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Abstract

Acts of prosociality, such as donating to charity, are often analyzed similarly as acts of conspicuous advertising; both involve costly signals revealing hidden qualities that increase the signaller's prestige. However, experimental work suggests that grand gestures, even if prosocial, may damage one's reputation for trustworthiness and cooperativeness if they are perceived as prestige-enhancing: individuals may gain some types of cooperative benefits only when they perform prosocial acts in particular ways. Here, we contrast subtle, less obviously costly, interpersonal forms of prosocial behaviour with high cost displays to a large audience, drawing on the example of food sharing in subsistence economies. This contrast highlights how highly visible prosocial displays may be effective for attracting new partners, while subtle signals may be crucial for ensuring trust and commitment with long-term partners. Subtle dyadic signals may be key to understanding the long-term maintenance of interpersonal networks that function to reduce unanticipated risks.

The many dilemmas of cooperation

The problem of cooperation is commonly framed by the Prisoner's Dilemma, which asks how cooperation is sustained between individuals who each stand to gain more from not cooperating. In the classic telling, two miscreants are interrogated by the police and faced with the temptation to testify against one another. However, before they were arrested and given the chance to defect, they had already grappled with another dilemma: whom to choose as a partner in crime. In real social situations, individuals typically are first faced with the choice of whom to interact with, as well as with the possibility of repeated interactions

with the same individual. Consequently, research on cooperation has increasingly focused on the dilemma of how to choose the best attainable partner from a set of possible partners of differing qualities[1–7], and how existing partners might demonstrate continued commitment to a mutually beneficial relationship[8–12].

When partner choice is the goal, individuals should be evaluating not only the quality of potential partners (which we narrowly define here as the quantity of benefits they can provide), but also the likelihood that those benefits would flow to them; that is, properties of relations should be evaluated as well as properties of individuals. A partner's perceived availability and cooperative tendencies are critical for imparting confidence in what future interactions with that individual will entail, and may sometimes be more important in shaping partner choice than partner quality[13]: a rich but greedy partner might be a poorer collaborator than a poor but generous one. Experimental research suggests that individuals looking for a cooperative partnership are often more sensitive to a partner's fairness than to quality, preferring fair partners over stingy ones even if they are poorer, especially when individual quality fluctuates over time[14,15]. Empirical observations in subsistence-based economies echo these experimental studies, showing that those who are more generous, but not those who are more productive per se, seem to reap the benefits of future cooperative rewards[16–18] (see Box 1).

Individuals also face decisions about whether to maintain existing relationships or invest in new ones, and therefore individuals should also be interested in assessing how committed their potential or current partners are to the relationship. There are also likely to be real

constraints on switching partners, including the cost of gathering information on potential partners, limits on the number of potential partners available, and trade-offs between the number of partnerships and the quality of relationships an individual can maintain. In making the choice to stick with an existing partner, the level of that partner's commitment to the relationship—the likelihood that benefits will flow to you, and not to someone else—is a critical piece of information[13]. Clearly, individuals want to avoid the possibility that their partners will abandon them, and should want evidence that their partners are willing to provide ongoing help to them specifically.

While cooperative partnerships can be utilized for a wide range of endeavours, the incentive to maintain partnerships may often stem not from the simple desire for eventual reciprocation, or from the need to accomplish a particular cooperative task, but from the broader value of long-term, committed relationships for coping with unanticipated events. While any one interaction may provide an immediate benefit, cooperative partnerships should be seen as broadly contributing to long-term strategies of building social capital: the resources embedded in a person's social network[19,20]. The long-term benefits of such relationships are clearly demonstrated by the large literature documenting the positive relationship between social support and health and well-being, both in humans[21–26] and non-human primates[27–30].

Building relationships through subtle signals

Making the right decisions about relationship investment is dependent upon being able to

92 access accurate information. Honest signalling by both parties is thus critical both in
93 perceiving an individual's quality (how much a partner might be able to help) and in
94 establishing that individual's commitment to the relationship and probability of helping
95 (how much to trust in their other-regarding motivations and reliability). Signalling theory
96 helps to explain how and under what circumstances honesty in communication can be
97 maintained when there are conflicts of interest and temptations to defect[31–33]. Developed in
98 biology as the 'handicap principle'[34], wherein signals are designed to reveal the hidden
99 qualities of an individual important for mate choice, predator evasion, or hunting skill,
100 signalling theory is most strongly associated with costly acts revealing one's intrinsic but
101 hidden qualities.
102
103 Signalling may be integral to explaining cooperation when signals take the form of costly
104 and often public acts that serve to benefit others[35,36]. Most work on signalling and
105 cooperation sees prosocial (or altruistic) signals as conveying something about the intrinsic
106 quality of the signaller. Donations to a public charity, for example, might reveal the wealth
107 and prosociality of the donor. Providing a large quantity of food or rare food items for a
108 feast might reveal something about a hunter's ability. Having observed such signals, people
109 can better assess the qualities of potential cooperators. In such cases, signallers may wish to
110 draw the attention of a large audience, as a highly visible, broadcast signal allows more
111 people to observe it and draw inferences about the suitability of the signaller as a mate or
112 cooperative partner, or of their formidability as a competitor[36]. However, as mentioned
113 earlier, individuals may want to assess not only properties of an individual, but also the
114 probable properties of a relationship with that individual, such as their availability for and

115 commitment to a particular relationship. While some dramatic broadcast signals may
116 provide clear evidence of the signaller's ability to provide a benefit, they may be less
117 convincing of the signaller's willingness or interest to provide those benefits to specific
118 individuals. This type of "public prosocial signal"—grand displays broadcast to a large
119 audience—might then do little to reassure any specific onlooker that they are the intended
120 target of the signal.
121
122 The prominence of public prosocial signals means that these signals can easily be viewed
123 with scepticism, seen as a selfish attempt to build renown rather than as an act of
124 commitment to others. Public prosocial signals may also be seen as advertising one's quality
125 to others in order to find new cooperative partners, which may undermine the confidence of
126 existing partners in an individual's commitment to them. Consequently, signal observers in
127 many contexts tend to discount prosocial acts when the actor stands to gain directly via
128 material benefits, or indirectly from improved social status[37–41]. The scepticism of public
129 prosocial signals extends to subtle considerations of whether or not individuals are acting
130 strategically to advance their own best interests rather than the mutual interests of
131 cooperators. For example, partners in a trust game are more willing to trust naïve individuals
132 who are generous playing a dictator game than individuals who are similarly generous in
133 the dictator game but who are informed that their initial generosity could be advantageous
134 later[42]. Signallers can work to reduce scepticism through a variety of mechanisms, such as
135 the signaller distancing him or herself from the act by remaining anonymous, using
136 intermediaries to distribute goods and services, or distributing in ways that make it clear
137 that reciprocation is not expected[18]. However, the potential tradeoff between the immediate

138 personal gains for such acts and the longer-term value of a committed relationship will
139 remain.
140
141 The solution to this dilemma may lie in the use of prosocial signals that are either subtle
142 (meaning, more discreet, rather than dramatic and flashy) and/or dyadic (directed to
143 particular individuals, rather than broadcast widely). Such signals are prevalent, and
144 potentially quite important communicative acts. For instance, Silk[43] contrasts loud primate
145 vocalizations that attract wide attention, such as warning calls, and quiet vocalizations that
146 are used to indicate intentions and dispositions towards particular others. Subtle and dyadic
147 signals have a number of characteristics that may make them particularly effective for
148 maintaining cooperative partnerships and affiliative social bonds. With subtle prosocial
149 signals, the observer's awareness that others are not similarly attentive to the signal
150 prevents scepticism that the act is being undertaken for individual aggrandizement. With
151 dyadic prosocial signals, the signallers' direct investment in a particular individual's well-
152 being (as opposed to an investment in others) assures the recipient/observer that the
153 signaller wishes to engage in a mutually-beneficial relationship. Investment in the well-being
154 of another, when accompanied by a manner of acting which demonstrates there are no
155 expectations of direct, in-kind reciprocation, allows the observer to trust that the signaller
156 actually does have her best interests at heart, and is not simply giving in order to get
157 something in return[18]. Indeed, strict account keeping and contingent behavior is often
158 detrimental to the relationship[44]. Observer confidence in the honesty of these signals is also
159 buttressed by a number of other reliability mechanisms that go well beyond simple signal
160 costs[45–48]. When individuals have a long history of repeated interaction, for example, each

partner has ample opportunity to directly observe the actions of the other, and evaluate their honesty[49]. Over time, each partner's continued investment in the relationship may also mean that their interests become more closely aligned, reducing their temptation to renege. Consequently, subtle dyadic prosocial signals, with their frequent, repeated, low cost demonstrations of a continued investment in the relationship, may most unambiguously provide reliable information of an individual's value as a friend or collaborator.

Both subtle, dyadic signals and dramatic, broadcast signals can take the form of other-regarding, non-contingent behaviours through which signallers may attempt to generate and maintain cooperative relationships with others. However, these signal forms may play different roles in supporting different types of cooperation. Public prosocial signals (dramatic, broadcast signals) may be particularly important in the task of recruiting new partners through reputation-building[50,51], while subtle, dyadic prosocial acts may be important for reaffirming and strengthening existing relationships. Because individuals generally interact on multiple occasions and in multiple settings, dyadic and broadcast signals may not be evaluated entirely independently of each other. When broadcast signals are consistently reinforced by subtle, dyadic signals of commitment and generosity, the two signal forms can reduce the scepticism with which public prosocial signals are viewed. However, while these two signal forms may often have reinforcing messages of a signaller's desire for cooperative relationships, there is also the potential for them to be at odds. In particular, widely broadcast signals may be viewed with more scepticism if one is always behaving selfishly in more private interactions. More generally, there is a constant tradeoff between signalling ongoing investment to a particular partner and signalling to other

potential or current partners. While one partner may appreciate demonstrations of commitment, other partners may feel slighted that they did not receive something at the same time.

Despite these tradeoffs, both signal forms contribute in distinct ways to fostering cooperative relationships, and signallers should often employ both. Because individuals differ in their own qualities as well as in the sets of relationships in which they are embedded, individuals also differ in the types of relationships they wish or need to engage in. Thus, not only do we expect individuals to employ multiple signal modalities, but the relative balance of each form of prosocial signalling will likely vary between individuals as well as within the same individual at different times. To illustrate the value of considering both dramatic broadcast and subtle dyadic signals, we now explore one type of prosocial behaviour that has been well-studied cross-culturally: food sharing.

Food sharing

One of the most common cross-cultural manifestations of prosocial behaviour is the transfer of food from those who acquired it to those who did not. Most applications of signalling models to sharing have focused on cases where food is made a common good, such as when hunters acquire large prey items associated with a high risk of failure, and share them widely throughout the community[52–55]. For example, Meriam turtle hunters send prosocial signals by giving away the entire catch to provision a public feast following a successful hunt, a signal that makes visible one's political motives and prosocial motivations[53]. This

sharing provides hunters with a means to send signals of support to the individual or families hosting the feast, as well as more indirect signals to those attending the feast who actually consume the turtle, which in turn benefit hunters through greater access to the sorts of alliances that translate into better marriage prospects.

Although grand displays have been the focus of applications of signalling theory to food sharing, signalling models may also provide insight into less obvious forms of sharing that are commonly explained through evolutionary models of reciprocity and kin selection. These forms of sharing generally involve dyadic transfers (or transfers to only a few partners) of a small amount of food, what we might call 'private' sharing as opposed to public distributions, and seem to be more common among women. Hiwi women exchange identical harvests of wild tubers[56]; Batek men and women engage in 'unnecessary' distributions of food when it is abundant, leaving families with the same amount they started with[57]; Hadza women coming together for a meal while out foraging pass roasted tubers back and forth[58]; Meriam women sometimes share sardines between households when sardines, as well as small reef fish and shellfish, are constantly available to everyone on the foreshore[59]; Martu women share monitor lizards (but not vegetable foods) in a similar fashion[18] (Box 1). Day-to-day sharing such as this is often assumed to be driven by the demands of contingent reciprocity or variance in individual need, but in many of these cases, food flows not only from haves to have-nots, but also between those who have identical amounts and types of resources.

Such sharing is puzzling for a number of reasons. First, it is seemingly low cost, and thus not consistent with 'wasteful display' signalling arguments, as only relatively small amounts tend to be transferred, and sometimes individuals end up with similar amounts of similar resources after sharing has concluded. Second, it often involves transfers of small-harvest, low-risk resources that are generally synchronously acquired, which make it unlikely that individuals are sharing in order to reduce the risk of failing to find food on any given day. Third, private sharing seems difficult to reconcile with signalling explanations that have traditionally relied on widespread advertising in which the act of generosity is directly observed by a large number of people. Instead, private sharing tends to involve direct transfers to few recipients, often in non-public contexts, which make it harder to build a widespread reputation for being a skilled or generous person. Finally, while private sharing may often be directed toward kin, it is also regularly done with non-kin, people with whom one does not have an obligation to share[60].

Given that private or "redundant" sharing[61] is common across many societies, it seems likely that it confers benefits on those who perform it. We suggest that the value of small acts of sharing, encompassing both 'unnecessary' sharing and many other day-to-day exchanges (not just food sharing) may lie more in signals conveyed and relationships affirmed than in the specific content of the exchange. As most quantitative studies of sharing demonstrate, contingency, kinship, scrounging, and other modes of sharing explain only a small proportion of most sharing transfers[62], suggesting that considerations of social relationships between individuals may account for types of sharing that are not well accounted for by classic models. This accords with sharers' own accounts of their actions: in many of these

cases, individuals talk about these small transfers not in terms of reciprocity (or even status gains), but in terms of morality, and the ethics of being a 'good person'[58,59,63,64]. In the case of subtle, dyadic food sharing, through such seemingly unnecessary transfers, recipients can infer the sharer's cooperative intent and commitment to a relationship because these signals demonstrate that the giver values the relationship over the benefits of consuming the resource herself.

Critically, while such sharing can be immediately reciprocated, these acts of sharing may be primarily motivated by the desire to ensure the availability of cooperative partners in the future through signalling a willingness to help[61,65]. The benefits of such relationships are manifested in varied, sometimes subtle ways, that do not reflect a strict accounting of transfers given and received. These benefits might include risk mitigation (e.g., aid during illness)[23,61], small economies of scale (e.g., turn-taking in tasks like wood collection or childcare)[66], and reduced stress[24]. People may not maintain these types of interpersonal relationships for these specific purposes, but rather invest in their social networks to more generally increase the likelihood of positive future impacts.

Conclusions and Future Directions

Signals should be understood inherently as attempts to influence others[67], and an important way to influence others is not just to show off abilities or physical qualities, but also to convey something about one's willingness to help. Expanding our focus from costly signals

of an individual's quality to more subtle signals of relational properties offers several ways forward in understanding both sharing in particular, and social systems more generally.

First, focusing on how signals can demonstrate cooperative intent or the properties of relations not just to a group but to specific partners encourages us to consider other types of interactions: the everyday, the subtle, and the cumulative, rather than attending solely to showy or solitary events. This further directs us to study the whole signal system, and to extend studies past isolated, short term, or one-off interactions. This can be facilitated by experimental work that considers realistic social contexts beyond simple anonymous games[68–70], by modelling work that better situates agents within chains of multiple interaction types[71–73], and critically, by long-term field projects that allow for a close and continued study of behaviour over time[17,74].

Second, if signalling is involved in subtle acts directed at specific others, this encourages us to focus on the complete range of actors and the mix of signals that they employ. As our food sharing example suggests, a focus on dyadic signalling of cooperative intent, in addition to broadcast signalling, may bring new attention to women's social strategies, which have often been neglected[75]. The goals and constraints that individuals face, as well as their positions within broader social networks, are variable and mutable. These factors shape the kinds of cooperative dilemmas that individuals are trying to solve (e.g., finding new or maintaining existing partners, as well as different kinds of cooperative tasks). More work should focus on how an individual's position and needs might shape the signalling strategies she employs, and how those decisions translate into differential benefits for

297 individuals with different social goals. The tools of social network analysis, especially those
298 being newly developed for temporal and multilayered network data[76], provide an important
299 methodological tool for documenting this process: both for concretely articulating the sets
300 of relationships within which individuals are embedded, and for tracing out the
301 consequences of their actions on these relationships[77]. Already, anthropologists have started
302 to look at networks of food sharing and social support[78–83], and some have begun to
303 consider the role of signalling in these relationships[74,84–86]. Future work should consider how
304 multiple signal forms, variably employed by different actors, correlate with different social
305 outcomes.
306
307 Finally, focusing on subtle signals shows how many signals may be aimed not (or not solely)
308 at conveying quality, but rather focused on conveying relationship commitment. This is in
309 large part because signal receivers (whether observing broadcast or dyadic signals) are
310 interested in ascertaining how that signaller is likely to act towards them in subsequent
311 interactions. While the signaller's attributes and qualities are relevant in that determination,
312 so too is an assessment of the essence of their relationship to date and the degree to which
313 the signaller has committed to future interactions. As our examples of "redundant" food
314 sharing make clear, a dry accounting of material exchanges fails to capture the longer-term
315 importance of the relationships formed through these short-term swaps. Indeed, this insight
316 echoes a long history of debate over whether exchange is about the movement of goods, or
317 is better viewed as a process that creates social relationships[87]. Concluding that prosocial
318 acts are "explained" if and when they are reciprocated may not be congruent with what
319 actually motivates the behaviour and fails to account for the fact that the information

conveyed through a prosocial act may be more important than the material content of the exchange. Similarly, seeing sharing among relatives as "explained" by the fitness benefits derived through fostering the well-being of close kin ignores the work that must be done over time to maintain those social ties.

One analytical frame that potentially has more purchase than seeing each partnership as a series of reciprocated exchanges is that of social capital, which defines the potential relationships and resources an individual has to call upon. Future work should investigate how an individual's various prosocial signals may influence her social capital. Here, too, network analysis holds particular promise, in that it allows for multiple renderings of an individual's network social capital[20], which may be differentially influenced by different prosocial signals. Broadcast prosocial signals, for example, may be most crucial for increasing network degree[23], while dyadic signals may have more effect on tie strength; both likely contribute to an individual's position within a network. Dyadic signals that are accompanied by unbalanced resource flows, demonstrating a lack of interest in account-keeping, may have more effect on tie strength between actors and produce more social capital, greater trust, and a greater likelihood of cooperation than those that are accompanied by more contingency in giving. Ultimately, we feel that situating each individual's actions within their broader social and temporal context, and rendering relationships rather than economic transactions or simple kinship benefits, will advance a more realistic view of the mechanisms that sustain cooperation.

Figure 1. Martu cooperative hunting network.

This network diagram depicts the cooperative hunting network of Martu small animal hunters. Red nodes are women; yellow are men; the ties between nodes are sized according to the frequency with which each person cooperated with each other, while the nodes themselves are sized according to observed generosity with meat.

BOX 1: Martu women's sharing

Martu women's sharing of small animals provides some insight into how subtle, sequentially dyadic transactions can send signals of cooperative intent[17,18]. Women, especially older women, spend most of their time hunting sand monitor lizards and other small reptilian and mammalian prey in the sand plains of the Western Desert of Australia. When women hunt, they form temporary camps away from the community, hunt alone or cooperatively, and assemble at the camp at the end of the day. At camp, they cook their harvests of around 2 kg of lizards each, and share with all those sitting around the fire. These sorts of harvests make up nearly 40% of the bushmeat that people consume on a daily basis, and women are successful 90% of the time. But on 23% of hunts, a successful hunter will take nothing for herself. More than 70% of the time, these harvests of small, synchronously acquired prey are shared well beyond their own families. The sharing itself proceeds in very unexpected ways: women exchange identical lizards, and the hunter will always give away the largest prey to someone else to distribute. While the goal is to distribute meat evenly among all present

(regardless of how hard anyone worked or how much they acquired), those who produced more that day usually end up with slightly less than everyone else, and this is the goal. By sharing in a slightly (but relatively) costly way, a productive hunter distances herself from the benefits she might achieve with her production; by sharing equally to freeloaders, other productive women, and hardworking but unlucky hunters, and by not distributing very large prey herself, a woman also distances herself from any hint that she is sharing only to receive something in return. The benefits of such sharing come in the form of greater access to cooperative partnerships, but only to those who share a higher percentage of what they acquire. Those who merely produce large harvests (and share some, but not proportionately more), while they may be considered skillful hunters, do not reap the rewards of generosity in the form of greater access to more generous cooperative hunting partners.

Conflict of interest statement

The authors declare no competing interests.

Author contributions

All authors contributed equally to the writing of the paper.

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