflicts often produce displays that predict their subsequent behavior, and such predictive displays occur even when repeated social interactions are infrequent. Moreover, studies on a taxonomically diverse set of organisms show that deception, in the form of withholding information, is prevalent. Deception through concealment of information may be widespread because it is more difficult to detect than active falsification of information.

During the 1970s, biologists using the conceptual framework of game theory^{1–3} raised an objection to the claim⁴ that animals should reveal information about their 'intentions' to perform a given behavior. They argued that in intraspecific conflict situations, signals conveying information about the probability of subsequent behavior (one operational definition of intention) would not be favored by selection because they could readily be exaggerated or concealed and thus would become unreliable signals over time. These early models stimulated much work on a wide diversity of species.

The term 'intentional' has also been used to describe a different

set of observations and experiments on animal communication. Research in this area has raised the possibility that the outcome of some social interactions is determined by complex mental processes rather than being the result of individuals responding to predictable situations.

Two senses of intentional signaling

When ethologists⁴ or behavioral ecologists³ discuss an animal's intentions, they typically mean that a given signal is predictive of the signaler's subsequent behavior. For example, Maynard Smith² defined intentions as information about 'the level to which they [signalers] would escalate', or intentions 'specify what an animal will do, or attempt to do, and can be changed with little cost in fitness'⁵. The latter qualification is important, although difficult to measure in practice, as it distinguishes information about intentions from that about fighting ability, or what has been termed resource-holding potential (RHP)⁶. There is little dispute that animals should reliably inform about, and respect, RHP⁷ because most attributes of RHP cannot be altered by animals without incurring significant costs. Instead, controversy has centered on the idea that animals should not provide information regarding subsequent behavior (see Box 1).

The other common usage of the term intentional is derived from philosophy and, as used by some ethologists^{12,13}, raises the possibility that complex mental processes guide the behavior of some animals. A useful framework for investigating intentionality in animals

is Dennett's 'intentional stance'¹⁴, which posits a hierarchy of increasingly complex mental states underlying behavior. Using this framework, the alarm-call system of the vervet monkey (*Cercopithecus aethiops*)^{15,16} has been scrutinized¹³. Observations do not support a higher-order intentional interpretation (e.g. A wants B to believe that A believes there is a leopard). Rather, results suggest that the production of alarm calls is guided by a motivation to inform others about danger or an appropriate escape response (e.g. A wants B to run up into a tree due to the presence of a leopard). As discussed below, however, alarm-calling behavior in vervet monkeys and other nonhuman animals is not simply a reflection of emotional state, since call production appears to be contingent upon the caller's 'audience'. As a result, animals can withhold information about predators and can use alarm calls that are functionally deceptive (see Table 1).

Thus, there are two quite different concepts associated with the use of 'intentional signaling'. To avoid confusion, it would be preferable if researchers were to use *predictive* signaling when discussing the association between a signal and the signaler's subsequent behavior, and *intentional* signaling when discussing the mental processes underlying signal production.

Cases of predictive signaling

In contrast to early predictions from game theory, recent theoretical⁸ and empirical research on agonistic interactions strongly suggests that in species where individuals engage in repeated interactions, signals accurately reveal information about subsequent behavior. However, two studies have also suggested that repeated interactions are not a necessary pre-

Marc Hauser and Douglas Nelson are at the Dept of Zoology, University of California, Davis, CA 95616, USA.

requisite for the evolution of signals that accurately reflect underlying motivation.

Predictive signaling among individuals with repeated encounters

Caldwell and his colleagues have investigated the fighting strategies of the stomatopod *Gonodactylus bredini* (a crustacean)¹⁷⁻¹⁹. In this species, individuals use their raptorial appendages to injure and even kill other conspecifics. Most aggressive interactions occur over defense of cavities. To understand how individuals assess the nature of an aggressive encounter, a detailed analysis of the 'meral-spread' display was carried out. In this display, the raptorial appendages are spread out while the maxillipeds are extended into a circular pattern; the size of the raptorial appendages is positively correlated with the individual's ability to deter intruders from attacking and, in non-molting individuals, the use of the meral spread correlates significantly with subsequent attacks.

Caldwell¹⁹ argues that 'the meral spread carries information available to receivers concerning the signaler's "intentions" to escalate'. Interestingly, post-molt individuals, who are literally defenseless, use the meral-spread display as an effective bluff because the signal's credibility was established during the pre-molting phase. Because there is a high risk associated with challenging the honesty of an individual's meral-spread display, this signal can be used deceptively.

Pigeon guillemots (*Cephus columba*) defend small (1-3 m²) territories immediately around their nesting burrows. Feeding is done at sea. Male-male interactions often include vocal and visual displays (hunch-whistle and neck-stretch) given either by the territory owner or by both birds¹¹. Territory owners win the majority of interactions and fights, regardless of size and age differences. While role differences explain most of the variation in the outcome of interactions, variation in the frequency (pitch) and duration of whistled notes in the hunch-whistle and neck-stretch displays predict when and whether the signaler will fly away or stay. No vocal or visual displays have been shown to predict tendency to attack. The

hunch-whistle and neck-stretch displays form a graded display series that accurately reveals the probability of subsequent behavior.

Musth in male African elephants (*Loxodonta africana*) has been described as a signal that announces a state of heightened aggressiveness²⁰. In general, larger males are in musth for longer periods than smaller males, and larger males typically outcompete smaller males. However, because relatively small adult males in poor condition and in musth can dominate larger non-musth males in good condition, this system provides an ideal opportunity to explore the honesty of signaling about motivation to fight²¹. When males compete for access to females, they readily make assessments of role asymmetries based on vocal, chemical and behavioral cues^{21,22}. As a result of their asynchronous periods of sexual activity, resource value changes with age and sexual state. Therefore, musth provides accurate information about resource value and about a male's willingness to fight with a given opponent, independently of differences in RHP.

Predictive signaling among individuals with infrequent interactions

Great skuas (*Stercorarius skua*) congregate on 'club' areas of their large breeding colonies. The club areas are composed of pre-breeders, failed breeders and old birds, the numbers of which change on a daily and seasonal basis. Birds in the centers of clubs show no site attachment, making it unlikely that there are repeated interactions between specific individuals. The neck-straight-bill-straight display has been shown to correlate significantly with escape by receivers, independent of the signaler's distance from the receiver²³. Eight other postures did not correlate with escape by receivers, but it remains possible that some of these postures provide other kinds of information that were not examined.

The aggressive communication of northern fulmars (*Fulmarus glacialis*), competing for food provided at sea, was studied to determine the relationship between risk and effectiveness of a given display⁹. Results show that individuals use signals that convey information

Box 1. Models and methodological approaches to signaling behavior

The 'war of attrition' model developed by Maynard Smith¹ was the first to make a novel prediction about the information conveyed by a signal. Assuming that the time spent in an interaction is the only cost incurred by participants, this model predicted that animals should not reveal when they will give up in a fight. Maynard Smith² and Caryl³ subsequently generalized the prediction to include information about the level to which individuals would escalate, but not in the context of formal models with relaxed assumptions. More realistic models followed by van Rhijn and Vodegel⁶, Maynard Smith⁶ and Enquist *et al.*⁹ In particular, van Rhijn and Vodegel⁶ argued that in cases where repeated interactions among individuals made individual recognition possible, truthful signaling of subsequent behavior should be favored. This model, which is most applicable to group-living animals, predicts that the tactics an animal adopts should vary as a function of prior experience with specific individuals.

Part of the problem with measuring information about an animal's intentions has been to disentangle it from information about RHP (fighting ability)⁷. For example, animals with high RHP might be expected to be more likely to attack, and those with low RHP, to flee. One operational distinction between the two concepts may be to consider associations between displays and future behavior as a function of time. Assuming that an animal's motivation to fight or flee varies over a shorter time course than its ability to fight, then the strength of association between displays and subsequent behavior should be negatively correlated with the time separating display and behavior. This has been observed in great skuas (*Stercorarius skua*)¹⁰ and pigeon guillemots (*Cephus columba*)¹¹.

regarding their motivation to fight for a food source. As the value of the resource increases, individuals use relatively more risky or costly displays.

In summary, these examples (see Table 1) demonstrate that predictive signaling is common. Several of the examples appear to meet the assumptions of Maynard Smith's territorial-bargaining model³, or the repeated-interactions model of van Rhijn and Vodegel⁶. Other data sets^{9,23}, which involved either encounters between unfamiliar individuals or seemingly random encounters among birds on a communal 'club', probably cannot be interpreted within the framework of these models and may be explicable in terms of Enquist's 'risk-effectiveness' model⁹. In agonistic situations, therefore, theory and data have converged on the view that signals can be reliable indicators of an individual's fighting

Table 1. Signaling behavior in nonhuman animals

A. Examples of predictive signaling				
Animal ^a	Individual recognition?	Repeated encounters?	Signal predicts subsequent behavior?	Refs
Stomatopod	Yes	Yes	Yes	17-19
Pigeon guillemot	Yes	Yes	Yes	11
Northern fulmar	?	No	Yes	9
African elephant	Yes	Yes	Yes	20-22
B. Examples of deceptive signaling				
Animal ^a	Context	Withhold information?	False information?	Refs
Chimpanzee	Food, sex, aggression	Yes	Yes	30,33
Great tit	Food		Yes	25
Domestic chicken	Food, predators	Yes	Yes	28,29
Vervet monkey	Predators	Yes	Yes	27
Baboon (<i>Papio</i>)	Aggression	Yes	Yes	12
Stomatopod	Aggression		Yes	19

^aSee text for Latin names of species.

ability or motivation. The opportunity for deceptive signaling is limited when recipients have access to other information (individual identity, size) to which the signal's meaning can be compared, or when the frequency of interaction between individuals is low²⁴. In other contexts, such as the alarm calling of birds and mammals discussed below, subtle deception by signalers may involve varying the frequency with which signals are given according to the composition of the audience.

Cases of intentional signaling

An intentional interpretation of behavior can assume different levels of cognitive complexity. As discussed by Cheney and Seyfarth¹³, however, it is important to recognize that ethologists often apply the same descriptive terminology to explain behavioral interactions that are guided by different mechanisms. This point is clearly illustrated by the use of the term 'deception'. For example, several studies (Table 1) have examined the question of deception by demonstrating that an animal either conceals information or uses a signal that provides false or misleading information about the socioecological environment¹⁴.

Møller²⁵, for instance, has shown that great tits (*Parus major*) produce alarm calls in the absence of predators. The consequence of such 'false' alarm calls is that individuals improve their chances of gaining access to highly valued food sources. Møller uses the term 'deceptive' to imply that the actor's behavior

functions to manipulate the behavior of the target in such a way that the actor benefits (e.g. the actor gains a food resource). Deception, in this functional sense, remains neutral with respect to underlying mechanisms. In contrast, Whiten and Byrne¹² have used a large set of anecdotal observations on tactical deception in nonhuman primates, especially chimpanzees (*Pan troglodytes*), to argue that individuals attribute beliefs to conspecifics and use this knowledge to manipulate each other.

Although there is substantial controversy regarding the use of anecdotes in the analysis of animal cognition²⁶, deception, as used here, implicitly refers to underlying mechanisms (i.e. complex mental states) and only secondarily considers functional issues. There are two sets of experimental studies, with vervet monkeys and chickens, respectively, that provide evidence of socially mediated call suppression, a subtle form of deception. These studies are of interest because they raise the possibility of higher-order intentional behavior.

East African vervet monkeys produce a variety of acoustically distinct alarm calls which appear to refer to different predators^{15,16}. Observations under natural conditions suggest that when individuals who are separated from their group encounter a predator, they do not give alarm calls. Moreover, low-ranking animals produce fewer alarm calls than high-ranking animals, even though there are no differences in the probability of sighting a pred-

ator based on rank. In captivity, females give more alarm calls to a predator when they are in the presence of kin than when in the presence of non-kin, and males give more alarm calls when they are in the presence of females than males²⁷. These results suggest that information about predators can be suppressed, and that the presence of conspecifics affects whether or not alarm calls are produced.

In domestic chickens (*Gallus domesticus*), males call when they find food. By presenting different types of food to males and by changing the social context in which the male finds food (i.e. changing the male's audience), it has been shown that call production is influenced by the kind of food presented and by the discoverer's audience²⁸. Just like the vervet alarm-call study, this study also shows that call production depends on the presence of conspecifics. In addition, Gyger and Marler²⁹ have shown that when sexually receptive females are set up as an audience, males will often (in 45% of cases) give food calls in response to non-food items. They argue that this result provides a potential example of deceptive calling behavior.

The vervet monkey and chicken studies raise the possibility that call production is mediated by the caller's intentions. For example, when a rooster calls in response to a nonfood item and thereby attracts a female, does he consciously intend to deceive the female into believing that there is food? Similarly, because vervets only appear to give alarm calls in the presence of group members, do they intend to inform others about predators? Researchers involved with this problem have concluded that such cognitively demanding interpretations are not yet warranted¹³. Rather, signal production in vervets and chickens can be explained by the rule 'Call when there is an appropriate audience and do not call when there is no audience'. Results from more recent studies suggest that the particular stimulus characteristics of the audience (e.g. familiar versus unfamiliar, kin versus non-kin) are important.

Although this rule is the most parsimonious explanation, results both from observations under natural

conditions and from experiments reveal that individuals control the frequency of signal production, apparently independently of other responses to the situation. For example, when female chimpanzees copulate with older males, they typically give loud copulation calls. In contrast, when females copulate with younger and presumably lower-ranking males, they occasionally do not call even though other behavioral responses to copulation (e.g. facial expressions) are expressed³⁰. Thus, nonhuman animals are capable both of withholding information and of falsely signaling about objects and events in the environment.

Conclusions and future directions

In conclusion, current research shows that in agonistic situations animals often use signals that accurately reflect their subsequent behavior. Such predictive signaling has been demonstrated in species with repeated interactions among individuals and in those where repeated interactions are infrequent. Our current theoretical and empirical understanding of predictive signaling needs to be extended to non-agonistic situations³¹. Although there is only suggestive evidence that nonhuman animals attribute mental states to one another, more detailed observations and experiments should allow us to show that nonhuman animals are not only good ethologists but also good cognitive scientists.

Lastly, it is important to recognize that predictive and intentional signaling may not generate different hypotheses regarding the outcome of an interaction and that tests of these hypotheses might lead us toward a better understanding of the evolutionary significance of using complex mental processes to guide one's behavior (see Ref. 13 for a detailed presentation of these ideas). Specifically, an individual using probabilities of expected behavior to guide behavioral decisions (i.e. predictive signaling) will be locked into a particular type of behavioral interaction (e.g. aggressive encounters with specific individuals, but not grooming interactions). In contrast, if one can attribute complex beliefs³² to others and use these to establish another individual's in-

tentions, then one escapes the constraints of having to respond to a given individual in a given context and can, instead, respond to what is generally known about individuals in the population for many different contexts¹³.

One way to bridge these perspectives would be through habituation-dishabituation experiments¹³. For example, one could cause an individual's recruitment screams to become unreliable through repeated playbacks (i.e. habituation), and then determine whether group members transfer this knowledge to another, perhaps closely related, domain such as intergroup aggression. A lack of revived response to intergroup aggression calls would imply that they had transferred knowledge about that individual's reliability as a signaler across contexts. If, on the other hand, they do respond to intergroup aggression calls, then this might suggest that their knowledge is specific to the context.

Acknowledgements

For comments on the manuscript we thank H. Dingle, P. Marler, J. Stamps, two anonymous reviewers and especially D. Cheney and R. Seyfarth. During the writing of this manuscript, MDH was supported by a NIH post-doctoral fellowship and National Geographic Society grant (with P. Marler).

References

- 1 Maynard Smith, J. (1974) *J. Theor. Biol.* 47, 209-221
- 2 Maynard Smith, J. (1979) *Proc. R. Soc. London, Ser. B* 205, 475-488
- 3 Caryl, P.G. (1979) *Behaviour* 68, 136-169
- 4 Hinde, R.A. (1981) *Anim. Behav.* 29, 535-542
- 5 Maynard Smith, J. (1982) *Evolution and the Theory of Games*, Cambridge University Press

- 6 Maynard Smith, J. (1982) *J. Theor. Biol.* 97, 1-5
- 7 Parker, G.A. (1974) *J. Theor. Biol.* 47, 223-243
- 8 van Rhijn, J.G. and Vodegel, R. (1980) *J. Theor. Biol.* 85, 623-641
- 9 Enquist, M., Plane, E. and Roed, J. (1985) *Anim. Behav.* 33, 1007-1020
- 10 Andersson, M. (1976) *Behaviour* 58, 40-77
- 11 Nelson, D.A. (1984) *Behaviour* 88, 145-189
- 12 Whiten, A. and Byrne, R. (1988) *Behav. Brain Sci.* 11, 233-273
- 13 Cheney, D.L. and Seyfarth, R.M. (1990) *How Monkeys see the World: Inside the Mind of Another Species*, University of Chicago Press
- 14 Dennett, D.C. (1983) *Behav. Brain Sci.* 6, 343-390
- 15 Struhsaker, T.T. (1967) in *Social Communication among Primates* (Altmann, S.A., ed.), pp. 281-324, University of Chicago Press
- 16 Seyfarth, R.M., Cheney, D.L. and Marler, P. (1980) *Anim. Behav.* 28, 1070-1094
- 17 Dingle, H. and Caldwell, R.L. (1969) *Behaviour* 33, 115-136
- 18 Steger, R. and Caldwell, R.L. (1983) *Science* 221, 558-560
- 19 Caldwell, R.L. (1986) in *Deception: Perspectives on Human and Nonhuman Deceit* (Mitchell, R.W. and Thompson, N.S., eds), pp. 129-145, SUNY Press
- 20 Poole, J.H. and Moss, C. (1980) *Nature* 292, 830-831
- 21 Poole, J.H. (1989) *Anim. Behav.* 37, 140-152
- 22 Poole, J.H. (1987) *Behaviour* 102, 283-316
- 23 Paton, D. (1986) *Behaviour* 99, 157-175
- 24 Cheney, D.L. and Seyfarth, R.M. (1988) *Anim. Behav.* 36, 477-486
- 25 Møller, A.P. (1988) *Ethology* 79, 25-30
- 26 Kummer, H., Dasser, V. and Hoyningen-Huene, P. (1990) *Behaviour* 112, 84-98
- 27 Cheney, D.L. and Seyfarth, R.M. (1985) *Behaviour* 94, 150-166
- 28 Marler, P., Dufty, A. and Pickert, R. (1986) *Anim. Behav.* 34, 194-198
- 29 Gyger, M. and Marler, P. (1988) *Anim. Behav.* 36, 358-365
- 30 Hauser, M.D. (1990) *Anim. Behav.* 39, 596-597
- 31 Masataka, N. (1988) *Ethology* 80, 265-273
- 32 Allen, C. and Hauser, M.D. *Philos. Sci.* (in press)
- 33 Hauser, M.D. and Wrangham, R.W. (1987) *Folia Primatol.* 48, 207-210

TREE for colleagues abroad

In some countries, the currency needed to pay for a personal subscription (US dollars or pounds sterling) is not available. If you wish to help a colleague abroad who is not able to benefit from TREE for this reason, we will accept your payment for another person's subscription. Simply complete the subscription order card bound into any issue, giving the recipient's name and address labelled 'send to'; after 'signature', give your own name and address and mark this 'bill to'. Renewal notices will be sent to your address and the recipient will receive the monthly copy of the journal. Please inform the recipient of your action.