**Moral Sentiments and Material Interests**

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# 4 Costly Signaling and Cooperative Behavior

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*There is, deep down within all of us, an instinct. It's a kind of drum major instinct—a desire to be first ... We all want to be important, to surpass others, to achieve distinction, to lead the parade ... Don't give it up. Keep feeling the need for being first. But I want you to be first in love. I want you to be first in moral excellence. I want you to be first in generosity.*

(From a sermon by Dr. Martin Luther King, Jr.)

## 4.1 Introduction

The last few decades have witnessed an increasing convergence and interaction between economic and evolutionary approaches to human behavior, a trend certainly exemplified in the present volume. In this chapter, we draw on a framework we will refer to as costly signaling theory (CST) that has been elaborated more or less independently in both economics (e.g., Veblen 1899; Spence 1973) and evolutionary biology (e.g., Zahavi 1975; Grafen 1990). In keeping with the theme of the present volume, we explore the ways in which CST might illuminate strong reciprocity and other forms of cooperative behavior.[1] In contrast to most of the contributors to this volume, we argue that many of the phenomena classed as strong reciprocity (as defined in chapter 1) might be individually optimal (i.e., produce a net fitness benefit) and thus not require cultural or genetic group selection, at least not for their evolutionary origins.

This chapter is organized as follows. Section 4.2 summarizes the fundamental features of costly signaling theory, and section 4.3 outlines a game-theoretical model of cooperative behavior based on this theory. Section 4.4 discusses the conditions under which we might expect group-beneficial signaling to be favored over neutral or "selfish" signaling. We then apply these arguments to a variety of contexts in which cooperative behavior is commonly observed, and for which standard models of conditional reciprocity seem inadequate. First, we consider cases of unconditional generosity involving the provisioning of collective goods, such as public feasts or fighting on behalf of one's community. Section 4.5.5 considers the special, but crucial, case of enforcement of group-beneficial norms and punishment of those who defect from them. We then discuss ways in which CST may illuminate situations involving trust and commitment (section 4.6). In each of these sections, we present a variety of ethnographic and historical examples that illustrate the application of CST to understanding cooperative behavior. Section 4.7 offers a brief set of conclusions that both review the material presented in this chapter and suggest the areas where major questions remain.

## 4.2 Costly Signaling Theory

Costly signaling theory proposes that expensive and often seemingly arbitrary or "wasteful" behavioral or morphological traits are designed to convey honest information benefiting both signalers and observers (Zahavi 1975; Grafen 1990; Johnstone 1997). These signals reveal information about underlying qualities of the signaling individuals (or groups). By "qualities," we mean characteristics of the signaler that are of importance to observers (i.e., elements that will affect their payoffs from social interaction with the signaler), but that are directly observable only with difficulty or not at all (e.g., disease resistance, competitive ability, resource endowment, dedication to an ongoing social relationship). Readers unfamiliar with CST should note that it is relevant to a much wider range of behavioral and morphological features than are considered here (see for example Johnstone 1995; Zahavi and Zahavi 1997).

There are two key conditions required for evolutionary stability of such signaling. First, both signalers and receivers must benefit from sharing information about signaler variation in the underlying quality. The second condition is that signals impose a cost on the signaler that is linked to the quality being advertised. This link can take one of two forms: either lower-quality signalers pay higher marginal costs for signaling or they reap lower marginal benefits. These two conditions are related, since quality-dependent cost (the second condition) serves to ensure that the signal honestly advertises the relevant underlying qualities of the signaler (the first condition).



CST provides a powerful framework for explaining how honest communication can be evolutionarily stable despite the pervasive conflicts of interest generated by natural selection. When the conditions outlined above are met, honest signals will be of benefit to both signaler and observer, even when their interests overlap very little. The payoff to the observer derives from the information inferred from the signal—he or she should be able to evaluate the signaler's qualities as competitor, mate, or ally by attending to the signal rather than through more costly means of assessing the signaler's abilities, qualities, or motivations. The payoff to the signaler results from the observer's response. Note that the mutuality of interest in information sharing can exist even when in a broad sense signaler and observer have strongly opposed interests and hence incentives to engage in deceit—for example, interactions between predator and prey, or between enemy soldiers.

It bears emphasizing that the logic of CST is not based on standard conditional reciprocity (see table 4.1). For example, when we say that signal observers may use the information they have received to choose someone as a (future) ally, we are *not* proposing that this is a favor reciprocated to the signaler, any more than a peahen that chooses the peacock with the showiest tail is "paying back" the cock for having expended high signaling costs. Rather, CST explanations propose that responding to signals in a way that benefits the signaler is simply the best move the responder can make given the available information. The mere fact that a costly action (e.g., hosting an expensive feast) results in a beneficial response (e.g., an increase in social status) does not entail conditional reciprocity. It is important to keep this distinction

**Table 4.1**
Comparison of conditional reciprocity and costly signaling accounts of cooperation.

| Are features below expected with: | Conditional reciprocity? | Costly signaling? |
|---|---|---|
| Donor obtains net gain in the long run | Yes | Yes |
| Donor is paid back by recipients | Yes | Not necessarily |
| Unilateral provisioning of public good | No | Possibly |
| Donors have higher status than recipients | No | Yes |
| Requires punishment of free riders | Yes | No |
| Stability less likely with larger group size | Yes | No |

in mind when considering the special case of group-beneficial signaling.

## 4.3 Group-Beneficial Signaling

In most cases, CST is applied to contexts where the benefits in question are privately consumed (e.g., mating opportunities) and any wider social benefits absent or incidental. In principle, signaler-observer relations can range from highly cooperative to blatantly antagonistic, as in the case of prey signaling their vigor to predators (Caro 1994), or individuals or social groups competing for social dominance (Neiman 1997). The situation that concerns us here is when costly signaling ensures that competitors for various social goods (e.g., alliances, mating opportunities, leadership positions) advertise their relevant qualities honestly, thus allowing observers to discriminate amongst the signalers and make their best move (such as ally with, mate with, or defer to those signaling more often or more intensely).

Several authors (Zahavi 1977, 1995; Boone 1998; Roberts 1998; Wright 1999) have proposed that costly signaling could provide an explanation for cooperation and group-beneficial behavior. In an earlier set of papers (Bliege Bird, Smith, and Bird 2001; Smith and Bliege Bird 2000), we argued that unconditionally providing a collective good when it was otherwise not in the provider's best interest to do so could be favored if such provisioning served as a reliable signal of the provider's quality. Those who provide this group benefit, or who provide more of it (i.e., signaling more intensively), assume costs greater than their personal share of the collective good, but in doing so honestly advertise their quality as allies, mates, or competitors. This information could then alter the behavior of other group members to act (for purely selfish motives) in ways that provide positive payoffs to signalers—for example, preferring them as allies or mates, or deferring to them in competitive situations (Smith and Bliege Bird 2000).

A formal model of this proposal, framed as an $n$-player public goods game, has been developed by Gintis, Smith, and Bowles (2001); we will refer to this as the GSB model.[2] In this model, cooperation involves providing a benefit to all members of the group regardless of any reciprocation in kind. Given the public goods game payoff structure and non-repeated interactions, the unique equilibrium of this game involves universal defection as the dominant strategy, and hence individually costly cooperation could not evolve (unless there were strong group selection in its favor). Even if interactions among group members were repeated, cooperation among more than a few individuals would require implausible forms of coordination (Boyd and Richerson 1988). The GSB model is meant to apply to such cases, where conditional reciprocity is unlikely to emerge and is vulnerable to free-riding.



It seems reasonable to suppose, however, that providing the group benefit serves as an honest signal of the provider's underlying quality (as defined in section 4.2). Specifically, suppose that providing the group benefit is differentially costly as a function of the provider's quality. For simplicity, GSB assume that members of the social group come in two types, high quality and low quality. The model further assumes that every individual knows his or her own quality (but not that of others) and that any other group member has probability $p$ of being high quality (and probability $q = 1 - p$ of being low quality).

In the GSB game, each member plays two roles in any given period: signaler and responder. The signaler role takes two forms: providing the collective benefit (e.g., hosting a feast) or not providing it. The responder role consists of observing signalers (including partaking in any collective benefits they may provide) and then making a decision whether or not to interact with one of them. This interaction, like the signal, is stated in the most general terms here, but could involve such things as mate choice, coalition formation, partner choice, deference in competitive situations, and so on.

With these options, in each role a player can use one of four strategies, as listed in table 4.2. Specifically, signalers can chose to signal (provide the collective benefit) (1) always, regardless of their quality;

**Table 4.2**
Strategies in the $n$-person signaling game.

| | |
|---|---|
| Signalers: | |
| AS | = always signal, regardless of quality |
| SH | = signal only if one is high quality |
| SL | = signal only if one is low quality |
| NS | = never signal |
| Responders: | |
| AR | = always respond, whether or not signaler signals |
| RS | = respond by interacting only with a signaler who signals |
| RN | = respond by interacting only with those who do not signal |
| NR | = never respond |

or they can make signaling conditional on their type—signaling (2) only if high quality, or (3) only if low quality; or (4) decide to never signal.

Similarly, responders can interact with an individual chosen at random (1) from all the other $n - 1$ group members; (2) from the subset of other members who provided the benefit; (3) from the subset of other members who did not provide the benefit; or (4) the responder can forgo interacting with any group member in this period.

A signaling equilibrium will occur if all players chose to a) signal only if high quality, and b) respond by interacting only with those who signal. Following the labels in table 4.2, this means that all play "SH" as signalers, and "RS" as responders. To determine if this signaling equilibrium will be favored (i.e., if it will be a strict Nash equilibrium), we need to specify some assumptions about payoffs from the various strategies. First, following the standard logic of CST, we assume that high-quality individuals pay a lower cost to signal than low-quality ones and that interacting with high-quality individuals will yield a higher payoff to responders than if they interact with low-quality individuals. We also assume that any signaler who interacts with a responder will gain a positive benefit from this interaction; in the GSB model, this benefit is the same irrespective of the signaler's type and regardless of whether or not the Signaler in fact signaled (provided the collective good).[3]

These assumptions produce the payoff matrix outlined in table 4.3 (for a full explication, see Gintis, Smith, and Bowles 2001). The analytical results discussed in GSB reveal that three conditions are necessary and sufficient for honest signaling (SH, RS) to be a strict Nash equilibrium. First, the benefits of signaling must exceed its expected cost for the high-quality type. Second, the opposite must hold for low-quality types. Finally, responders must gain greater benefits from interacting with a high-quality type than with a low-quality type. Note that these conditions are essentially the minimal assumptions needed to apply a costly signaling framework.

In addition, as long as $p$ (responder's payoff from interacting with a high-quality individual) + $q$ (responder's payoff from interacting with a low-quality individual) > 0, there is a non-signaling equilibrium (NS, AR) in which no one signals and responders choose randomly from all other group members. Similarly, if the above inequality is reversed, there is a non-signaling equilibrium (NS, NR) in which no



**Table 4.3**
Payoff matrix for the $n$-person signaling game. Adapted from Gintis, Smith, and Bowles 2001. See table 4.2 for key to strategy abbreviations.

| | AR | RS | RN | NR |
|---|---|---|---|---|
| AS | $s - pc - qc'$<br>$ph + ql$ | $s/p - pc - qc'$<br>$ph + ql$ | $-pc - qc'$<br>0 | $-pc - qc'$<br>0 |
| SH | $s - pc$<br>$ph + ql$ | $s - pc$<br>$h$ | $s - pc$<br>$l$ | $-pc$<br>0 |
| SL | $s - qc'$<br>$ph + ql$ | $qs/p - qc'$<br>$l$ | $s - qc'$<br>$h$ | $-qc'$<br>0 |
| NS | $s$<br>$ph + ql$ | 0<br>0 | $s$<br>$ph + ql$ | 0<br>0 |

Note:
$s$ = signaler's payoff from interacting with a responder
$c$ = signaling cost for a high-quality type
$c'$ = signaling cost for a low-quality type
$h$ = responder's payoff from interacting with a high-quality type
$l$ = responder's payoff from interacting with a low-quality type
$p$ = proportion of $n$ group members who are high-quality types
$q = 1 - p$ = proportion of $n$ group members who are low-quality types

one signals and responders never choose interaction partners. The GSB analysis indicates that the honest signaling equilibrium will have higher payoffs than either non-signaling equilibria when, holding all other parameters of the model fixed, (a) high quality types are sufficiently rare ($p$ is small); (b) the responder's benefit from consuming the collective good provided by the Signaler is sufficiently large; (c) the advantage of interacting with high quality types is sufficiently large; and (d) the cost of signaling is sufficiently small (for high-quality types).

GSB also show that the form of signaling outlined in the previous paragraphs will proliferate when rare and be evolutionarily stable, as long as the cost of signaling is sufficiently greater for low-quality than for high-quality players, and high-quality individuals are neither too common nor too rare. The reason for the latter condition is that if high-quality individuals become too common ($p$ is very high), responders have a very high probability of interacting with such individuals even if they choose randomly, and thus those who avoid the costs of signaling will still have a high probability of being chosen for beneficial interactions. GSB provide an analysis showing that $p$ will attain an equilibrium value under a range of plausible conditions.

In summary, the $n$-player costly signaling model developed by Gintis, Smith and Bowles (2001) shows that cooperative acts can function as ordinary costly signals and be favored by selection acting on either cultural or genetic variation. Over a broad range of parameter values, honest signaling of high quality by providing collective benefits is a strict Nash equilibrium, and a large basin of attraction grants it robust evolutionary stability. The conditions for this equilibrium are simply that (a) low-quality types pay greater marginal signal costs than do high-quality types; (b) other group members benefit more from interacting with high-quality than with low-quality types; and (c) this interaction provides benefits to high-quality signalers that exceed the signaling cost.

All of these results, however, apply equally to ordinary noncooperative signals, and thus the GSB model in itself specifies only necessary, but not sufficient, conditions for understanding why cooperative signaling might be favored over other forms with equivalent individual costs and benefits. The remainder of this chapter examines this last issue, both theoretically and empirically.

## 4.4 Why Group-Beneficial Signaling?

Honest signaling of quality need not be beneficial to the signaler's group. Indeed, the GSB model applies equally well to socially neutral or harmful forms of costly signaling. This raises the question of why costly signaling should ever take the form of providing collective goods. After all, in other species such signaling generally involves displays such as peacock's tails, roaring contests between red deer, or ritualized struggles between male elephant seals, which provide no overall group benefits. Furthermore, there appear to be numerous human examples of such socially wasteful displays: foot-binding, headhunting, various forms of conspicuous consumption, duels, violent brawling, and even the conspicuous flouting of social norms.

We can think of three possible answers to this question. One—invoking group selection among alternative evolutionarily stable equilibria (Boyd and Richerson 1990)—will be discussed briefly in a later section of this chapter. First, we explore two other explanations in greater detail, one involving the superiority of collective goods in attracting a larger audience and the other proposing that such provisioning is a superior signal of group-beneficial qualities (i.e., that cooperation is an intrinsic element of the qualities being signaled).



### 4.4.1 Broadcast Efficiency and Signal Escalation

Because signals evolve not only to convey honest information, but also to attract the attention of observers, advertising levels can escalate as a result of competition among signalers over such attention (Arak and Enquist 1995; Guilford and Dawkins 1993). Signal design may thus be directly related to competition over observer attention. This process could transform a socially neutral signal, such as an individual showing off his skill by spearing a few small fish, into a socially beneficial one, such as investing in construction of a stone fish weir allowing hundreds of kilograms of fish to be caught and shared throughout the community. Providing larger amounts of food than a competitor for "no-strings-attached" public consumption will tend to attract more attention from more observers (Hawkes 1993). This argument could easily be generalized to a wide range of public goods and corresponding appetites.

Put another way, one of the advantages *to the signaler* of providing a collective good over some more "wasteful" display of handicap may lie in the broadcast efficiency of the signal (Smith and Bliege Bird 2000). By "broadcast efficiency," we mean the number of observers attracted per unit of signaling effort. A man who expends a given amount of energy and risk in fighting with his neighbor might broadcast his abilities to far fewer people than one who assumes the same costs in publicly defending his village against an attack. We would expect individuals to take advantage of any means for increasing broadcast efficiency when they can benefit from increasing the number of observers and thus to signal by providing collective goods if doing so has such an effect. Furthermore, we expect that competition among such signalers will often result in increasing quantities of collective goods being provided to attract larger audiences (up to some equilibrium level, of course).

Grafen (1990) has modeled the role of differential quality in setting levels of competition in costly signaling games. His analysis indicates that as differences among competitors become more acute (e.g., as the differences in quality between the best and worst males increases), the level of advertising effort among all competitors increases correspondingly. Individuals near the low end invest heavily in advertising to distinguish themselves from slightly worse males; those of higher quality have no choice but to increase their effort to outdo those below them. This effect will be strongest when there are many competitors, especially if quality is continuously varying, rather than discrete. For example, male frogs will call more frequently and produce calls of longer duration when the number or density of competitive callers increases (Wells 1988). Levels of advertising tend to spiral upward under these conditions, in an arms race to outdo one's competitors.

Note that this broadcast efficiency argument does not reduce to saying that signalers gain benefits by providing goods that attract an audience. For CST to apply, there must also be a relation between the signal (in this case, the goods used to attract an audience) and variation in the underlying qualities being signaled. If signaling were simply a matter of attracting audiences by supplying collective goods, we would expect that quantity of goods supplied would be the only relevant dimension. Yet this fails to account for observations that only certain resources—and often relatively scarce ones at that—are provided for public consumption. The argument we are making here is that certain types of collective goods yield greater signal value per unit produced because they reveal relevant underlying qualities of the signaler. Resources that are more sensitive to marginal differences in levels of skill, strength, knowledge, or leadership will allow observers to discriminate amongst competing signalers in terms of these qualities more effectively.

For example, in a foraging economy, large game (e.g., marine turtles) is usually harder to locate and capture than smaller, more abundant game (e.g., sardines) or most plant resources. When the amount of a resource harvested does not reflect differences in underlying quality, the marginal payoff to the signaler of harvesting enough to provide a public good might not be high enough to justify the increased labor costs. In addition, if observers are interested in qualities such as skill or dedication, harvests of gathered resources or low-variance game should generally attract a smaller audience than an equivalent amount of a more challenging resource that does facilitate such discrimination. This would further increase the difference in payoff to the signaler of producing and providing quality-correlated collective goods versus other resources. This may explain why the marine foragers we have studied (see section 4.5.3) voluntarily assume higher labor costs and failure rates to provision a feast with 50 kilograms of turtle meat, rather than providing 50 kilograms of sardines with greater reliability and at lower labor costs.

### 4.4.2 Signaling Cooperative Qualities

Ordinarily, CST views signals as "indicator traits" of underlying qualities, with simply a contingent connection between signal and quality.



Thus, a signal such as a peacock's tail is an indicator of male vigor and hence (on average) genetic quality; only those cocks who are vigorous, disease-resistant, and excellent foragers can afford the cost of producing, maintaining, and dragging around a heavy and showy tail (Petrie 1994). But any trait that reliably indicated genetic quality would serve as well; there is no inherent reason that peahens should favor showy tails over some other equally reliable indicator. However, signal observers may value cooperative traits in themselves. Consequently, such traits may have intrinsic value to observers that extends beyond their role as indicator traits.

We can expect that responders will prefer signals that provide a collective good worth $G$ over some equally informative signal that provides no collective good because, in addition to the gains from the information transferred in the signal, each of the $n$ responders' payoffs will also be increased by $G/n$. Note, however, that this responder preference will not be enough to favor group-beneficial signaling if (as assumed earlier in this chapter) the interaction is a one-shot game, and all group members receive a share of the collective good whether they ally with the signaler producing it or not. In a more realistic model, however, group-beneficial signals may enhance the signaler's value to a potential ally because they strongly predict the signaler's ability to produce such signals in the future. For instance an individual who punishes wrongdoers within the group has honestly signaled his ability to also punish enemies of the political alliances of which he is part. Similarly, one who harvests surplus resources and generously shares them with others rather than conspicuously consuming them personally has honestly signaled his ability to do the same with an ally or mate. In both cases, we are proposing that a high-quality individual is more likely to provide the social benefit because the cost of doing so is lower than the cost for a low-quality one. The quality being signaled might be anything that lowers the cost of behaving in a cooperative manner, such as superior strength or greater foraging skills.

The important point here is that the potential ally may prefer not just good indicator traits, but ones that will provide additional benefits to him or her. In many cases, group-beneficial signals will be more likely to have this quality than other types of signals. Note that this explanation, like the broadcast efficiency one in the previous section, relies solely on individual advantages (to signaler and to observer) of group-beneficial signaling; it is based on mutualism rather than altruism and thus provides an alternative to both reciprocal altruism and strong reciprocity.

## 4.5 Signaling and Collective Action

### 4.5.1 The Problem of Collective Goods

Generosity—such phenomena as sharing food outside the immediate family, giving gifts, hosting public events, or helping neighbors in need, all at some cost to one's self—seems to be a ubiquitous cross-cultural feature of human social life. But generosity is not universally nor randomly extended. Instead, it appears to be strategic—the contexts in which such acts occur, as well as the characteristics of donors and recipients, seem to be highly constrained and patterned. Some of this variability may be adaptive and therefore explicable using theory from evolutionary ecology. Such explanations have most frequently been framed in terms of conditional reciprocity, involving such concepts as reciprocal altruism, tit-for-tat, iterated Prisoner's Dilemma, and the like (Trivers 1971; Axelrod and Hamilton 1981; Cosmides and Tooby 1989). Others have argued that sharing or other forms of putative generosity are due to coercion on the part of recipients and hence are a form of "tolerated theft" (Blurton Jones 1984; Hawkes 1992). CST provides a third explanation, involving mutualism rather than reciprocity or coercion (Dugatkin 1997), although as we will argue, these need not be mutually exclusive and indeed can work in concert.

One classic example of public generosity is the widespread practice among hunter-gatherers of sharing individually harvested resources with nonkin. This practice is commonly explained as a means of reducing the risk associated with acquiring productive but highly variable resources such as big game (Smith 1988). Pooling individually harvested resources smoothes out consumption variance for all participants, a considerable benefit when harvests are so unpredictable that individual hunters can expect many days or weeks to elapse between successes (Winterhalder 1990). While risk-reduction effects are plausible and can be demonstrated to exist (Cashdan 1985; Kaplan, Hill, and Hurtado 1990), these effects might be an outcome rather than a cause of food-sharing. Sharing in order to reduce consumption variance involves a Prisoner's Dilemma payoff structure (Smith and Boyd 1990) and thus creates incentives to slack off and free-ride on the efforts of others (Blurton Jones 1986; Hawkes 1993). This insight has led to an active debate about how to explain the undisputed fact of extensive food-sharing by hunter-gatherers (Winterhalder 1996).

We believe that while conditional reciprocity may explain some cases of hunter-gatherer food sharing, it cannot explain them all. When all



group members have rights to consume the resource regardless of their past contribution, and the number partaking is dozens or more, the conditions for conditional reciprocity are not met (Hawkes 1992). Such lack of contingency (failure to direct shares so as to repay debts or create indebtedness) occurs where there are strong social norms governing the distribution of shares and when resources are distributed to individuals regardless of whether they ever repay the donor. This situation applies most obviously in public ceremonial contexts such as funerary rites (Smith and Bliege Bird 2000), big-man feasting (Wiessner and Schiefenhövel 1995), Northwest Coast Indian potlatching (Boone 1998), or charity galas in capitalist society (Veblen 1899). Here, generosity takes place within a broad social arena, and resources are distributed as a collective good simultaneously to large numbers of recipients. The generous individual cannot ensure that the targets of his generosity will return the favor. If sharing or generosity cannot be made contingent upon reciprocation, then the fundamental condition for evolutionarily stable reciprocity is absent.

Lack of attention to a recipient's past history or future probability of reciprocating has been described as part of food sharing patterns in many hunter-gatherer societies, such as the Ache Indians of the Paraguayan forest (Kaplan and Hill 1985a), and the Hadza of the East African savanna (Hawkes 1993). In these cases (and others), at least some types of harvested resources are shared unconditionally with most or all members of the community, and some hunters consistently provide more than others while sharing more or less equally in the catch. These "altruistic" providers in fact enjoy higher social status and reproductive success than their less productive peers, despite the absence of any conditional exchange of "meat for mates" (Kaplan and Hill 1985b; Marlowe 2000; Bliege Bird, Smith, and Bird 2001; Smith in press). Enhanced reputations, social status, and its subsequent mating advantages could be the "selective incentive" (Olson 1965) that motivates certain individuals to provide collective goods. But why should recipients reward generous providers with high status? Is this not just another form of reciprocity? If so, we would seem to have solved one collective action problem by posing another (Smith 1993).

### 4.5.2 Is "Indirect Reciprocity" a Solution?

Early social theorists analyzing public generosity interpreted some of its many forms as an outgrowth of social competition, a rivalry in divesting oneself of goods where the most generous individual gains the highest prestige, and the recipients of goods gain material benefit at the expense of their reputations (Veblen 1899; Mauss 1926; Fried 1967). Recently, behavioral biologists have begun to modify models of reciprocal altruism to account for reputation enhancement and status benefits associated with giving, what Alexander (1987, 85) termed "indirect reciprocity." Indirect reciprocity, in Alexander's scheme, results when "the return explicitly comes from someone other than the recipient of the original beneficence."

Nowak and Sigmund (1998) proposed that the benefit gained from advertising one's cooperative tendencies through costly acts of altruism is the increased chance of becoming the recipient of another's altruistic act at a later date. They constructed computer simulations in which one of a pair of players could choose whether or not to donate help based on the potential recipient's behavior in previous pairings with others, as measured in their "image score." While their simulation showed that reputations did matter in choosing partners, others have demonstrated that the particular form by which the "image score" is instantiated in Nowak and Sigmund's analysis is not evolutionarily stable (Leimar and Hammerstein 2001). However, a related form of indirect reciprocity, the "standing strategy" (Sugden 1986), can both invade a noncooperative population and resist invasion by other strategies, even when errors and incomplete information are allowed (Panchanathan and Boyd 2003).

While this work illuminates theoretical possibilities, it will take empirical research to determine if altruists are indeed preferred targets of the altruism of third parties. For example, experiments conducted by Wedekind and Milinski (2000) showed that those who were more generous in dyadic semi-anonymous interactions received more donations in return, which the experimenters interpret as support for the "image scoring" version of indirect reciprocity. However, the more generous players preferred to give indiscriminately, rewarding the generous and stingy alike. This is precisely the behavior one would predict if generosity were a costly signal of the ability to donate resources. Milinski, Semmann, and Krambeck (2002) report experimental results showing that players who donated more to a charity (information which was known to other players in the game) received both more aid from fellow players in an indirect reciprocity game and more votes for election to a student organization. As the authors note (p. 883), "Donating to those who are in need might serve as an honest and efficient (because it is done in public) signal for one's reciprocity reliability."



Boyd and Richerson (1989) also modeled indirect reciprocity and concluded that strategies based on the principle "be nice to people who are nice to others" were relatively successful. However, they and others have noted that the evolutionary stability of indirect reciprocity is likely only in small groups, where there is some way of keeping score of one's giving and receiving and of targeting cooperation conditionally at reciprocators—precisely the same limitations faced in direct conditional reciprocity. Roberts (1998) proposed a solution to this problem by arguing that reputation could be an indirect benefit of altruistic behavior if interactions are modeled in two stages: (1) an assessment stage, in which individuals establish reputations for generosity through public and non-reciprocal displays; and (2) a subsequent stage involving dyadic interactions, where individuals choose a cooperating partner based on reputations previously established. Like Milinski et al., Roberts is thus proposing essentially a costly signaling argument, where the key function of establishing reputations through costly public displays of altruism is to facilitate trust in dyadic partnerships.

While "indirect reciprocity" models tend to focus on benefits gained through subsequent pair-wise cooperative interactions following display, CST helps us see that these may not be necessary in order for both signalers and observers to benefit. As we have pointed out (Smith and Bliege Bird 2000), observers might respond to signals by subsequently avoiding the signaler altogether, in much the same way as red deer roaring provides a way for competitors to evaluate the probability of winning a fight without actually risking injury (Clutton-Brock and Albon 1979). Indirect reciprocity explanations also overlook the possibility that there may be benefits gained simply as a function of the display, both by those who display and those who observe.

### 4.5.3 The Costly Signaling Solution: An Ethnographic Example

Meriam turtle hunting provides an interesting test of the ability of CST to explain seemingly inefficient (and costly) foraging and food distribution patterns (Smith and Bliege Bird 2000; Bliege Bird, Smith, and Bird 2001). There are two primary types of marine turtle acquisition on Mer (an island in Torres Strait, northern Australia)—hunting and collecting. Turtle hunting occurs primarily in the context of public feasting events; hunters choose to hunt in response to a request from feast organizers to provide turtles for consumption at a previously announced feast. Among Meriam turtle hunters, there are three distinct roles: hunt leader, jumper, and driver. In addition, turtles are also collected, primarily in the context of household provisioning, but also for feasts, by men of all ages, women, and children. This occurs only when they can be harvested on beaches during the nesting season (October through April).

Hunting turtles is a competitive pursuit, with a very different complement of participants than collecting. As the Meriam put it, "*Anyone* can collect turtle in the nesting season, but only certain men have the ability to succeed at turtle hunting." Compared to collecting, hunting is more costly (in terms of time, energy, and risk), provides meat less efficiently (due to higher travel, search, and pursuit costs), and is associated with wider distributions of meat (figure 4.1). Hunters keep no meat for themselves, except in the rare occasion when they are hunting for household consumption, in which case they still keep less and share more than turtle collectors. Hunters take on a variety of costs for which they are not materially compensated, including time and energy

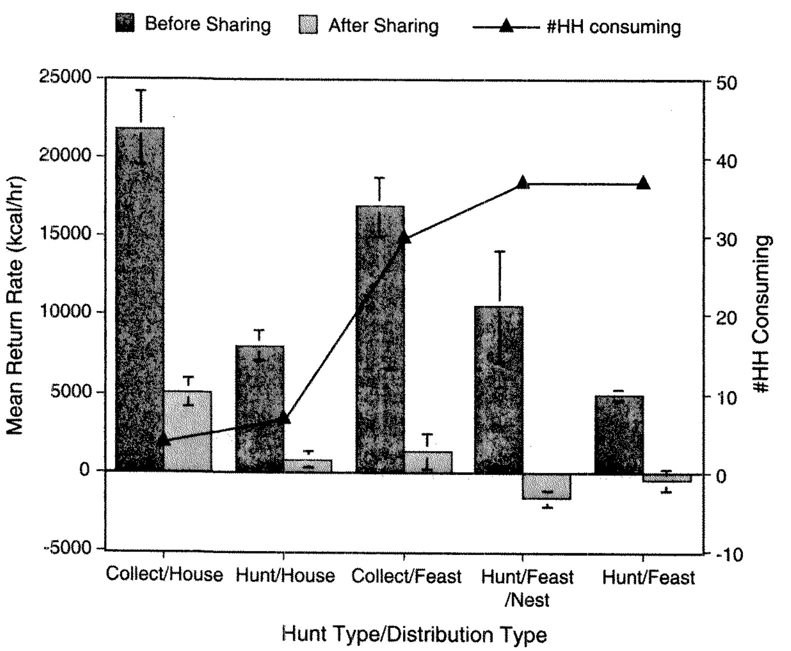



**Figure 4.1**
Meriam turtle hunting versus collecting returns before and after sharing, and number of households consuming for each hunt/distribution type.



in hunting, money for fuel, and time organizing and preparing the hunting team and its equipment prior to the hunt. The ability to bear such costs appears to be linked to hunter quality: because a hunt leader is an organizer and decision-maker, his abilities peak as he gains skill and experience. The signals sent by hunting also are efficiently broadcast: hunts are associated with larger numbers of consumers and thus attract a broader audience than collections during the nesting season and during household consumption events (figure 4.1). When quizzed, most feast-goers (audience members) know the identity of hunters, while the identity of jumpers seems to be common knowledge only among their own peer group of young males.

The benefits hunters receive from generously providing turtle for public consumption do not appear to come in the form of increased shares of collected turtle or other foods, as we might predict if risk reduction reciprocity were structuring the payoffs for hunting (Bliege Bird et al. 2002). Those who acquire turtle (both hunted and collected) more frequently and share more widely (figure 4.2) or acquire turtle in greater quantity (figure 4.3) do not receive turtle more frequently as compared to those who share less or not at all. In addition, generous turtle sharing does not appear to be repaid through receiving shares of fish or other foods (figure 4.4).

The CS explanation of collective goods provisioning as applied to the Meriam turtle hunting case proposes that turtle hunters benefit from unconditional sharing because their harvesting success sends honest signals about their quality to the community in which they will

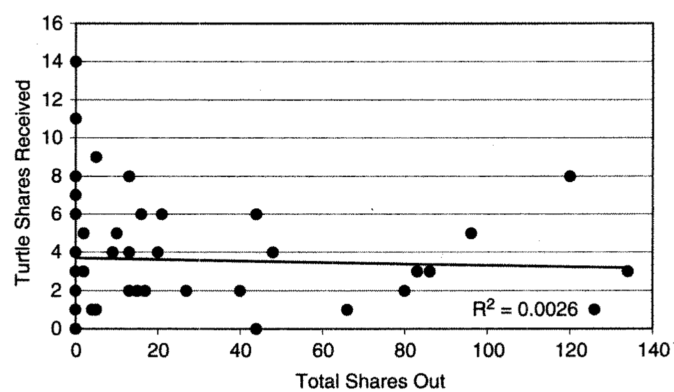
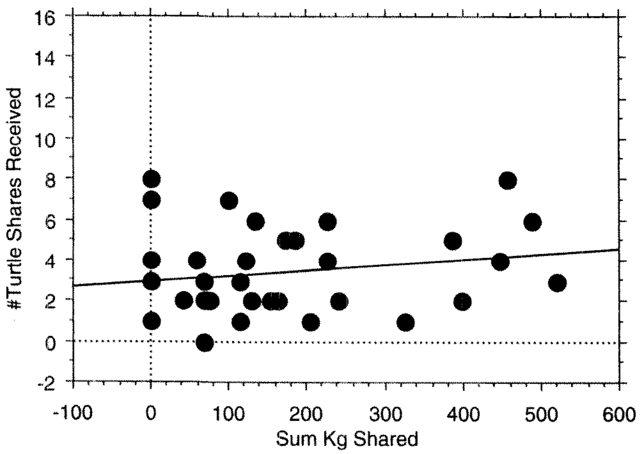



**Figure 4.2**
Do those who give turtle to more households receive turtle more frequently?




Y = 2.978 + .003 * X; $R^2$ = .037

**Regression Coefficients**
**#Turtle Shares Received vs. Sum Kg Shared**

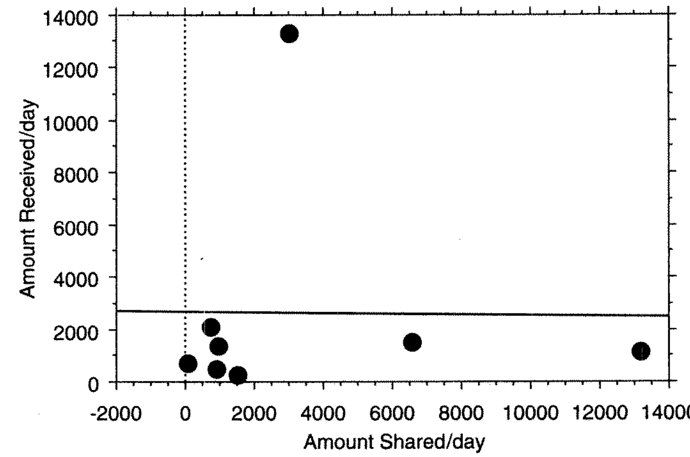
| | Coefficient | Std. Error | Std. Coeff. | t-Value | P-Value |
|---|---|---|---|---|---|
| Intercept | 2.978 | .541 | 2.978 | 5.506 | <.0001 |
| Sum Kg Sh | .003 | .002 | .192 | 1.127 | .2680 |

**Figure 4.3**
Do those who share more kilograms of turtle receive more frequently?

play out their lives as mates, allies, and competitors. Paying attention to such signals can benefit observers because the costs and potential for complete failure inherent in the signal guarantee that it is an honest measure of the underlying qualities at issue. Only those endowed with the necessary skills will succeed and be asked to serve regularly on crews or as hunt leaders. The benefits accruing to signalers (hunters) will depend upon the specific signal and audience. For hunt leaders, they might consist of being deferred to by elders or obtaining benefits of a hard working wife's labor (Smith, Bliege Bird, and Bird 2003). For jumpers, they might include a means of establishing social dominance among peers and hence preferential access to various social resources, including enhanced mating opportunities.

Interestingly, the Meriam themselves interpret unconditional generosity such as donating turtles to feasts or sharing collected turtles with neighbors as different from conditional reciprocity (which also has a






Y = 2657.796 - .012 * X; $R^2 = 1.39 * 10^{-4}$

**Regression Coefficients**
**Amt Rec/day vs. Amt Sh/day**

| | Coefficient | Std. Error | Std. Coeff. | t-Value | P-Value |
|---|---|---|---|---|---|
| Intercept | 2657.796 | 2139.059 | 2657.796 | 1.243 | .2604 |
| Amt Sh/day | -.012 | .399 | -.012 | -.029 | .9779 |

**Figure 4.4**
Do those who share more food receive more food?

place in their social and economic lives). The Meriam conception of generosity involves reference to a concept called "*debe tonar*," which means "the good way." *Debe tonar* is a set of principles for everyday social interactions, and adhering to those principles is considered a signal of Meriam identity. Following *debe tonar* is said to provide long-term benefits in the form of an enhanced social reputation as a "good person." Subsistence decisions intersect with that aspect of *debe tonar* that incorporates generosity with food. There are strong social sanctions against conditional or contingent sharing of "table food" (*derapeili*—to share portions out) between households following the harvesting of wild or cultivated foods. Similarly, there are social norms governing the provisioning of food to feasts: such foods are explicitly designated public goods (*kies*), open to unconditional consumption. *Debe tonar* states that such unconditional sharing is its own reward; to share with the expectation of a return in kind is to share selfishly, and to return a portion given freely is to imply that the giver had selfish motives. A Meriam adage goes, "When you expect payment back, you do not *esak gem blo em*" (make an lasting impression). Sharing selfishly is equivalent to not sharing at all: both are referred to as being *"gobar,"* greedy with food. While *derapeili* and *kies* sharing are explicitly unconditional, there are conditional sharing contexts within which reciprocal exchange is considered proper: markets (*tama*), labor exchange/work party feasts (*irapu*), ceremonial exchange partners (*wauri tebud*), and repayments (*bodomelam*) for use-rights to certain individually or corporately owned items (land, foraging areas, boats, or tools).

### 4.5.4 Why Does Crowding Out Occur?

As discussed in chapter 1 and elsewhere in this volume, it often happens that voluntary contributions to a public good will decrease when such contribution is supplemented or replaced by direct material incentives (e.g., payments to blood donors). The costly signaling framework can be used to generate the hypothesis that this "crowding out" may be due to a dilution of signaling value. If the social value of donating blood is cheapened by an increased supply from sellers or if blood donation might be conflated with blood selling, the signaling value of donating is likely to fall, perhaps sufficiently to lie below the donation cost for many former donors.

We are not arguing that all examples of "crowding out" can be explained by costly signaling processes, nor that we are certain that some can be so explained. However, it appears to be a plausible hypothesis, supported by a formal model and empirically testable under the right circumstances. The alternative explanations in terms of strong reciprocity and histories of group selection proposed elsewhere in this volume are equally testable, but it appears in most cases that the data to distinguish between the explanatory efficacy of the two explanations are lacking.

### 4.5.5 Signaling and Group-Beneficial Enforcement

Another type of collective good that may be a form of costly signaling involves punishing those who free-ride on the group's cooperative activities or otherwise violate group-beneficial norms. It is well known that although enforcing cooperation by punishing defectors will solve collective action problems, such enforcement is costly to those who carry out the enforcement and is itself a collective good, thus posing



a second-order collective action problem (Hardin 1982)—albeit a less demanding one at the cooperative (low–enforcement-frequency) equilibrium (Boyd et al. 2003). Boyd and Richerson (1992) demonstrated that if enforcement takes the form of punishing both noncooperators and nonpunishers, then cooperation (or anything else) can be evolutionarily stable, even in large groups and even if enforcement is only carried out by a small fraction of the group's members. Such enforcement may be a potent element in stabilizing cooperation in many types of social systems (Clutton-Brock and Parker 1995; Frank 1995; Richerson and Boyd 1998; chapter 7 in this volume).

Note, however, that enforcement can serve as a costly signal in its own right, as long as the costs of enforcement are quality-dependent. If the qualities that make one a good (low-cost) enforcer also make one attractive as a potential ally or someone it will pay to defer to in other contexts, enforcement costs can be recouped by signaling benefits. This costly signaling dynamic can then provide a private benefit to the enforcer and thus in principle solve the second-order collective action problem. The GSB model provides one mechanism for the evolution of such a system. In this version, enforcement—punishment of noncooperators—is itself the behavior that signals high quality. This model readily allows such punishment or enforcement to serve as the costly signal and hence to be maintained when the conditions for evolutionary stability specified in the model are met.

Here is a brief account to show how the model captures this form of signaling (adapted from Gintis, Smith, and Bowles 2001). Suppose that a group of $n$ members can cooperate to provide some collective good. By cooperating, each member contributes a total benefit of $\gamma$ to others at a fitness cost of $\delta$ to himself. Thus, the gain from defecting is $\delta$, and to prevent this, members must be punished at least $\delta$ for defecting. Now suppose that a high-quality individual can impose $\delta$ on defectors at a personal cost of $c$, whereas a low-quality individual must incur cost $c' > c$ to achieve the same effect. Following the model summarized in section 4.3, under the range of parameter values noted, there will be an equilibrium in which high-quality individuals will punish and low-quality ones will not. In turn, observers will benefit by using such punishment behavior as a signal of underlying qualities that will provide useful information for future social interactions. And of course, all group members will benefit from the effect of punishment in enforcing cooperation in collective action. To our knowledge, this argument has not been directly applied to any empirical cases of group-beneficial punishment. However, it does seem to be consistent with a variety of ethnographic observations (e.g., Boehm 1999, chapter 5 of this volume).

A common observation that can be experimentally replicated (see chapter 5 of this volume), is that in many circumstances people enforce a norm of fairness or equity. Of course, the specific meaning of "fairness" is culturally variable and often highly contested within any given culture or society (compare the arguments of U.S. Democratic versus Republican lawmakers on tax policy, for example). Nevertheless, even if subject to conflicting interpretations and strategies of deception and manipulation, enforcement of fairness or redistributive equity in division of the social product is a pervasive feature of human social life (see various chapters of the present volume for evidence and discussion). While models of strong reciprocity (chapter 6) and conditional reciprocity (chapter 3) offer plausible hypotheses to explain this phenomenon, in the spirit of theoretical pluralism we want to sketch how CST might have something to contribute to this topic.

In brief, we suggest that fairness norms allow assessment of the ability (or willingness) of individuals or coalitions to "pay their share"—that is, to pay the cost that ensures signal reliability. This could apply equally (but with different forms and signaling details) to both egalitarian systems—where fairness means contributing equally—and to hierarchical systems—where some are allowed to possess more wealth and power than others but are expected to contribute to the common good (e.g., hosting ceremonial events) according to their greater abilities. In either case, norms that require members of a collective to donate their surplus to have-nots (Boone 1998) or to contribute equally to production of a public good could be motivated by signaling concerns.

Given this multiplicity of social contexts and underlying qualities being signaled, failure to pay one's share could have one of several distinct meanings and consequences, including:

1) inability to do so (a signal of low quality, leading to reduced social status),

2) defection from the game (a decision to withdraw from a given arena of status competition), and

3) flaunting the norm (a signal of social power or superior status, reliable to the extent that norm violation is more costly than simply "paying one's share," and hence not viable for low-status or subordinate individuals).



Thus, we suggest that the meaning of fairness-norm violations must be interpreted in light of contextual information. In any case, the CS framework suggests that attention must be paid to the information value of fairness norms, and that enforcement of these norms may be aimed at ensuring signal reliability and solving status-competition games as much as (or more than) ensuring equity *per se*.

### 4.5.6 Signaling and Inter-Group Conflict

A related set of phenomena involve individually costly contributions to violent conflict between social groups. Participating in group raiding or defense is common among chimpanzees as well as human societies (Boehm 1992; Manson and Wrangham 1991), yet this kind of activity poses some thorny challenges to evolutionary analysis. Such behavior provides benefits that are available to all group members and cannot be hoarded or individually consumed, and therefore approach the classic definition of a pure public good. Yet the costs to contributors can be extraordinarily high (including of course death), which means that the payoffs to free-riding should be considerable. Some have argued that the widespread occurrence of organized intergroup violence thus can only be explained as the result of a history of genetic group selection (Alexander 1979, 1987; Hamilton 1975; Eibl-Eibesfeldt 1982). Others suggest that group selection acting on *cultural* variation could be responsible for favoring self-sacrificial aspects of intergroup conflict (Peoples 1982; Richerson and Boyd 1998; chapter 7 of this volume). CST offers a possible alternative to both of these views, with participation in group military defense and offense serving as a display of underlying qualities useful for status competition within one's group.

The evidence that military contribution and self-sacrificial bravery is a primary avenue to male status enhancement in small-scale societies is substantial (Chagnon 1990; Otterbein 1970; Patton 2000). It is easy to see that status enhancement may ensure the spread of even dangerous status-enhancing behavior if it has sufficient benefits to material, reproductive, or cultural success. The key question, as we saw with the issue of unconditional generosity, is *why* others grant such status to warriors. The CS explanation is that success in warfare signals underlying qualities that are valued by prospective allies and deferred to by prospective competitors. In turn, females may mate preferentially with successful warriors (Chagnon 1988) because they benefit from the social dominance of such individuals, even if the particular qualities signaled are not of direct benefit to a spouse.

The group-level benefits of status-seeking by warriors is thus incidental to the CS explanation, and indeed the CS dynamic could produce an oversupply of military adventuring as well as an undersupply of dedicated warriors. We read the ethnographic and historical record as providing ample evidence of both (e.g., Boone 1983; Keeley 1996; Mesquida and Wiener 1996; Otterbein 1970). Of course, CS dynamics could work in concert with multilevel selection of either genetic or cultural variation. For example, depending on initial conditions, CS might yield a variety of equilibria in the intensity of intergroup conflict, and those equilibria that happen to optimize the supply of belligerence (as measured by enhanced persistence and/or spread of the social group) would then be favored. This would be an example of the process of group selection among alternative local equilibria modeled by Boyd and Richerson (1990) (see also chapter 7 in this volume).

## 4.6 Signaling and Commitment

### 4.6.1 Signaling and Common Goals

The presence of conflicting interests among social organisms often sets high barriers to cooperation. Gender can be a source of profound disparities in reproductive interests such that "even when cooperating in a joint task, male and female interests are rarely identical" (Trivers 1972, 174). Even the most closely related groups of cooperating individuals have imperfectly coincident genetic interests and can therefore exhibit intense conflict and competition. Although siblings share a considerable degree of common genetic interest, they also often compete more with each other (for parental investment and other resources) than with other individuals in the social group (Sulloway 1996). Conflicting genetic interests between mother and fetus institute a form of maternal-fetal warfare during gestation, even though by cooperating each could maintain an outcome better for both (Haig 1993).

Individuals often come into conflict about working toward a shared goal when each faces different tradeoffs and gains different benefits from working toward that goal. For example, given the fact that males and females have different reproductive strategies and life histories, they will often face conflicts between working toward a common goal of household provisioning (in effect, an investment in self-maintenance and the rearing of children) and alternative productive and reproductive goals, such as gaining status in the wider community, producing children with other mates, acquiring more mates, or accumulating wealth. To have an incentive to cooperate, however, partners must have goals in common to some degree, such that both benefit more from the partnership than each would if they acted independently.



In choosing a partner for a dyadic cooperative endeavor—such as a mate to cooperatively raise offspring, a research colleague, or a coauthor—each partner must be convinced that he or she will gain a net benefit from the interaction. This is particularly important if the association will be a long-term one, with opportunities for cheating or periods of one-sided costs for one partner (e.g., carrying a child to term or writing the first draft of a manuscript) that would allow the other partner to maximize short-term returns by defecting. How can the potential partners discern each other's intentions with any degree of reliability?

One way they might do so is by sending honest signals of commitment to common goals for the project or relationship in question. Pursuing our coauthorship example, conflict can occur when one partner seeks individual status over the collective status achieved through coauthorship or seeks to free-ride on the efforts of a harder-working coauthor. In order to honestly signal his commitment to common goals, he must show that when given the opportunity to gain individual status at the expense of his partner, he chooses to forgo this in favor of promoting the interests of the partnership. For example, one partner might be approached by a publisher interested in securing the rights to a book deal based on jointly conducted research. If this partner accepts the deal and promotes himself as sole author, he gains individual benefits but jeopardizes the continuation of the partnership. If he declines the publisher's offer (or brings the partner into the deal), he pays an opportunity cost in terms of his own individual status but signals his ongoing commitment to the partnership. Since the tempted partner can only expect the short-term cost of forgoing sole authorship to be repaid if he expects the relationship to last long enough to produce benefits greater than these costs, his actions are an honest signal of commitment. Thus, the cost paid by not defecting (if sufficiently high) guarantees the honesty of the signal.

### 4.6.2 Coalition Commitment

Signaling of common goals applies not only to dyadic partnerships, but might also help solve multi-agent cooperative dilemmas. Relationships among members of relatively stable social groups often involve such interactions; for example, some of the most important interactions are cooperative behaviors involving group territorial defense. When challenges by neighboring groups come at unpredictable times, periodic testing of the commitment of group members to engage in costly territorial defense helps ensure that they can be relied upon when the time comes to fight. Zahavi and Zahavi (1997) suggest that among Arabian Babblers (a group-living bird), many social behaviors such as huddling, grooming, and group dances serve to test the social bond and, by extension, demonstrate commitment to group defense. Dances and ceremonies in many human groups that are performed prior to heading into battle might serve much the same function. However, plausibility arguments such as this one need to be stated in a more directly falsifiable manner and then subjected to careful empirical tests.

Cooperative dilemmas also arise in the context of within-group competition, involving political coalitions and alliances. Most models of political power assume that politicians gain power as part of a reciprocal exchange: a politician promises "pork" to his constituents in return for the favor of their vote. Given the delayed return here ("If I support you now, you will return the favor by providing collective goods in the future"), defection is always a distinct possibility. Costly signaling may not eliminate the risk of defection, but it could help in predicting which individuals are less likely to do so. If a politician can reliably signal a superior ability to obtain resources for redistribution during period 1, he should be more likely to actually do so in period 2.

Here, costly signaling does not guarantee honesty of intent to deliver collective goods, but it may guarantee honest advertisement of the ability to do so. A variety of political systems, ranging from the semi-egalitarian "big-man" systems of Melanesia to the stratified chiefdoms of the Northwest Coast Indians, appear to display various elements of this costly signaling dynamic of garnering and maintaining political support through magnanimity (Boone 1998). In these cases, and arguably in many instances of electoral politics in modern industrialized democracies, political candidates use distributions of goods to honestly signal their ability to benefit supporters in the future. The big man, chief, or congressional candidate encourages others to donate wealth or labor in his support by displaying honest signals of his skill in accumulating resources, thus ameliorating the most problematic aspect of delayed reciprocity: the risk of default.



## 4.7 Conclusions

Costly signaling theory provides the basis for arguing that generosity—incurring the costs of providing collective goods (including those shared with partners in dyadic relationships)—is one means by which individuals and coalitions compete for status, and ultimately for the material and fitness-enhancing correlates of status (such as political power, mates, and economic resources). The quality-dependent cost of providing the collective good guarantees the honesty of the signaler's claim to such qualities as resource control, leadership abilities, kin-group solidarity, economic productivity, or good health and vigor—information that is useful to the signaler's potential mates, allies, and competitors (Boone 1998; Smith and Bliege Bird 2000). If this explanation is correct, it means that those who engage in acts of unconditional generosity by providing collective goods are not acting in hope of reciprocation in kind, nor sacrificing for the good of the group or their partner, but rather are competing for status and its perquisites. We extended these arguments to address the issue of *commitment* in cases of both dyadic reciprocity and $n$-person coalitions and argued that signaling might provide an alternative to (or at least strengthen) more conventional analyses of these phenomena.

The $n$-player game-theoretical model summarized earlier in this chapter (and developed more fully in Gintis, Smith, and Bowles 2001) specifies conditions under which an honest-signaling equilibrium will be stable. At this equilibrium, only high-quality individuals signal while observers respond only to signalers (these being the player's respective best moves). This model shows that group-beneficial signals (such as unconditionally providing a collective good) can meet the conditions for a signaling equilibrium. However, these results apply equally well to socially neutral or even harmful signals, and hence this model alone cannot tell us why group-beneficial signals would be favored over other signals.

To address this last question, we briefly discussed three distinct (but not mutually exclusive) hypotheses. One of these involves equilibrium selection among alternative (some more group-beneficial, some less) signaling equilibria, possibly through a process of cultural group selection. A second proposes that the value *to the signaler* of providing a collective good over some more "wasteful" display may lie in the broadcast efficiency of the signal in competing for observer attention, given that observers are more likely to be attracted to signals that provide an additional consumption benefit. Our third hypothesis is that when members of a social group benefit directly from cooperative signals, these signals can be favored because they serve as reliable indicators that the signaler's allies have an increased probability of receiving similar private benefits from the signaler in the future.

While the costly-signaling approach to cooperation and collective action opens up some exciting vistas, it raises many questions that will require extensive theoretical and empirical work. Of these, we will mention three major ones: figuring out (1) what underlying qualities are being signaled, (2) who the intended signal recipients are, and (3) under what conditions signaling to the field is a better strategy than targeting specific signal recipients. The first two questions are primarily empirical, although potentially very difficult ones to answer in particular cases. The third question is one that is side-stepped in the GSB model—which simply presumes that attracting a large audience by providing a collective good will increase the payoff to the signaler. This is likely to be the case under at least two circumstances: 1) when each signaler can benefit from attracting multiple partners of a single type (e.g., multiple potential mates), and 2) when each signaler can benefit from influencing multiple types of observers (e.g., attracting allies and mates, intimidating competitors).

Another issue that presents intriguing possibilities for theoretical development is to extend the one-shot analysis of the GSB model to situations of repeated signaling and extended interaction. Repeated signaling is likely to occur when reputations need to be built or maintained. We suspect that this is likely to be important under two main (but not mutually exclusive) conditions: (1) where there is lots of "noise" (i.e., variation in signaling that is not due to underlying qualities), and (2) where the qualities being signaled are likely to change quickly over time (e.g., due to ecological and economic variations). The first situation is exemplified by the hunting of large game. In this scenario, elements not controlled by the hunter can have a large but unpredictable effect on success, yet underlying qualities (such as ethological knowledge, visual acuity, stamina, and so forth) can lead to consistent differences between individuals in long-term average returns. The second situation—where underlying qualities are subject to rapid decay—is characteristic of a variety of economic situations, ranging from subsistence regimes subject to severe ecological fluctuation (e.g., pastoralists in arid lands) to a speculative capitalist economy, where entrepreneurs and members of the underclass are subject to boom-and-bust conditions. We can expect the first situation to feature repeated signaling early in an individual's career, in order to establish a reputation that will then be relatively stable and require little or no future reinforcement (e.g., the turtle-hunting careers of Meriam that typically take a decade or so to establish and may then persist for only a few years more, yet result in long-term social and reproductive gains). The second situation is likely to be much more dynamic, with signalers' fortunes (and signaling intensities) rising and falling rapidly with changing circumstances; this scenario will presumably present a more challenging arena for formal modeling.



## 4.8 Acknowledgments

For many fruitful discussions that have strongly influenced the ideas developed in this paper, we thank Doug Bird, Carl Bergstrom, Sam Bowles, Herb Gintis, Kristen Hawkes, Hillard Kaplan, and Joan Silk. The $n$-player signaling model outlined in this chapter was developed in collaboration with Gintis and Bowles and a more detailed version is published elsewhere (Gintis, Smith, and Bowles 2001). Fieldwork among the Meriam was carried out in close collaboration with Doug Bird, Craig Hadley, and many Meriam friends, especially members of the Passi family. This fieldwork was supported by grants from the National Science Foundation, the Leakey Foundation, the Wenner-Gren Foundation, and the Australian Institute of Aboriginal and Torres Strait Islander Studies.

## Notes

1. By "cooperative behavior" we mean any actions by Ego that enhance the well-being of members of Ego's social group beyond his or her immediate kin. Such actions need not impose a net cost on Ego in the short term, and the social benefits need not be evenly distributed among Ego's social group, though these special cases are of particular interest in this chapter and elsewhere in the present volume.

2. Lotem, Fishman and Stone (2002) subsequently published a model of the evolution of cooperation via costly signaling that shares some aspects of the GSB model. However, Lotem et al. model only dyadic interactions, and start with a population containing high frequencies of conditional reciprocators, whereas Gintis et al. (2001) develop a multi-player game with no initial (pre-signaling) levels of cooperation.

3. GSB show that the results are unchanged if (following Johnstone 1997 and Getty 1998) signaling benefits rather than signaling costs are made quality-dependent. They did not, however, analyze the effect of allowing Responders to vary in ways that affect the

interaction payoff to Signalers. This two-sided matching problem is difficult to model, and has not been attempted in the costly signaling framework, though it has been developed for marriage markets and mate choice (e.g., Bergstrom and Real 2000).

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