

Lee Cronk

The application of animal signaling theory to human phenomena: some thoughts and clarifications

Abstract. Animal signaling theory has recently become popular among anthropologists as a way to study human communication. One aspect of animal signaling theory, often known as costly signaling or handicap theory, has been used particularly often. This article makes four points regarding these developments: (1) signaling theory is broader than existing studies may make it seem; (2) costly signaling theory has roots in the social as well as the biological sciences; (3) not all honest signals are costly and not all costs borne by signalers serve to ensure honesty; and (4) hard-to-fake signals are favored when the interests of broad categories of signalers and receivers conflict but the interests of individual signalers and receivers converge.

Key words. Costly signaling theory – Costly signals – Hard-to-fake signals – Honest signals – Receiver psychology – Signaling theory – Signals

Résumé. La théorie des systèmes de signaux chez l'animal est récemment devenue populaire parmi les anthropologues en tant qu'outil d'étude de la communication humaine. L'un des aspects de cette théorie, souvent connu sous le nom de théorie des systèmes de signaux coûteux, a été le plus souvent utilisé. Cet article tente de faire quatre points sur la question: (1) la théorie des systèmes de signaux chez l'animal est plus large que les études actuelles peuvent le laisser croire; (2) la théorie des systèmes de signaux coûteux prend ses racines dans les sciences sociales et les sciences biologiques;

I should like to thank Carl Bergstrom, William Irons, Beth L. Leech, Eric Alden Smith, Richard Sosis, and Robert Trivers for their comments on a draft of this article. Of course, I retain responsibility for any errors or shortcomings.

Social Science Information © 2005 SAGE Publications (London, Thousand Oaks, CA and New Delhi), 0539-0184

DOI: 10.1177/0539018405058203 Vol 44(4), pp. 603–620; 058203

(3) tous les signaux honnêtes ne sont pas nécessairement coûteux pour l'émetteur et tous les coûts supportés par l'émetteur n'ont pas nécessairement un but honnête; (4) les signaux difficiles à feindre sont favorisés dans le cas où les intérêts de larges catégories d'émetteurs et de récepteurs sont conflictuels mais où les intérêts des émetteurs et des récepteurs individuels convergent.

Mots-clés. Psychologie du récepteur – Signaux – Signaux coûteux – Signaux difficiles à feindre – Signaux honnêtes – Théorie des systèmes de signaux – Théorie des systèmes de signaux coûteux

Introduction

For nearly two decades, anthropologists have been pointing out the potential for animal signaling theory to form the basis of a rigorous, systematic, and scientific approach to human signals (e.g. Cronk, 1991a, 1991b, 1993a, 1993b, 1994a, 1994b, 1995a, 1995b, 1996, 1999, 2001, 2003, in press; Harpending et al., 1987; Kaplan, 1987). That potential is now being realized thanks to several recent field-work-based studies of human signaling systems (e.g. Bliege Bird et al., 2001; Boone, 1998; Gurven et al., 2000; Hagen and Bryant, 2003; Hawkes and Bliege, Bird 2002; Irons, 2001; Smith and Bliege Bird, 2000; Smith et al., 2003; Sosis, 2000, 2003; Sosis and Alcorta, 2003; Sosis and Bressler, 2003; Sosis and Ruffle, 2003; Strassmann, 1996; see Bliege Bird and Smith, 2005 for a recent review). However, as leading signaling theorists themselves have pointed out (e.g. Maynard Smith and Harper, 2003), terminological and theoretical confusion has slowed the development and use of animal signaling theory. The purpose of this article is to clarify a few key issues in this rapidly developing field, with particular emphasis on the application of animal signaling theory to human phenomena. It makes four main points, moving from the general to the specific:

- (1) Signaling theory is broader than existing studies may make it seem;
- (2) Costly signaling theory has roots in the social as well as the biological sciences;
- (3) Not all honest signals are costly and not all costs borne by signalers serve to ensure honesty;

- (4) Hard-to-fake signals are favored when the interests of broad categories of signalers and receivers conflict but the interests of individual signalers and receivers converge.

The breadth and variety of signaling theory

Anyone examining recent reviews of the anthropological study of human signaling systems (e.g. Alvard, 2003; Bliege Bird and Smith, 2005; Sosis and Alcorta, 2003) could be forgiven for thinking that animal signaling theory consists mostly or entirely of costly signaling theory, mostly as developed by Amotz Zahavi (1975; see also Zahavi and Zahavi, 1997). Indeed, most of this article itself deals with costly signaling theory in one way or another.

Costly signaling theory's dominance arises from its undeniable usefulness and power in explaining many human and nonhuman signals. However, it is worth taking a moment to acknowledge that animal signaling theory offers insights independent of costly signaling theory and that signals among both humans and nonhumans are often either not very costly at all or not costly for the reasons given by costly signaling theory. The reasons why natural selection might favor costly signals and the relationship between costliness and honesty will be discussed below. Here my focus is on the narrow point that signaling theory offers insights not related to costly signaling theory.

One area in which costly signaling theory has proven particularly valuable recently is the study of religious behavior (e.g. Irons, 2001; Sosis and Alcorta, 2003). Following Irons' Durkheimian suggestion that religious rituals might serve as hard-to-fake signs of commitment and thus enhance the success of some groups over others, Sosis and his colleagues have shown that religious communes tend to survive longer than secular communes (Sosis, 2003) and that a higher number of costly rituals and taboos imposed on members is associated with greater longevity of religious but not secular communes (Sosis and Bressler, 2003). Building on these findings, Sosis and Ruffle (2003) recently used an experimental game to compare the cooperation in religious and secular kibbutzim in Israel, finding that men in the religious kibbutzim tended to behave more cooperatively than men in the secular ones.

Such important findings are in no way diminished by the observation that much of the religious and moralistic signaling that goes on

in human societies does not fit the predictions of costly signaling theory. Rather, it consists of exhortations to behave or to refrain from behaving in particular ways. Such exhortations typically occur where there is at least the potential for a conflict of interests between signalers and receivers. The commonplace use of religious rhetoric by social, political, and economic elites to justify and thus perpetuate the status quo is a case in point (Cronk, 1994a, 1994b), but conflicts of interests that lead to such exhortations can also exist in relatively egalitarian societies. Common examples include public denunciations of adultery, particularly if committed by women, and admonitions to younger people to obey their elders. Such statements are important parts of human social life, but they are not necessarily costly, and even when they are costly they are not necessarily “honest” in terms of providing accurate information about the signaler. The costliness that such signals do have may be better explained by Krebs and Dawkins’ proposal (1984; see also Dawkins, 1982; Dawkins and Krebs, 1978) that conspicuous signals may help signalers to overcome receivers’ resistance to being manipulated in ways that are in the interests of the signaler but not necessarily of the receiver.

Obviously, we should expect receivers to evolve or learn to resist being manipulated in ways that are detrimental to their own interests. But for a variety of reasons there may still be a large opening for manipulative signals, particularly among humans. For example, human receivers may often lack sufficient information to accurately evaluate the truthfulness of a signal. Religious admonitions to behave in particular ways in order to avoid an unpleasant afterlife are a dramatic case in point. As Pascal pointed out, although one might find it hard to believe in supernatural beings and an afterlife, the possible cost of not believing in such things may seem so great that most receivers will choose to believe (or behave as if they believe, which to the signaler may be good enough). Similarly, the possible cost to a would-be rebel of assessing the truthfulness of a declaration by a political elite that certain types of behavior will be met by certain punishment in this life may be too great for it to be worth the risk. The ability of humans to use their signals to make claims that are difficult, risky, or even impossible to evaluate may help explain why animal signals are often so honest (Maynard Smith and Harper, 2003) while human signaling systems seem, to many observers, to be arenas for a great deal of

deception and exaggeration (e.g. Alexander, 1987; Harpending et al., 1987).

Another aspect of animal signaling theory that has been underused by those studying humans is the importance of receiver psychology to signal design. Guilford and Stamp Dawkins (1991) argued that what receivers find easy to detect, discriminate, and remember constitute major forces in the evolution of signals. Noting that male birds frequently sing from high perches and that male frogs croak in frequencies suited to the ears of female frogs, they suggested that warning displays, such as the coloration of bees and wasps, might be designed not just to be conspicuous but also to be more easily remembered. Rowe (1999) expanded this idea to include multicomponent signals, noting that signalers can increase the chance that a message is received by sending it in more than one way.

The idea that signals are designed, whether by the signalers themselves or by evolutionary processes, in order to take advantage of receiver psychology is something that researchers in the human sciences have long understood. For example, mothers around the world speak to their babies in a special singsong, high-pitched fashion that researchers have labeled “motherese” (Fernald, 1992). Motherese differs from normal speech not only in terms of rhythm and intonation but also in that sentence structure is simplified and a lot of repetition is used. Interestingly, the babies themselves seem to prefer motherese to normal speech, paying more attention to people who speak in motherese than to those who speak as they would to adults.

Toy manufacturers are also keenly aware of the importance of appealing to the psychology of potential customers. This was nicely demonstrated by Hinde and Barden’s (1985) documentation of how teddy bears have evolved since they first became popular due to an association with Teddy Roosevelt. Teddy bears started out with prominent snouts, looking something like actual bears. Over the years, however, they shifted to a more baby-like appearance, with a reduced snout and a rounder face. Because the toy bears were being designed by their manufacturers to appeal to buyers, mainly adults, this evolution appears to reflect a process of signal evolution strongly influenced by a receiver psychology that includes a preference for babyish over more mature-looking faces. Perhaps that aspect of receiver psychology is particularly prone to activation when the receiver is shopping for a gift to give a child.

Whether by deliberate design, a process of cultural evolution, or some combination of the two, religious ideas may tend to have certain characteristics because they fit better with aspects of human psychology. Boyer (1999) has argued that concepts that are minimally counterintuitive are easier for people to remember and more likely to be transmitted to others than concepts that are not counterintuitive or so counterintuitive as to seem bizarre. Thus, men who can walk on water, women who can give birth without ever having had sexual intercourse, and lamps that burn for much longer than they normally do with a given amount of fuel all violate our intuition about the categories to which they belong, but they are not so bizarre as to violate our intuition about things in general. This quality of many religious beliefs may also allow us to link Boyer's insights to the costly signaling approach to religion. Minimally counterintuitive religious beliefs often make complete sense to those who believe them while appearing to be complete nonsense to those who do not. Believers' willingness to suspend reason and to embrace beliefs that appear ridiculous to nonbelievers is itself a hard-to-fake sign of commitment to the religion and a defining feature of the boundary dividing believers from nonbelievers. Religious rituals are also clearly shaped by human psychology, being well designed for "eliciting arousal, directing attention, enhancing memory, and improving associations" (Sosis and Alcorta, 2003: 265).

When I was shopping for a car recently, a salesman said that he hoped to keep me and my wife "in the Mazda family". Given that humans evolved in societies structured around kin relationships, it is reasonable to predict that we may be susceptible to such kinship-based rhetoric even when no real kin ties exist and that signalers, including not only salesmen but also politicians, will be aware of this susceptibility. Salmon (1998) assessed the persuasive power of three different versions of a single political speech, which differed only in terms of the rhetoric used. One used kin terms such as "brothers and sisters", one used the term "friends", and one used "fellow citizens". The version using kin terminologies proved to be more persuasive than either of the other two. Of course, not all kinship-based rhetoric is persuasive to all receivers: my wife and I bought a Honda.

Signaling theory's breadth has implications for the way that evolutionary anthropologists choose how to use it. Thus far, most published studies that use animal signaling theory to shed light on

human signals begin with the observation that a particular behavior (e.g. public generosity, certain kinds of hunting and fishing, and certain religious practices) are remarkably costly for those who choose to engage in them. Costly signaling theory is then offered as a possible explanation of the behavior and tested against other possible explanations. This is simply the scientific method, and as such it is unassailable. However, the selection of phenomena for study based on their apparent costliness is vulnerable to the criticism that it stacks the deck in favor of costly signaling theory.

This criticism can be avoided by first identifying a type of signal or signals without regard to its apparent costliness and then exploring a variety of explanations, including but not limited to costly signaling theory, for its design features. An example of this approach is a study of cosmetics currently being conducted by some colleagues and me in evolutionary psychology (Cronk et al., 2003; Milroy et al., 2002; Wigington et al., 2004). We chose to study cosmetics not because of their costs but because of their ubiquity, their importance in the social lives of people in many contemporary societies, and their relevance to the study of facial attractiveness. While it is possible for women to spend a great deal of time and money on cosmetics, such costs are not related to their underlying qualities in the way predicted by costly signaling theory. Some of our preliminary findings are that while a minority of women deliberately use cosmetics to appear healthier and more attractive, most women neither seek nor achieve deceptive effects using cosmetics. We hypothesize that most women use cosmetics not to deceive but rather to make their faces more noticeable and memorable. Thus, most women's use of cosmetics may be similar to advertising campaigns that convey little information about a product but make it more memorable and draw attention away from competitors' advertisements and products.

The many sources of costly signaling theory

Although signaling theory has much else to offer, there is no denying the centrality of costly signaling theory to this rapidly developing approach. Costly signaling theory seems likely to retain its importance both because it is a relatively well developed aspect of signaling theory and because it is useful for explaining signals that, due to their costs, are prominent, interesting, and attention-grabbing.

Anthropologists, following the lead of animal behavior studies, typically trace the idea that there is a relationship between the cost of a signal and its honesty to the work of Amotz Zahavi (1975; see also Zahavi and Zahavi, 1997) despite the fact that Zahavi's idea was anticipated several different times by social scientists. The list of social scientists and their ideas that are similar to Zahavi's includes Thorstein Veblen (1899) and the idea of conspicuous consumption, Thomas Schelling (1960) and his insights about signals of commitment, Michael Spence (1973) and his theory of job market signaling, and Robert Frank (1988) and his argument that moral commitments are hard-to-fake signs of one's reliability as a cooperator. Also, Bliege Bird and Smith (2005) have pointed out similarities between costly signaling theory and both Marcel Mauss's insights on competitive gift-giving (1924) and Pierre Bourdieu's (1977) idea of social capital.

The fact that costly signaling theory is common to both the social and biological sciences is more than just a curiosity. It also highlights the generality of signal design problems, whether they are solved by engineers, advertisers, or natural selection, and creates opportunities for fruitful exchanges of insights across disciplines. For researchers working in an evolutionary framework, such borrowing is also justified by the phenotypic gambit (Grafen, 1984), which posits that, because in the long run natural selection will tend to favor adaptive phenotypes regardless of how they are inherited, related to particular genotypes, or shaped during an organism's development, it is usually a worthwhile risk to focus on phenotypes and to set aside questions about how they are inherited and their proximate, ontological, and phylogenetic causes.

The relationship between honesty and cost

Maynard Smith and Harper (2003) have recently made an attempt to clear up some of the terminological, conceptual, and theoretical confusion in animal signaling theory. Much of the confusion surrounds the relationship between honesty and cost. The emphasis on costly signaling may lead to the impression that costliness is a necessary guarantor of honesty. Although that is true in certain circumstances (see below), it is not always so. For example, when signalers and receivers have common interests, selection (or signal design principles more broadly) may favor a signal that is only as

costly as it needs to be in order to get the message across (Krebs and Dawkins, 1984; Maynard Smith and Harper, 2003). Such signals are said to have only “efficacy costs” (Guilford and Stamp Dawkins, 1991), i.e. the costs necessary to ensure that the information conveyed by the signal reaches the receiver. While efficacy costs can be substantial, they are not the sorts of costs referred to in the phrase “costly signaling theory”. Costly signaling theory is concerned, rather, with strategic costs (Grafen, 1990a, 1990b), often referred to as handicaps. Strategic costs are necessary to ensure not that information is conveyed but rather that the signal is perceived as honest. The cosmetics study mentioned above provides an example of a signaling system with the potential for high efficacy costs but without strategic costs. Although women can spend a great deal of time and money on cosmetics, those costs are not related to the qualities such as health, beauty, and youth that some women report that they are trying to convey with cosmetics.

Other signals may be honest not because they are particularly costly for the signaler but because they are simply impossible for those without the quality being signaled to successfully fake. Maynard Smith and Harper (1995, 2003) call these sorts of signals “indices”, which is related to the way that term is used in semiotics. For example, Hamilton and Zuk (1982) suggested that bare patches of skin on birds might serve as indices of their resistance to parasites, an idea supported by experiments on red jungle fowl (Zuk et al., 1992). Among humans, some markers of group membership, such as the ability to speak a specific dialect with the proper accent and complete fluency, have a similar quality of being either impossible or extraordinarily difficult to fake.

The literature on human signals also contains the category of “hard-to-fake” signals. This includes signals that are hard to fake either because they are indices or because they impose on signalers strategic costs which honest signalers can afford but which are difficult for dishonest signalers to bear. As we will see in the next section, sometimes the distinction between indices and costly signals is less important than the similarity of the circumstances in which signal design processes, including natural selection, may favor their development and maintenance. It is also sometimes helpful to avoid the word “costly” in order not to confuse strategic and efficacy costs. For both of these reasons, the “hard-to-fake” label is sometimes very useful.

Confluent interests, conflicting interests, and selection for hard-to-fake signals

One common feature of the literature on costly signaling is the idea that natural selection will favor costliness as a guarantor of signal honesty when there is a conflict of interests between signaler and receiver. A complementary idea is that when signaler and receiver have common interests, natural selection will favor expenditure on efficacy costs but none on strategic costs. In this section I argue that this understanding of the circumstances that favor costly signals and, more broadly, hard-to-fake signals is not quite right. Specifically, costly signaling theory is relevant to circumstances in which there are broad conflicts of interests between categories of signalers and receivers but *confluences* of interest – common interests that are real though they may be fleeting – between *particular* signalers and *particular* receivers.

In evolutionary terms, a conflict of interests exists between two parties when natural selection would favor a different outcome for their interaction if it were determined solely by selection on genes in one party or the other (Maynard Smith, 1991; Trivers, 1974). The complement of this is that two parties share common interests when natural selection acting on genes in both of them would favor the same outcome from their interaction. Some categories of organisms are locked in permanent and perpetual conflicts of interests. Natural selection favors prey that can escape predators and predators that capture prey. It favors males that succeed in mating with many females regardless of their own quality and females that mate with only the highest-quality males. The relationships between other categories of organisms, such as parasites and hosts and parents and offspring (Trivers, 1974), are more complex but have potential for conflicts of interests. However, even in the context of such broad and permanent conflicts of interests, particular signalers and particular receivers can have common interests. It is in these situations that hard-to-fake signals will be favored. It is the difficulty of faking them, whether because they are indices or because they are costly, that ensures their honesty in a milieu in which honesty is not expected.

Stotting, a peculiar sort of hopping behavior performed by Thomson's gazelles and some other ungulates when faced with a predator, is an example of a signal that is likely to have resulted from this evolutionary scenario. Field research has shown that the ability

to stot correlates with an organism's physical condition and may help dissuade predators from wasting time and effort in pursuit of an individual that is likely to escape capture (Caro, 1986a, 1986b, 1995; FitzGibbon and Fanshawe, 1988). While a prey species such as a gazelle and its main predators, such as African wild dogs, are certainly engaged in a long-term conflict of interests, a confluence of interests exists between an alert and physically fit gazelle that is capable of eluding a predator it spots and the predator. Natural selection would favor the same outcome from the interaction for both of them: abandonment of the pursuit. The gazelle saves the time and energy of eluding capture and the predator saves the time and energy of a failed pursuit. One might say that a conflict of interests still exists because natural selection would favor a successful hunt by the predators, but that is irrelevant. Only outcomes that are actually possible are relevant. Because the gazelle in question is alert and physically fit enough to avoid being caught, a successful hunt is so unlikely that it is not worth the predator's bother. At the beginning of the encounter, this information is possessed by the gazelle but not by the predator. Stotting is a way of transferring that information to the predator in a way designed to overcome the resistance to signals by the prey that selection has favored in it because of the broader conflict of interests between the two categories of organism. The conflict of interest in this scenario is not between an individual alert, physically fit gazelle and a specific pack of wild dogs but rather between an alert, fit gazelle and relatively inattentive, unfit gazelles in its vicinity.

A similar confluence of interests in the midst of a broader conflict of interests arises when a male that is of truly high quality relative to competing males attempts to convince a female to mate with him. Despite the broad conflict of interests between males in general and females in general, individual males and females can (and routinely do) experience confluences of interest. The male that is truly of high quality relative to competing males benefits from the encounter in an obvious way, i.e. by mating. The female benefits because she makes a good choice and mates with a male that is truly of high quality compared to other available males. Hard-to-fake signals about male quality, whether they are indices or costly signals, serve to transfer honest information about the male's quality to a female that is likely to be skeptical due to past selection against females who made poor mate choices. As in the case of predators and prey, the conflict of interests in this situation is not between

the female and the prospective male mate that is of truly high quality but rather between the high-quality male and low-quality males in its vicinity that would also like to mate with the female in question.

Such situations also arise routinely in human communication. For example, lobbyists use a variety of techniques in their efforts to influence people in government, some quiet and others elaborate (see Baumgartner and Leech, 1998). Among the more dramatic types of lobbying is a grassroots campaign, in which an interest group encourages a large number of citizens to contact their legislators directly about a particular issue. Grassroots campaigns are one form of “outside lobbying”, which contrasts with the “inside lobbying” style of personal contacts with legislators and their staffs (Kollman, 1998; Walker, 1991). Because “astroturf” campaigns – fake grassroots campaigns mounted by interest groups that lack a large number of motivated members – are costly and difficult to organize, both policy makers and political scientists see grassroots campaigns as usually being honest indicators of how voters feel about issues (Kollman, 1998). Given the reasoning presented here, we would expect to find lobbyists using grassroots campaigns when trying to influence legislators with whom they are usually at odds. Such campaigns inform legislators that, although they may usually be opposed to the positions taken by the interest group, in this particular case there is a confluence of interests between the desires of the interest group to see certain bills passed or defeated and the legislators’ desires to remain in office. This technique can be very effective. One congressional staff member explained why his boss reversed his position on catastrophic health insurance in 1990 by explaining, “It was a no-brainer. He got over five thousand letters for the repeal of the insurance, and literally eight letters in favor of the current insurance. He didn’t have much choice really. He had to vote for repeal” (quoted by Kollman, 1998: 5).

The problems faced by job applicants signaling employers are analogous to those experienced by male organisms signaling potential mates. The broad context is adversarial, but if a particular job applicant is truly of high quality then there is a confluence of interests between him or her and potential employers. The details of job market signaling were explored by Spence (1973). Following the logic presented above, the most successful applicants will be those who honestly advertise their high quality with signals that would be too costly for low-quality applicants to fake. An example

might be holding a degree with honors from an elite university (Frank, 1988: 102).

Axelrod's analysis of the live-and-let-live system during the trench warfare of the First World War, in which belligerents would develop tacit agreements to avoid killing one another, includes the observation that hard-to-fake signals were a key to the success of the system:

During the periods of mutual restraint, the enemy soldiers took pains to show each other that they could indeed retaliate if necessary. For example, German snipers showed their prowess to the British by aiming at spots on the walls of cottages and firing until they had cut a hole Likewise the artillery would often demonstrate with a few accurately aimed shots that they could do more damage if they wished. (1984: 79)

This is a clear case of a confluence of interests within a broader context of conflict leading to hard-to-fake, honest signals. Despite the fact that combatants on both sides would have preferred different outcomes for the conflict in general, they had enough common interests (e.g. short-term survival) for there to be an incentive to develop signals that overcame the conflictual milieu.¹

While I hope that I have clarified an important point, I also realize that I have barely scratched the surface of the complex relationship between signal design and the competing and convergent interests of signalers and receivers. Signaling theory is a rich source of interesting ideas about how the varying interests of signalers and receivers can influence signal design. For instance, Farrell and Rabin (1996) have shown that low-cost signals can evolve when there is a conflict of interests between signalers and receivers so long as both parties benefit enough from coordinating their actions. Silk et al. (2000) have gone beyond that by arguing that low-cost signals can evolve when there is a conflict of interests and no benefits to coordination so long as particular signalers and receivers interact repeatedly, such as in a social group, and Johnstone (1998, 2000) has pointed out that even in situations where both signalers and receivers are aware at the outset that they share broad common interests, there may be a conflict about which party will bear the costs of ensuring that a signal is reliably detected. How this conflict is resolved will determine whether the resulting signal is muted or conspicuous. Anthropologists and other social scientists wishing to apply signaling theory to human signaling systems would do well to explore these and other ideas about signal design.

Conclusion

Whether one studies humans or nonhumans, signaling theory is one of the most exciting areas in current behavioral ecology. The points made in this article are intended to make it easier for anthropologists and other social scientists to use signaling theory to shed light on human phenomena.

Lee Cronk is Associate Professor in the Department of Anthropology at Rutgers University. *Author's address:* Department of Anthropology, Rutgers University, 131 George St, New Brunswick, NJ 08901-1414, USA.
[*email:* lcronk@anthropology.rutgers.edu]

Note

1. This idea is similar to a model developed by Bradbury and Vehrencamp (2000). They examined four cases that vary in terms of whether signalers and receivers have conflicts of interest. Their Case II is a situation in which signaler and receiver disagree on the optimal action by the receiver in the absence of a signal but agree when there is a signal. They note that this describes “many situations in which receivers seek information about some trait in a sender and in the absence of signals assume the worst (from the sender’s point of view)” (2000: 264). As they explain, this appears to accurately describe the situation when a gazelle stots. In the absence of a signal, the predator will assume that the gazelle is a good choice for a pursuit. Even if the gazelle is fit enough to be able to elude the predator, this is still not the choice that is in the best interests of the gazelle because of the time, energetic cost, and risk associated with being pursued. When there is a signal, predators usually do not pursue, a choice that is in the best interests of both the individual gazelle and the predators.

References

- Alexander, R. D. (1975) “The Search for a General Theory of Behavior”, *Behavioral Science* 20: 77–100.
- Alvard, M. (2003) “The Adaptive Nature of Culture”, *Evolutionary Anthropology* 12: 136–49.
- Axelrod, R. (1984) *The Evolution of Cooperation*. New York: Basic Books.
- Baumgartner, F. R. and Leech, B. L. (1998) *Basic Interests: The Importance of Groups in Politics and Political Science*. Princeton, NJ: Princeton University Press.
- Bliege Bird, R. and Smith, E. A. (2005) “Signaling Theory, Strategic Interaction, and Symbolic Capital”, *Current Anthropology* 46(1–2): 000–000.
- Bliege Bird, R., Smith, E. A. and Bird, D. W. (2001) “The Hunting Handicap: Costly Signaling in Human Foraging Strategies”, *Behavioral Ecology and Sociobiology* 50: 9–19.

- Boone, J. L. (1998) "The Evolution of Magnanimity: When is it Better to Give than to Receive?", *Human Nature* 9(1): 1–21.
- Bourdieu, P. (1977) *Outline of a Theory of Practice*. Cambridge: Cambridge University Press.
- Boyer, P. (1999) "Cognitive Tracks of Cultural Inheritance: How Evolved Intuitive Ontology Governs Cultural Transmission", *American Anthropologist* 100(4): 876–89.
- Bradbury, J. W. and Vehrencamp, S. L. (2000) "Economic Models of Animal Communication", *Animal Behaviour* 59: 259–68.
- Caro, T. M. (1986a) "The Functions of Stotting: A Review of the Hypotheses", *Animal Behaviour* 34: 649–62.
- Caro, T. M. (1986b) "The Functions of Stotting in Thomson's Gazelles: Some Tests of the Predictions", *Animal Behaviour* 34: 663–84.
- Caro, T. M. (1995) "Pursuit-Deterrence Revisited", *Trends in Ecology and Evolution* 10: 500–3.
- Cronk, L. (1991a) "Communication as Manipulation: Implications for Biosociological Research", paper presented at the annual meetings of the American Sociological Association, Cincinnati, OH.
- Cronk, L. (1991b) "Human Behavioral Ecology", *Annual Review of Anthropology* 20: 25–53.
- Cronk, L. (1993a) "Signals, Manipulation, and Biocultural Evolution", paper presented at the annual meetings of the American Association for the Advancement of Science, Boston, MA.
- Cronk, L. (1993b) "Signals, Manipulation, and Darwinian Models of Culture", paper presented at the annual meetings of the American Anthropological Association, Washington, DC.
- Cronk, L. (1994a) "Evolutionary Theories of Morality and the Manipulative Use of Signals", *Zygon: Journal of Religion and Science* 29(1): 81–101.
- Cronk, L. (1994b) "The Use of Moralistic Statements in Social Manipulation: A Reply to Roy A. Rappaport", *Zygon: Journal of Religion and Science* 29(3): 351–5.
- Cronk, L. (1995a) "The Bathwater and the Baby: What the Culture Concept Can and Cannot Do for Human Behavioral Ecology", plenary address to the annual meeting of the Human Behavior and Evolution Society, Santa Barbara, CA.
- Cronk, L. (1995b) "Is There a Role for Culture in Human Behavioral Ecology?", *Evolution and Human Behavior* 16(3): 181–205.
- Cronk, L. (1996) "Culture, Signals, and the Creation of a Cross-Specific Behavioral Science", paper presented at the 42nd annual convention of the Southwestern Psychological Association, Houston, TX.
- Cronk, L. (1999) *That Complex Whole: Culture and the Evolution of Human Behavior*. Boulder, CO: Westview Press.
- Cronk, L. (2001) "Anthropology and the Evolutionary Study of Human Behavior", *Research in Biopolitics* 8: 1–30.
- Cronk, L. (2003) "Otics", paper presented at a conference at Stanford University, CA entitled "Toward a Scientific Concept of Culture".
- Cronk, L. (In press) "Behavioral Ecology and the Social Sciences", in J. Barkow (ed.) *Missing the Revolution: Evolutionary Psychology for Social Scientists*. Oxford: Oxford University Press.

- Cronk, L., Campbell, L., Milroy, A. and Simpson, J. A. (2002) "Cosmetics as a Signaling System", paper presented at the annual meeting of the American Anthropological Association, New Orleans, LA.
- Dawkins, R. (1982) *The Extended Phenotype: The Gene as the Unit of Selection*. Oxford: Oxford University Press.
- Dawkins, R. and Krebs, J. R. (1978) "Animal Signals: Information or Manipulation?", in J. R. Krebs and N. B. Davies (eds) *Behavioural Ecology*, pp. 282–309. Oxford: Blackwell Scientific Publications.
- Farrell, J. and Rabin, M. (1996) "Cheap Talk", *Journal of Economic Perspectives* 10: 110–18.
- Fernald, A. (1992) "Human Maternal Vocalizations to Infants as Biologically Relevant Signals: An Evolutionary Perspective", in J. Barkow, L. Cosmides and J. Tooby (eds) *The Adapted Mind*. Oxford: Oxford University Press.
- FitzGibbon, C. D. and Fanshawe, J. H. (1988) "Stotting in Thomson's Gazelle: An Honest Signal of Condition", *Behavioral Ecology and Sociobiology* 23: 69–74.
- Frank, R. H. (1988) *Passions Within Reason: The Strategic Role of Emotions*. New York: W. W. Norton.
- Grafen, A. (1984) "Natural Selection, Kin Selection and Group Selection", in J. R. Krebs and N. B. Davies (eds) *Behavioural Ecology: An Evolutionary Approach*, 2nd edn, pp. 62–84. Oxford: Blackwell Scientific Publications.
- Grafen, A. (1990a) "Biological Signals as Handicaps", *Journal of Theoretical Biology* 144: 517–46.
- Grafen, A. (1990b) "Sexual Selection Unhandicapped by the Fisher Process", *Journal of Theoretical Biology* 144: 473–516.
- Guilford, T. and Stamp Dawkins, M. (1991) "Receiver Psychology and the Evolution of Animal Signals", *Animal Behaviour* 42(1): 1–14.
- Gurven, M., Allen-Arave, W., Hill, K. and Hurtado, M. (2000) "'It's a Wonderful Life': Signaling Generosity Among the Ache of Paraguay", *Evolution and Human Behavior* 21(4): 263–82.
- Hagen, E. H. and Bryant, G. A. (2003) "Music and Dance as a Coalition Signaling System", *Human Nature* 14(1): 21–51.
- Hamilton, W. D. and Zuk, M. (1982) "Heritable True Fitness and Bright Birds: A Role for Parasites", *Science* 218: 384–7.
- Harpending, H., Draper, P. and Rogers, A. (1987) "Human Sociobiology", *Yearbook of Physical Anthropology* 30: 127–50.
- Hawkes, K. and Blige Bird, R. (2002) "Showing Off, Handicap Signaling, and the Evolution of Men's Work", *Evolutionary Anthropology* 11(2): 58–67.
- Hinde, R. A. and Barden, L. A. (1985) "The Evolution of the Teddy Bear", *Animal Behaviour* 33: 1371–3.
- Irons, W. (2001) "Religion as a Hard-to-Fake Sign of Commitment", in Randolph Nesse (ed.) *Evolution and the Capacity for Commitment*, pp. 292–309. New York: Russell Sage Foundation.
- Johnstone, R. A. (1998) "Conspiratorial Whispers and Conspicuous Displays: Games of Signal Detection", *Evolution* 52: 1554–63.
- Johnstone, R. A. (2000) "Conflicts of Interest in Signal Evolution", in Y. Espmark, T. Amundsen and G. Rosenqvist (eds) *Animal Signals: Signalling and Signal Design in Animal Communication*, pp. 465–85. Trondheim: Tapir Academic Press.
- Kaplan, H. (1987) "Human Communication and Contemporary Evolutionary Theory", *Research on Language and Social Interaction* 20: 79–139.

- Kollman, K. (1998) *Outside Lobbying: Public Opinion and Interest Group Strategies*. Princeton, NJ: Princeton University Press.
- Krebs, J. R. and Dawkins, R. (1984) "Animal Signals: Mind-Reading and Manipulation", in J. R. Krebs and N. B. Davies (eds) *Behavioural Ecology*, 2nd edn, pp. 380–402. Oxford: Blackwell Scientific Publications.
- Mauss, M. (1924) *The Gift*. London: Cohen and West.
- Maynard Smith, J. (1991) "Honest Signalling: The Sir Philip Sidney Game", *Animal Behaviour* 47: 1115–20.
- Maynard Smith, J. and Harper, D. (1995) "Animal Signals: Models and Terminology", *Journal of Theoretical Biology* 177: 305–11.
- Maynard Smith, J. and Harper, D. (2003) *Animal Signals*. Oxford: Oxford University Press.
- Milroy, A., Cronk, L., Campbell, L. and Simpson, J. A. (2002) "Health and Cosmetics: Can Female Signals of Health and Beauty be Faked by the Use of Cosmetics?", paper presented at the annual meeting of the Human Behavior and Evolution Society, Rutgers University, New Brunswick, NJ.
- Rowe, C. (1999) "Receiver Psychology and the Evolution of Multicomponent Signals", *Animal Behaviour* 58: 921–31.
- Salmon, C. (1998) "The Evocative Nature of Kin Terminology in Political Rhetoric", *Politics and the Life Sciences* 17(1): 51–7.
- Schelling, T. C. (1960) *The Strategy of Conflict*. Cambridge: Harvard University Press.
- Silk, J. B., Kaldor, E. and Boyd, R. (2000) "Cheap Talk When Interests Conflict", *Animal Behaviours* 9: 423–32.
- Smith, E. A. and Bliege Bird, R. (2000) "Turtle Hunting and Tombstone Opening. Public Generosity as Costly Signaling", *Evolution and Human Behavior* 21(4): 245–61.
- Smith, E. A., Bliege Bird, R. and Bird, D. W. (2003) "The Benefits of Costly Signaling: Meriam Turtle Hunters", *Behavioral Ecology* 14(1): 116–26.
- Sosis, R. (2000) "Costly Signaling and Torch Fishing on Ifaluk Atoll", *Evolution and Human Behavior* 21(4): 223–44.
- Sosis, R. (2003) "Why Aren't We All Hutterites? Costly Signaling Theory and Religious Behavior", *Human Nature* 14(2): 91–127.
- Sosis, R. and Alcorta, C. (2003) "Signaling, Solidarity, and the Sacred: The Evolution of Religious Behavior", *Evolutionary Anthropology* 12: 264–74.
- Sosis, R. and Bressler, E. (2003) "Cooperation and Commune Longevity: A Test of the Costly Signaling Theory of Religion", *Cross-Cultural Research* 37: 211–39.
- Sosis, R. and Ruffle, B. J. (2003) "Religious Ritual and Cooperation: Testing for a Relationship on Israeli Religious and Secular Kibbutzim", *Current Anthropology* 44(5): 713–22.
- Spence, M. (1973) "Job Market Signaling", *Quarterly Journal of Economics* 87: 355–74.
- Strassmann, B. (1996) "Menstrual Hut Visits by Dogon Women: A Hormonal Test Distinguishes Deceit from Honest Signaling", *Behavioral Ecology* 7: 304–15.
- Trivers, R. L. (1974) "Parent–Offspring Conflict", *American Zoologist* 14: 249–64.
- Veblen, T. (1899) *The Theory of the Leisure Class*. New York: Macmillan.
- Walker, J. W. (1991) *Mobilizing Interest Groups in America*. Ann Arbor: University of Michigan Press.

- Wigington, T., Campbell, L., Cronk, L., Simpson, J. A., Milroy, A. and Wilson, C. L. (2004) "Do Women's Faces Honestly Signal Long-Term Mate Quality?", paper presented at the annual meeting of the Human Behavior and Evolution Society, Free University of Berlin, Germany.
- Zahavi, A. (1975) "Mate Selection – a Selection for a Handicap", *Journal of Theoretical Biology* 53: 205–14.
- Zahavi, A. and Zahavi, A. (1997) *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. Oxford: Oxford University Press.
- Zuk, M., Ligon, J. D. and Thornhill, R. (1992) "Effects of Experimental Manipulation of Male Secondary Sex Characters on Female Mate Preference in Red Jungle Fowl", *Animal Behaviour* 44: 999–1006.