

Forum

The overlooked signaling component of nonsignaling behavior

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The handicap principle (Zahavi, 1975, 1987; Zahavi and Zahavi, 1997) is now widely used to explain the evolution of conspicuous signals such as tail ornaments, courtship displays, and nestling begging (Godfray, 1991; Grafen, 1990a,b; Johnston, 1997; Maynard Smith and Harper, 1995). The essence of the model is that signals must be costly to be honest. Females have evolved preferences for males with longer tails or brighter plumage, for example, because only males of high quality can survive and perform with handicapping ornaments. Despite the general acceptance that the handicap principle explains extravagant morphological and behavioral signals, the model's mechanism has not been broadly applied to explain a host of other behaviors. Here we suggest that the selection on animal behavior to be performed differently when observed by other animals can lead to significant quantitative changes in behavior. Although such changes in the level or intensity of a behavior may not justify calling the behavior a signal, they can evolve as signaling components to behaviors whose primary function is not signaling (i.e., they can shift the level of the behavior from its nonsignaling optimum). We call this idea the overlooked signaling component of behavior. We explore this issue using three examples: (1) prey fleeing a predator; (2) human behavior in the presence of others; and (3) parental care behavior. We then apply the overlooked signaling component to reexamine Zahavi's (1977, 1995) suggestion that altruism is a signal of social prestige. Whereas Zahavi presents his "prestige hypothesis" as an alternative to kin selection, we show how both theories can work together. We suggest that helping behavior among kin, which increases inclusive fitness, may also eventually evolve into signals of individual quality, condition or need. We conclude by suggesting ways to test for signaling components of animal behaviors.

Speed of prey fleeing a predator

An animal fleeing from a predator may use conspicuous pursuit deterrent signals. Stotting behavior in Thomson's gazelles *Gazella thomsoni* (Fitzgibbon and Fanshaw, 1988) and flight song in skylarks *Alauda arvensis* (Cresswell, 1994) are examples of behaviors used by prey animals to signal predators that they are in sufficiently good condition to avoid capture (see Hasson, 1991, for a review). Although the prey's running behavior itself is not considered a signal (Maynard Smith and Harper, 1995), running speed can provide information to the predator about capture probabilities. Speed may thus play a role in predator-prey communication. Animals fleeing from predators probably adjust their running speeds according to several factors, such as their ability to sustain speed for the expected length of pursuit, the predator's speed, and their need to conserve energy. Because individuals vary in quality, and thus in the cost they incur by running, the speed at which

they run should differ among individuals. If predators can assess capture probabilities by comparing the running speeds of different potential prey and use running speed to decide whether to begin, continue, or cease their pursuit, then the prey's optimal running speed may be selected to shift upward. Prey animals will benefit by running faster than is necessary to escape. This extra investment in running speed is what we call the signaling component of running.

Note that we do not claim that prey running speed is necessarily correlated with capture probabilities in all predator-prey systems. Nevertheless, in cases where such correlations do exist, and predators therefore benefit from selecting slow runners, a signaling component of running is expected to evolve. Hasson (1994) and Maynard Smith and Harper (1995) considered this predator-prey example and predicted a change in the prey running speed to result from the predator's attention to the prey speed. They used this example to illustrate the difficulties in defining biological signals. According to Hasson's (1994) definition, the prey's increased speed is a signal because the added cost of running faster is not balanced by improving running efficiency, but only by altering the behavior of the predators (see also Hasson, 1997, for a mathematical definition). According to Maynard Smith and Harper, on the other hand, the change in prey running speed cannot be viewed as a signal because it has no characteristics that have evolved specifically to alter the predator's behavior. They explain, for example, that although a trait such as body size could have changed as a result of its role as a source of information, only structures that emphasize size, such as manes and ruffs, can be viewed as signals (Maynard Smith and Harper, 1995). Accordingly, stotting behavior in gazelles that emphasize running ability is a signal, but the extra running speed discussed here is not. Hence, by making signal definitions more specific, cases like the change in prey running speed were left out. We suggest that in these cases the concept of signaling components may be useful.

Many models of signal evolution assume that the first step toward a signal is a trait or behavior that was not a signal initially (Krebs and Dawkins, 1984; Michod and Hasson, 1990; Rodriguez-Gironés, 1996; Rodriguez-Gironés et al., 1996; Zahavi, 1987). Our novel point is that although many traits or behaviors may never evolve into full-blown signals, they may nonetheless be shaped by a subtle signaling component. In the example of predator-prey pursuits, the signaling component may simply cause running speed to change, but the act of running does not change.

Signaling components of human behavior: performing slightly better in the presence of others

Humans commonly modify their performance of everyday activities if observed by others (or merely suspect they are observed). The amount that we alter our performance when being watched defines the signaling component of our behavior. For example, a young man who jogs daily may "optimize" his running speed according to several factors such as his ability to sustain a given speed, the risk of straining a muscle, and his motivation to improve. When he passes a group of young women, however, he might increase his running speed, improve his posture and attempt to conceal his fatigue. Although we would not claim that the man's motivation for running was to signal to the women (i.e., that jogging is a

signal), it is apparent that the women can affect the runner's speed and behavior. It is hard to tell whether such behavior still contributes to male fitness in modern society or simply reflects its evolutionary heritage. However, the logic is basically the same as in the predator-prey example: if the speed or mode of running is correlated with certain male qualities that women use for selecting potential mates (such as health or body condition), the women should use running as a source of information. When they do, the man may benefit from changing his jogging speed or behavior, thus advertising his quality and increasing his sexual attractiveness.

Humans may use their well-developed cognitive skills and self-awareness to produce signaling components. The phenomenon, however, is simple, and its evolution does not require cognitive skills. Selection can simply operate on variations in the tendency of animals to perform slightly better when they are observed. We present this human example to illustrate the ease with which one can overlook the signaling component of many common behaviors. The difficulties in detection arise because the signaling component primarily changes the magnitude of the behavior rather than its nature. However, considering the prevalence of the phenomenon in humans and its simple evolutionary mechanism, it is reasonable to expect signaling components to evolve in many aspects of behavior.

Sexually selected signaling components of parental care

The signaling component idea is especially relevant to studies that link male parental care and sexual selection. In many species, males were originally selected to perform parental chores such as nest building and offspring feeding, and a signaling component to these behaviors could have evolved subsequently. For example, courtship feeding by male birds can increase the female's clutch size (Nisbet, 1973, 1977), leading to higher fitness. But if females choose males based on their parental ability, sexual selection may favor males that can procure food at extravagant rates. Reyer (1980, 1986) implicitly assumed a signaling component to parental care when he suggested that male pied kingfishers (*Ceryle rudis*) become helpers in order to impress unrelated females with their parental ability. Evans and Burn (1996) have shown that in the wren (*Troglodytes troglodytes*), the number of nests that males build in their territories is correlated with the number of females they attract and suggested that extra investment in nest building advertises the male's quality (although, as we note below, alternative interpretations exist). In all these examples, the behavior did not evolve changes in their original function, but the optimal level of the males' performance apparently shifted as a result of its signaling effect.

In many monogamous bird species, certain males have low or even no paternity (Birkhead and Møller, 1992), yet often feed offspring at the same rates as males with complete paternity. Numerous reasons have been proposed to explain the lack of male response to lowered paternity, including the idea that a signaling component exists in male parental performance. Males that reduce their effort and allow offspring to starve in view of their mates and neighbors may suffer lower mating success in the future (Wagner, 1992; Wagner et al., 1996). This is an extension of Zahavi's idea (Carlisle and Zahavi, 1986; Zahavi, 1977, 1995) that individuals help others in cooperative groups in order to increase their prestige and thereby their direct fitness. Evidence consistent with the prestige hypothesis in a monogamous species was found in savannah sparrows *Passerculus sandwichensis*, in which males achieved paternity in the second brood in proportion to the amount they provisioned in the first brood, suggesting that females preferentially allowed fertilizations from their mates

when they performed better as parents (Freeman-Gallant, 1997). Thus, it is possible that a signaling component of chick-feeding behavior has evolved.

Extra investment in helping: reconciling kin selection and social prestige

Zahavi (1977, 1987, 1995) proposes that seemingly altruistic acts are actually costly signals of quality (i.e., handicaps) by which the performer gains social prestige. By advertising its quality to group members through the performance of costly helping behaviors, a helper might gain direct benefits (such as mate acquisition). This idea is not widely accepted as one of the major explanations of apparent altruism (Emlen, 1991; Pusey and Packer, 1997). A difficulty that many behavioral ecologists might have with the social prestige hypothesis is that Zahavi presents it as an alternative to kin selection, a theory that he rejects but that most behavioral ecologists accept. We suggest that kin selection is not inconsistent with Zahavi's prestige hypothesis and that the two models may often operate in tandem. Moreover, we suggest that the evolution of signaling components in kin-selected helping behaviors is actually expected by optimization reasoning.

Let us take for example a group of cooperatively breeding birds that are related to each other and in which helping has evolved via indirect benefits (i.e., kin selection). The level of helping performed by three helpers that are equally related to the breeding pair can be derived from Hamilton's rule; i.e., at any particular moment, helpers help when $r(b) > c$, where r = the coefficient of relatedness, b = the benefit of helping, and c = the cost of helping. Because r is equal for the three helpers, they are expected to help at the same level (or as frequently) as long as c and b are also equal. However, whereas the benefit of helping is likely to be the same in this case (because all three helpers help the same breeding pair), the cost of helping is likely to vary among the three helpers (because the performance of a certain act of helping should be easier for high-quality helpers). Individual differences in quality, therefore, should enable some helpers to help more than others. Considering this variation in the cost of helping, the optimal level of helping according to Hamilton's rule will actually differ among the three helpers and will be positively correlated with their quality (the term "quality" can be used for both genotypic or phenotypic quality, or even for phenotypic condition at the moment the help is given). Hence, a situation in which the level of help is correlated with helper quality may be common. This does not imply that the level of helping is already affected by a signaling component, but under such circumstances it has the potential to become affected. If other group members begin to use the level of helping to assess the quality of the helper and adjust their behavior toward that helper accordingly, then selection should favor the modification of the level of helping according to its value as a signal.

Why should individuals use the level of helping by other group members as a source of information? The answer is that group members are not only cooperative partners, they often are also competitors or potential mates. Having information about each other's quality would allow them to make better decisions regarding their competitive and sexual interactions within the group. Take for example two male group members who cooperatively defend a territory. By so doing, they can also appraise each other's fighting ability without engaging in costly fights with one another. Thus, information gathered in intergroup conflicts may help to settle intragroup conflicts at a lower cost. Considering that social animals frequently inspect each others' activities (Pusey and Packer, 1997) and that helping behavior such as feeding nestlings or defending a territory can easily be observed by other group members (e.g., Heinsohn

and Packer, 1995; Reyer, 1986; Zahavi, 1990), it is reasonable to expect that a mutant that uses helping behavior to assess an individual's quality or condition would have a selective advantage. We predict that when the level of helping provides visible and reliable information about individual quality, animals will eventually use it, and when they do, the level of helping will shift into a new equilibrium that is modified by a signaling component. In other words, it will become adaptive to help at higher levels than would be predicted by Hamilton's rule because helpers also benefit directly by advertising their quality to other group members. At equilibrium, even poor-quality individuals may help slightly more than predicted by Hamilton's rule in order to advertise that they are still above the lowest possible quality. In summary, the evolution of a signaling component of helping behavior can be favored in a system in which helping initially evolved via kin selection.

A complementary argument is that, whereas all social animals need some information about the quality of their group members to make decisions about competitive and sexual interactions, cooperative animals additionally need this information to optimize their level of cooperation. When helping is maintained by kin selection, the relative quality of the recipient can determine how much help should be given because the quality of this recipient has a direct effect on the benefit parameter " b " in Hamilton's rule. Consider a group of related individuals cooperating in territorial defense or in mobbing a predator. An individual will gain greater indirect benefits by helping a brother of high quality, who is likely to produce many viable offspring, than by helping a brother of lower quality (assuming that both brothers benefit equally from receiving help). Hence, when r and c are equal, donors need information about the quality of prospective recipients in order to determine b . The same logic has been applied in the context of parental investment in offspring that vary in quality (Godfray, 1995; Haig, 1990; O'Connor, 1978). Thus, just as parents choose which offspring to feed, group members must choose which relative to help. Under these circumstances, group members may benefit from advertising their quality by performing predominately nonsignaling behaviors (such as territorial defense or feeding offspring) at exaggerated levels to prove they are worthy of receiving help.

The evolution of a signaling component of helping behavior can also be favored when unrelated individuals cooperate for direct benefits (e.g., reciprocity, territory inheritance, or parental experience). Regardless of relatedness, the optimal level of helping should vary among individuals of different quality because a given level of helping is cheaper for high-quality individuals. Hence, high-quality individuals can afford to help more. Again, the level of helping has the potential to be a source of information about an individual's quality, and if used as such, will eventually be modified by a signaling component (see also Roberts, 1998, for a related discussion on the evolution of handicap-based altruism from reciprocity). In short, the evolution of a signaling component of helping behavior can be favored in systems in which helping initially evolved for either direct or indirect benefits.

Signaling components may also provide information about need

Throughout this paper we have suggested that signaling components can provide information about the quality of the individual performing a certain behavior. This idea can be extended to the signaling of need. Costly signals of need have been suggested to evolve when parents seek information about the food requirements of their offspring (Godfray, 1991), or when individuals must assess the amount of help their close kin require (Maynard Smith, 1991). In this context,

some traits or behaviors may not evolve into signals of need (like nestling begging), yet may evolve signaling components. A model by Rodriguez-Gironés (1996) has shown that sibling aggression can evolve a signaling role and shift from its non-signaling optimum into a new higher level. Initially, the aggressive behavior evolved as direct competition for food, with large chicks often killing their smaller siblings, resulting in some level of parent-offspring conflict. However, the model illustrates that the parents' best response to such aggression is to provide more food to the aggressor to prevent siblicide. As a result, large siblings were selected to exaggerate aggression, thus blackmailing their parents to give them more food. Hence, although we do not in general consider sibling aggression as a signal to the parents, the model suggests that a signaling component of chick need can greatly affect the larger sibling's level of aggression. In a similar manner, signaling components of need may also evolve in helping behavior. If helpers adjust their effort in relation to their need to participate in helping (i.e., in relation to the expected benefit a helper gains from helping), variations in the level of help may evolve to signal the helper's need or motivation to help, rather than to signal its individual quality. To date, most models treat signaling of quality and signaling of need separately, even though a combined effect of a signaler's need and quality may be inevitable in some cases. The possibility that a signal, or a signaling component, will reflect the product of both is yet to be explored.

Testing for signaling components of animal behavior

Some evidence supports the idea that there is a signaling component of parental care or helping behavior. However, the evidence is indirect and subject to alternative interpretations. For example, a correlation between feeding rates and mating success (Freeman-Gallant, 1997), might be explained by confounding variables, such as male age or phenotypic condition (Freeman-Gallant, 1997; Wright, 1998). Similarly, apparent competition for helping opportunities, which was suggested as evidence that helpers compete for signaling benefits (Carlisle and Zahavi, 1986), has been recently interpreted to be a result of a high density of helpers around the nest (Wright, 1997). Experimental manipulation of individual quality (e.g., by providing extra food or by handicapping physical performance) can test the extent to which a behavior is correlated with quality, but it cannot determine whether other individuals use it as a source of information. It will be more convincing if manipulating the presence or size of an audience will cause animals to alter their level of behavior. It might be difficult, however, to manipulate the size of the audience without affecting the need for help or the cost of helping. For example, mobbing a predator may become less dangerous as the number of group members increases.

The best and perhaps only way to test for the existence of signaling components in animal behavior is by experimentally manipulating the behavior itself. However, because signaling components may affect a trait or a behavior only in a quantitative way, a rigorous test requires several stages. First, one has to manipulate the level or intensity of the behavior and to show that other individuals respond to the change in the behavior (i.e., that they use the behavior as a source of information). This type of experimental manipulation has been applied successfully to illustrate that long tail ornaments of males attract females (Andersson, 1982; Møller, 1988). The second and more difficult stage is showing quantitatively that the observed level of performance is indeed influenced by a signaling effect (i.e., that it is influenced by the fact that other individuals use the behavior as a source of information). This stage should be followed by a detailed measurement of the

behavior's costs and benefits to test whether (1) the level or intensity of the behavior is considerably higher than could be explained by the primary function of the behavior (i.e., than could be explained without the existence of a signaling component), and (2) the level of exaggeration in the behavior is related to quality (or need), as required by a handicap mechanism. This type of experiment has been used to in some degree to study sexually selected signals. Other studies that experimentally manipulated tail ornaments were able to quantify the costs and benefits of a signal in relation to an individual's quality (Evans and Hatchwell, 1992; Evans and Thomas, 1992; Møller, 1989). The main challenge is to find practical ways to manipulate behaviors in the way we manipulate morphological traits.

Unfortunately, it is difficult to manipulate behaviors to demonstrate their hypothetical signaling effects. We need to find ways to alter the behavior of some individuals without affecting their other traits. Much originality and effort is required. However, we suspect that the reason such tests have rarely been attempted is not because they are impractical but because few researchers believe that the role of signaling components of predominately nonsignaling behaviors is worth testing. Our main motivation in writing this paper is to convince them that it is.

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