Content, Cost and Context: A Framework for Understanding Human Signaling Systems

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Humans frequently perform extravagant and seemingly costly behaviors, such as widely sharing hunted resources, erecting conspicuous monumental structures, and performing dramatic acts of religious devotion. Evolutionary anthropologists and archaeologists have used signaling theory to explain the function of such displays[1–4], drawing inspiration from behavioral ecology[3–5], economics,[6] and the social sciences[7,8]. While signaling theory is broadly aimed at explaining honest communication, it has come to be strongly associated with the handicap principle[9], which proposes that such costly extravagance is in fact an adaptation for signal reliability[3–5]. Most empirical studies of signaling theory have focused on obviously costly acts, and consequently anthropologists have likely overlooked a wide range of signals that also promote reliable communication[10]. Here, we aim to build on recent developments in signaling theory and animal communication, developing an updated framework that highlights the diversity of signal contents, costs, contexts, and reliability mechanisms present within human signaling systems. By broadening the perspective of signaling theory in human systems, we strive to identify promising areas for further empirical and theoretical work.

INTRODUCTION

How do individuals manage to communicate honestly with one another when there is so often the temptation to deceive others for personal gain? Signaling theory delineates the conditions under which honest communication can evolve (in more technical terms, when a receiver can have confidence in the reliability of a signal; see Box 1 for more detail on these conditions). One well-studied mechanism for maintaining honest communication is costly signaling[3–6], in which the costs of dishonest signaling are high enough that only honest signaling will be favored by

selection. For example, if successfully hunting hard-to-catch prey requires skill from the hunter—as well as time and energy investments—then regularly acquiring and sharing such prey could reliably indicate that hunter's expertise[11]. Similarly, if holding a feast entails cajoling and coordinating many contributors, then successfully doing so could provide evidence of the host's social support and status[12]. Often, the costs involved in such displays would otherwise remain unexplained by standard evolutionary models, with the costs appearing to be wasteful expenditures. Signaling theory has therefore been widely adopted in the evolutionary sciences as a possible explanation for many behaviors that appear to impose a net cost on performers.

Within evolutionary anthropology, early applications of signaling theory extended narrow ecological models of decision-making to include the pursuit of symbolic and culturally specific measures of status[10,13]. For example, anthropologists found evidence suggesting that signal senders convey information about their strength[11], skill[14], prosociality[15,16], commitments[17–19], and social status[2,20], with one signal potentially conveying information about multiple attributes simultaneously. In this work, signaling theory has largely been used to explain three broad types of behavior: i) the pursuit of risky resources, especially when the resources are widely shared[11,12,14,21–23] (Box 2A); ii) contribution to a public good, as with blood donation[24,25] (Box 2B); iii) religious behaviors that entail sizable investments of time, money, and energy in the name of the divine[17,19,26–30] (Box 2C). Empirical investigations have suggested that signals result in improved status and reputational standing[27], leading to increased social support and well-being[16,19,23,29,31], and ultimately reproductive success[32–34].

Behavioral ecologists have continued to develop and refine signaling theory since its initial

introduction to anthropology in the late 1990s. While models of signaling theory in behavioral ecology initially focused on a single signal and pairwise interaction between sender and receiver, more recent work on animal communication has called attention to the complex reality of signaling systems, with the potential for multiple signal components and multiple interacting individuals[35–41]. Here we review the foundations of signaling theory and synthesize these recent developments, discussing their relevance to human signaling systems. While acknowledging the empirical challenges, we offer a framework that is intended to guide studies of human signals in all their diversity and complexity. In so doing, we build on earlier efforts to bring some of the insights from behavioral ecology to anthropology[11,13,21,42], emphasizing the avenues for future research that are consequently opened.

SIGNALING FRAMEWORK

Applications of signaling theory to human signals often start by noting an obviously costly behavior, hypothesizing that it may hold some signal value, and evaluating that hypothesis by assessing whether costly senders are honestly signaling high quality (e.g., whether putative signals of generosity are being given by individuals who are "actually" more generous). This "costs-first" approach contrasts with how signals are typically studied in behavioral ecology, which can be thought of as a "content-first" approach. Researchers start by identifying a putative signal and then construct hypotheses about what factors have shaped it, e.g. what are the benefits of signaling versus not signaling[43] or what (if any) costs signaling may entail.

Consider a female sedge warbler hearing the song of a male[44]. In this example the male is the *sender*, who produces a *signal* (the song). The signal is then transmitted through the environment to a *receiver* (the female), prompting a possible response[45]. The signal is part of a *system* that includes multiple signalers (e.g., competing males), multiple signals (e.g., elaborate displays combining flight with song), and multiple receivers (e.g., females and predators who use the song as a cue to locate prey), operating within a particular socioecological context. Understanding how a particular signal functions requires attention to all these elements.

To investigate the function of a signal, we start by asking why senders send signals in the first place, and why receivers respond. Senders benefit by shaping the actions of others to serve their own interests (for example, the male warbler attracting the female to mate with him) and receivers benefit by responding to the signal in an appropriate way (the female chooses the most desirable mate). Thus, signals are behaviors or structures that have evolved (whether through natural or cultural selection) in order to generate a response that on average benefits both senders and receivers[9,38,45–49].

Signals function to change the behavior of the receiver, but it is not as straightforward as simply communicating one's desired outcomes. This is because the interests of sender and receiver can diverge, and thus receivers benefit by being skeptical of the senders' intentions. However, there are a number of mechanisms, discussed in Box 1, which can maintain signal reliability, and so overcome such skepticism. In the case of the sedge warbler, the ability of a male to produce a difficult song is related to his health, so females benefit by mating with a male who produces a complex song[50].

Human signals are often more complicated than the song of a male warbler, yet they are also the product of selection and thus can be profitably analyzed using behavioral ecological methods. In order to facilitate such an approach, we present a framework structured along three sources of variation in signals: content, cost, and context. First, we categorize signal content (Figure 1): the attributes of the sender that are encoded in a signal. Second, we categorize the cost structure of signals, with an emphasis on how costs can promote signal reliability (Figure 2). Third, we consider the context in which signaling interactions occur, highlighting the socioecological factors that may influence the form or forms that signals take. By calling attention to these aspects of signaling systems, we are suggesting a different orientation for researchers that focuses on the full systemic process of communication and interaction rather than simply the production costs of a potential signal. We illustrate our approach with three case studies (Box 2).

Signal content

What is it that might comprise signal content? What is, for example, the signal content of the male sedge warbler's song? Turning to humans, what of a Tlingit chief carrying out a potlatch, a Tamil devotee participating in the monthly worship at the temple, or a Hadza forager sharing collected honey (Box 2)? By signal content, we refer to the attributes of the sender or the environment that the receiver(s) assess from the signal. Content is typically considered as an advertisement of the sender's "quality"[5,6], which can denote a range of attributes including wealth, skills, status, and social commitments, or reveals information about the environment, such as the location of food or predators. However, it is important to realize that it is the

161 receivers who are responsible for interpreting the signal and acting upon it. Receivers vary in
162 their needs and interests, and hence also in their responses to signals. We thus ground signal
163 content in the strategic value of its outcome to the sender and receiver. While signals about the
164 environment are common, they are also often more easily assessed by receivers, so we
165 consequently focus our attention on signals about sender quality. Specifically, we see the content
166 of such signals as generally relating to i) the sender's capital (e.g., her wealth or fighting ability)
167 and/or ii) the sender's character in terms of her values and commitments (e.g., her commitment
168 to reproductive fidelity or her willingness to give) (Figure 1).
169
170 *Senders' attributes*
171
172 The sender's capital comprises sources or supplies of resources that confer adaptive benefits to
173 those with access. Drawing on previous literature, we delineate three forms of capital: material,
174 embodied, and social[7,51]. Material capital is the tangible and alienable resources often associated
175 with economic wealth, including land, money, food, and property. Embodied capital refers to the
176 sender's physiological and noetic attributes, such as her immune function, physical strength,
177 skill, or intelligence[51,52]. Social capital stems from the sender's location in a social network, her
178 interpersonal relationships, and the resources that can be gained through social contacts[7]. The
179 sender's character represents the subjective values and commitments of the sender, which derive
180 from the sender's mental representations and perspectives of the world. These include
181 dispositions, emotional states, and moral values, which can typify a sender and inform the
182 receiver about the sender's expected behavior. Hence, character refers to expectations of future
183 states and actions, and so can only be verified with time. For instance, the attribute of

reproductive fidelity can only be verified so long as the sender continues to remain faithful. Any given putative signal may contain one or more aspects of signal content, and this may be especially true for human signals. While the male sedge warbler's song is indicative of what we term here embodied capital (healthy males have more complex songs[50]), the act of attending a *puja* (Hindu worship) by Tamil devotees may demonstrate their material capital through the commitment of time and offerings, as well as their character[27] (Figure 1).

Receivers' interpretations and responses

Receivers can vary in how they respond to the same signal, meaning that signals can be "pluripotent"[41]. For instance, the male sedge warbler's song is not only heard by females, but also by other males who may interpret the song as a territorial intrusion. In humans, yet again the situation can be more complex: for example, extravagant gift-giving could be interpreted as an indicator of generosity (sender's character) or wealth (sender's capital). This potential multiplicity of meanings does not imply that the signal will not have a reliable probabilistic effect on receiver behavior; it simply implies that the effect will be different for different classes of receiver (e.g. males versus females, in-group versus out-group)[41].

Signal costs

Why should the female sedge warbler pay attention to the male's song? In order to make any inferences, a receiver must have some confidence in the reliability of the signal, that is, the degree to which the signal is correlated with the sender's underlying character and/or capital.

There are multiple ways in which signals may be kept reliable[38,47,53], which we discuss further in Box 1. Here, however, we focus on signal costs, because they have received considerable attention in the anthropological literature and have also been a source of misunderstanding[9].

Models of costly signaling have shown that signal costs function to maintain reliability when signaling at the same level is more costly to a lower quality individual than it is to a higher quality individual[3–6]. Strictly, what is important are the differential *marginal* costs: for example, the marginal cost of donating $100 to charity would be extremely high for a donor with little material capital, but relatively low for a rich philanthropist. As anthropologists applying signaling theory have long recognized, these costs can be paid in many different currencies (e.g., calories, time, money), which we again categorize in terms of capital. As an individual's capital determines her productive capacity, delineating costs in terms of capital explicitly draws the connection between the costs associated with a signal and its ultimate fitness consequences. Just as there are three forms of capital conveyed in signal content, signal costs are likewise composed of these same three forms: material capital (e.g., gift-giving displays), embodied capital (e.g., competitive physical performances), and social capital (e.g., pledges not to associate with out-group members). Importantly, signals often entail costs across multiple capitals simultaneously (Figure 2). For example, torch fishing on Ifaluk, which has been analyzed as a costly signal of male fishers' matriline investments, entails the material capital costs of the required technology, including torches, hooks, and nets; the embodied capital costs of time and energy expenditure; and the social capital costs of forgoing investments in other matrilines[22].

How and when costs can be paid

Costs need not be limited to those entailed in the immediate production of the signal. Some costs may instead be ongoing, periodic, or delayed, and other costs may never be realized[49,54]. To emphasize the different ways in which costs may be paid, we distinguish between capital that is spent, risked, and/or forgone (Figure 2). Capital that is spent can be transferred to others (e.g., when food is shared, Box 2A) or burned via irretrievable expenditure (e.g., when blankets are literally burned in a potlatch, or when calories are burned in a performance, Box 2B). Capital can also be risked, and risked in different ways. Some risks may be entailed in the production of a signal (e.g., firewalkers risk bodily harm, Box 2C), whereas other risks are delayed and ongoing (e.g., scars marking group membership exposing their bearer to risk of injury from enemies long after the original physical toll of scarification[55]). Finally, capital can also be forgone (i.e. opportunity costs) when an individual gives up the opportunity to gain from capital that they have or could secure (e.g., food taboos and religious dietary restrictions).

While risked and forgone capital are only "potential", not "realized" (spent), costs—leading many to dismiss them as beyond the scope of costly signaling[9,38,47,48]—we suggest that such costs are in fact compatible with signaling theory[46,54] and may often be crucial elements of many signaling systems. The vast economic literature on risk and uncertainty already demonstrates the importance of potential costs in shaping behavior. Including such potential costs in our framework highlights that signal costs may be paid at different times, if at all: for example, while costs involving spent capital (burnt or transferred) are paid immediately, costs from risked capital are probabilistic, and costs from forgone opportunities are also dependent on outside options.

Audience independent and dependent costs

Costs also differ in whether they are paid without the involvement of others (audience independent) or are socially imposed (audience dependent)[36,38,53,56–58]. In this regard, spent costs are paid in the production of the signal and are thus necessarily independent of the audience. Risked and forgone costs, however, may or may not be shaped by the audience. For example, risked embodied capital may be audience independent, as when a Tamil villager walks across a bed of hot coals (Box 2C), or audience dependent, as when a Maring man dances at a kaiko, publicly committing himself to participate in the next round of inter-tribal warfare[59]. Forgone costs can similarly be audience independent, such as fasting as part of a religious vow, or audience dependent, such as wearing markers of devotion that lead members of the religious out-group to distance themselves.

Importantly, some audience-dependent costs are paid not by the honest sender, but by the (revealed) deceptive sender (e.g., reporters who are fired after their stories are revealed to be unsubstantiated). Such costs may be particularly prevalent and potent in human signaling systems[53,60]. For example, many religions require private practices, such as prayer and morning ablutions, whose primary costs are the social stigma involved in failing to exhibit the practices when, on the rare occasion, they are expected in a public setting[61]. The large literature on monitoring and punishment makes clear the power of audience-dependent costs to drive behavior[62]. The scope for audience-dependent costs is large, and including them within the rubric of signaling theory connects it with the wide literature on cooperation, free-riders, and “cheap

276 talk"[63].

277

278 *Costs can be combined*

279

280 Finally, we note that signals can entail costs that are paid in multiple ways. For example,
281 accompanying the spent material and embodied costs of firewalking (Box 2C), there are
282 additionally audience-independent risked embodied costs (if a person was to fall and get burned)
283 as well as audience-dependent risked social costs (the gossip that would follow from such a fall).
284 This example underscores two points. First, although all audience-dependent costs are potential
285 costs (risked or opportunity costs), not all potential costs are audience-dependent. Second, costs
286 can be paid in different capitals (as well as in different resources within each capital), which has
287 largely been overlooked in studies of signaling. Our inclusion of these diverse forms of cost is
288 aimed at ensuring that even inconspicuous costs are uncovered and analyzed.

289

290 **Signal context**

291

292 Returning to the male sedge warbler singing, there is in fact more to his signal than just a single
293 song. For example, females assess the male's entire repertoire of songs, his activity in song flight
294 displays, and also the size of his territory[44]. That is, signals are embedded within a context that
295 involves other signals and the socioecological context. This context influences all aspects of
296 signaling, including the functions the signals serve and the forms the signals take.

297

298 What factors of the socioecological context might moderate human signals? Aspects of the

299 environment can shape whether and how a signal is received and the set of signals available to
300 the sender. These factors can be elements of the physical environment (e.g., background noise,
301 visibility) and the social environment (e.g., laws or social norms that shape receivers' baseline
302 expectation of behavior). Consequently, some of the costs that are entailed in a signal may not be
303 strategic costs (those that ensure that the signal is effective at promoting a beneficial response in
304 the receiver) but instead may be efficacy costs (those costs that are necessary to simply ensure
305 that the signal, regardless of its reliability, is encountered by the receiver)[42,64,65].
306
307 Studies of receiver psychology have shown that signals are often comprised of multiple
308 elements: they may be "multimodal" (involving multiple sensory modalities) or
309 "multicomponent" (occurring within the same sensory channel)[66–70], at least in part to ensure a
310 signal's observability, robustness, and memorability[64,66,67,71]. The multiple elements of the sedge
311 warbler's signaling system (including multiple songs and flight displays) are likely to have been
312 selected for these reasons, as are the pageantry of religious rituals with their elaborate ceremonial
313 procedures, costumes, chants and songs. Finally, more immediate contextual factors include the
314 number and identity of receivers (e.g., in-group versus out-group members[72]) and the proportion
315 of receivers who are unintended, i.e. "eavesdroppers"[37,73]. Senders may calibrate signals to avoid
316 eavesdroppers or to minimize receiver skepticism about the degree to which the signal is
317 intended for them.
318
319 In sum, contextual factors can both constrain and enhance the potential for signals. For example,
320 signals can be constrained by high efficacy costs from increased background noise (resulting in
321 signals that have multiple redundant elements, potentially across multiple channels of

communication), or facilitated by social norms and institutions that provide space for signaling. Signals may vary between socioecological settings not only due to different selection pressures on signal function, but also due to different contextual constraints. For example, male ultra-Orthodox Jews in Israel often remain in yeshivot until after 40 years of age, which results in a draft deferment and extreme poverty, to signal their commitment to the ultra-Orthodox community. But in the U.S., without the draft, remaining in yeshivot for such a long time among ultra-Orthodox Jews rather implies some dysfunction and inability to enter the mainstream market economy[74]. Any signal system can only be evaluated in light of its particular context.

FUTURE DIRECTIONS

Our framework raises several outstanding theoretical and methodological issues, which we now sketch out here, as they highlight promising avenues for future research.

Theoretical issues

Signal cost and content

Our inclusive view of costs reveals ways in which cost may have a more complex relationship to content than is often assumed[43]. It is not always as straightforward as recognizing the physiological and cognitive effort (spent embodied capital), as is the case for the male sedge warbler's song. While spent costs such as these are dependent on the sender's capital, risked and forgone costs may not be so tightly constrained. Future modeling work should help clarify the relationship between the sender's capital and the types of signal costs borne. For example, it may

346 be that senders holding less capital are more likely to take on risked costs, because they do not
347 have sufficient capital to spend[75]. Alternatively, senders who hold *more* capital may be more
348 willing to take on risked costs because of their greater ability to buffer in case of loss.
349
350 While spent costs may be more tightly linked to the signal content, audience-dependent costs
351 may often have an arbitrary link to signal content[53,56]. For example, many religious markers,
352 such as head coverings or adornments, are not intrinsically linked to their bearer's character, but
353 are, however, policed by others. Such arbitrary links could be sustained when signals are at least
354 partially verifiable: that is, receivers can in the long term evaluate when signals are
355 dishonest[53,63,76]. Establishing the conditions under which signal costs should, or should not, be
356 tightly related to signal content is an important area for further study.
357
358 *Who pays the costs?*
359
360 While audience-independent costs are inherently borne by all senders, audience-dependent costs
361 may be more variable. First, audience-dependent costs may be meted out to senders who are
362 revealed to be deceptive, such as warriors who feign injury to avoid a raid[55] or academics who
363 falsify their curriculum vitae, rather than those who are revealed to be honest[9,46,48,49]. This means
364 that it is important to consider not only the cost of displaying an honest signal, but also the cost
365 of displaying a dishonest one. Second, imposing a cost on a sender can itself be costly, whether
366 the punisher risks injury or forgoes social opportunities in order to avoid and shun a deceptive
367 sender. From a theoretical standpoint, this is important because it implies a second-order free-
368 rider problem, especially when there are multiple receivers: which receivers are willing to bear

the cost of ensuring sender honesty by imposing these audience-dependent costs? Receivers generally have different incentives to bear these costs: for example, group leaders may stand to gain a higher net benefit from imposing punishment than do other group members[77]. Future work should investigate when costs are expected to be borne by the honest or dishonest sender, and whether the receiver bears any costs as well.

Context and signal evolution

An additional theoretical issue is the feedback between socioecological context—both the social and physical environment—and signaling systems. First, the context may influence the set of signals that are available for members of the population to use, as with the ultra-Orthodox Jewish men in Israel versus the U.S. in the example described above[74]. All social environments may have, at least theoretically, a multitude of potential signaling solutions to particular local problems, yet only a few may actually be observed[43,53]. How researchers can make predictions about which signaling solution(s) to a given dilemma may arise in a given environment remains unexplored. Second, signals themselves may affect the socioecological context as they are transformed from voluntary to compulsory acts. Future work will need to develop a plausible theory for how signals become institutionalized in this way.

Methodological issues

We recognize that the task of operationalizing the categories in our framework is not without challenges, as definitively establishing the relevant elements of signal context, content, and cost

can be difficult empirically. Here, we identify some of the likely hurdles and suggest some potential methodological tools to overcome them.

Context

Identifying and understanding content and cost requires a full characterization of the context in which putative signaling is occurring. It is clear that local context is essential for uncovering the function and meaning of signaling behaviors. Not only does a characterization of local context help researchers identify the fitness-relevant problems driving signal evolution, but local context further shapes the particular form that the evolved signals may take. On Ifaluk, for example, the local norms that constrain canoe ownership to matrilines enable torch fishing to indicate matriline strength (social capital), but in communities with different canoe ownership norms, torch fishing may be unrelated to matriline strength[22], and any signal of social capital would necessarily take a different form. Ethnographic fieldwork, still the central methodological tool for all anthropologists studying extant cultures, can provide the essential details of local context. The anthropological staple of cross-cultural comparison may be one way to identify which features of the local context are most relevant to shaping signal content and cost.

Content

We have tried to broaden our conception of the content of any signal, particularly emphasizing its multiplicity. This does not imply an infinite set of possibilities for signal content. Often, anthropologists drawing on signaling theory have remained somewhat agnostic about signal

content, assuming that it may be conveying multiple meanings (e.g., commitment to the group, strength, and hunting ability). We agree with such multiplicity, but call for a more active attempt to delineate these potential meanings and their attendant influences on receivers. Practically, this could be achieved by assessing the relationship between the actions and traits of potential senders and receivers' perceptions and responses to them. This can be done through such techniques as reputational sorting tasks and observational studies of behavior, and ideally would involve measurement of many potential traits, actions, and reputational assessments in order to pinpoint the actual signal content[78,79]. Broadly, researchers should aim to identify the payoffs of signaling for both the sender and receiver under a range of receiver responses, in order to ultimately identify signal function.

Costs

In our framework, we describe a wide range of costs that can help ensure signal honesty. While we may be able to distinguish them readily in the abstract, the process of cataloguing and measuring them empirically may not always be straightforward. First, the presence of costs does not mean that they are implicated in maintaining honesty: as discussed above, they may be efficacy costs, which may be empirically hard to distinguish from strategic costs, as they may be paid simultaneously and inseparably[49]. A careful attention to context in observational studies should help in the task of distinguishing the two, as could experimental or vignette manipulations of context. Second, the equality of costs across individuals need not imply that signaling is dishonest: it could be that individuals gain differential benefit. This means that benefits to the sender—and eventually the overall cost-benefit ratio—should be assessed empirically. This

could entail observing senders before and after signaling events, for example measuring reputational change[27]. Third, the absence of cost is also an empirical challenge: when costs are meted out to deceptive signalers, the costs may be empirically invisible when most or all signalers are honest. Given the rarity of observing such punishment, vignettes may offer a promising technique to determine what receivers' likely response would be to such infractions by a sender[48,80]. The economic approach of choice modeling may also be useful in quantifying opportunity costs.

Even for those costs which are spent (e.g., handicaps) and are easily recognized, such as the fulfillment of religious vows (see Box 2C), the fundamental task of empirically measuring them can be challenging[9]. Simply getting an average measure of cost (and benefit) across individuals can entail sizable amounts of work, and getting individual measures may be prohibitive. Another issue is that potential variation differs across forms of capital: material capital, for example, seems to have a much wider inter-individual range than social or embodied capital, cross-culturally[51]. Furthermore, some forms of capital may be more difficult to quantify than others (e.g., it is easier to quantify spent money or calories than it is to measure spent social capital). This makes the task of establishing the commensurability of costs across different forms of capital yet more challenging[55,81]. How are we to establish the "exchange value" of costs that bridge different forms of capital? And how do we evaluate the relative costs and benefits across all these currencies for different actors? Individuals vary in their ability and willingness to exchange across currencies (taking on a cost in one capital in order to build another) based on the capital(s) they have and need. Ethnographic insight will of course be crucial in this endeavor, as it can provide an appreciation of the relative importance of each form of capital to individual

461 livelihood[51]. Choice modeling may again also be of use, though here in particular we expect that
462 different individuals may have different revealed preferences.
463
464 **CONCLUSIONS**
465
466 The handicap principle[3,4] is a compelling idea and its application to explain extravagant behavior
467 in humans and other animals has been influential[9]. Certainly, it compelled a number of us to
468 pursue research aimed at testing some of its predictions. In the course of applying it—both in
469 ethnographic fieldwork settings and in experimental game settings—we have each recognized
470 the need for signaling theory to be extended. It is telling that much of the work extending
471 signaling theory in the animal communication literature has been prompted by empirical
472 research. We feel that the anthropological investigations of signals have similar potential to
473 advance signaling theory. Here, we have tried to synthesize this work to create a framework that
474 can demonstrate the full breadth and complexity of signaling systems. We hope this framework
475 will stimulate further discussion and development of signaling theory of both human and non-
476 human signaling systems.

BOXES AND FIGURES

Box 1: Evolution of reliable communication

Receivers are constantly attending to the many inputs around them that provide information about the environment. Many of these inputs are cues: acts or structures that reliably inform the receiver about some feature of the world to which they benefit from responding. For example, the whine of a mosquito is a cue that prompts a quick swat. In contrast to signals, cues have not been selected for the purpose of altering receiver behavior[47]. However, if the sender benefits, cues can evolve into signals, making the boundary between signals and cues sometimes fuzzy[82].

What then prevents the sender from using signals to exploit a receiver? As many have noted, there are multiple ways in which reliable communication can be maintained by selection beyond the handicap principle and its easily observable production costs[9,10,13,46,49,80,83].

Relationship between sender and receiver

Alignment of interests: when sender and receiver interests are aligned, there is no incentive for dishonesty and thus no need for an honesty enforcing mechanism. This results in low-cost "conventional" signals[56] that can be used to coordinate actions (e.g., similar jerseys on a sports team).

Repeated interactions: honesty can be maintained without high cost when senders and receivers interact repeatedly because receivers can call the sender's bluff[84].

Differential benefits

Honesty can be maintained by differential benefits, rather than differential costs[85]. For example, a need can be honestly signaled when those most lacking benefit more, such as when chicks beg for food[86].

Intrinsic properties of the display

Indices: reliability may be assured when the signal is intrinsically correlated with the sender's quality and is thus inherently "unfakeable" (e.g., the pitch of a red deer's roar is an index of his size)[47,65,87,46,88]. There is some debate among biologists concerning the boundary between indices and costly signals[89], but it is generally thought that since indices are physiologically constrained, they do not require additional costs to be reliable.

Box 2: Signaling case studies

Here we explore three well known examples to which signaling theory has been applied, and illustrate how our framework could allow them to be interpreted in a new light. We briefly describe these settings in order to give concrete examples of the complexity of signaling systems, and how our framework can be applied to make sense of such complexity.

A: Hadza foraging

Among the Hadza, a group of mobile hunter-gatherers living in northern Tanzania[90,91], there is a strong sexual division of labor in which women pursue relatively reliable resources (e.g., tubers,

523 berries, and baobab pods) and men pursue higher variance resources, particularly meat and
524 honey. Hawkes and colleagues[92] have suggested that men's consistent pursuit of these risky
525 resources (especially large game) is more readily explained as their attempts to "show off" and
526 gain status, rather than as their effort to provision their families. Male hunting has therefore been
527 framed as a costly signal of the hunter's quality, with only truly skilled hunters able to regularly
528 capture large game and share it with others[14]. This interpretation of men's hunting has been
529 critiqued[93–95], including recent concerns that hunting is too noisy to serve as an honest signal of
530 quality[79]. Wood and Marlowe[96], for example, demonstrate that men are actually more able to
531 provision their own family than suggested, arguing that men's hunting can therefore be
532 understood primarily as effort directed toward provisioning, with the additional burden of
533 tolerated scrounging leading to the observed pattern of food distribution. In this light, some
534 men's foraging and provisioning may be a cue rather than a signal[47], insofar as men may benefit
535 from inclusive fitness and reciprocity, rather than from communication alone.
536
537 Whether a cue or signal, observers benefit by attending and responding to the foragers' behavior,
538 and foragers may be motivated by both the provisioning and the communicative potential
539 entailed in the pursuit of large game. Regardless, the view that we promote with our framework
540 suggests that single signals such as the pursuit of large game should not be studied in isolation,
541 but rather in their broader context.
542
543 Broadening our focus in this way reveals the communicative potential inherent in other Hadza
544 foraging activities. Hadza men and women forage for a wide range of resources, notably
545 including honey and small game. When men collect honey, a highly desired resource, they often

546 exert more effort to try to direct it to their kin and other desired partners. The collector's ability
547 to direct the foraged goods to particular partners, including kin and others, could convey to the
548 recipients the collector's continued commitment to their partnership. When women forage
549 collectively for tubers, their returns are dictated largely by the amount of time and effort
550 invested, so even an effort primarily seen as provisioning kin may additionally hold signal
551 content of the skill and dedication of the forager, as well as her potential value as a foraging
552 partner. In accordance with this, Hadza women who are known as the best tuber diggers are
553 preferred as campmates, and while men known as good hunters are more often named as friends,
554 it is those who are known as the best honey collectors who are yet more often named as "best
555 friends"[90]. As our framework aims to make clear, it need not only be conspicuous and seemingly
556 costly acts that have signal value.
557
558 *B: Tlingit potlatch*
559
560 "So much has been written about the potlatch of the Northwest Coast tribes that almost everyone
561 has some ideas about it"[97]—indeed, the potlatch is not only an iconic cultural practice
562 extensively discussed by anthropologists, but it is also the archetypical anthropological example
563 of costly signaling in the biological literature. While the best-known feature of the potlatch is the
564 hosts' extravagant spending of material capital, potlatch systems entail multiple signals and
565 responses.
566
567 Although there is some variation in potlatches among the different groups who practice(d) it, the
568 core concept is the same: it is a ritual festival held in order to repay a favor given to the potlatch

569 hosts by the guests. As a more specific case study, we focus on the Tlingit people from Southeast
570 Alaska, where a common occasion for potlatches was to pay back help given after someone had
571 died. Tlingit society is divided into two matrilineal moieties (descent groups), each of which
572 comprises a number of kin-based clans, which in turn may be geographically distributed across
573 many communities. Maintenance of balance between the moieties is strongly emphasized: for
574 example, marriages must occur between moieties, and major help (such as in building a house)
575 can only be given by members of the opposite moiety. After a death, the funeral is held by the
576 opposite moiety (patrilineal kin of the deceased), and the potlatch given after around forty days
577 by the matrilineal kin marks the end of the mourning period and the repayment of the debt they
578 incurred to the opposite moiety[98].
579
580 What signals are given during a potlatch? The most conspicuous are the enormous quantities of
581 food and gifts given by the hosts to the guests (transferred material capital) and the hosts'
582 destruction of their own property, including sacrificing slaves as well as destroying valuable
583 copper plates (burnt material capital – in some cases literally). These acts are widely interpreted
584 as hosts signaling their status (social capital) to the guests[97–99]. However, there are likely multiple
585 audiences at play, with rival hosts signaling to each other as well as to the guests. The sender's
586 message may be his own status as an individual, but also the status of his clan, communicated in
587 terms of his lineage validating its ownership over sacred clan objects, such as crests[99]. That is,
588 such signals may be multiplex.
589
590 While these dramatic signals of spent capital are the main event of the potlatch[98], they are by no
591 means the only event. The ceremony traditionally began with a mock battle, where the hosts

592 symbolically submitted to the guests' staged attack. The potlatch continued with multiple stages
593 of singing, dancing and oratory, which Kan[98] views as a form of exchange between hosts and
594 guests. These included songs of condolence, whose additional meaning was to confirm the
595 singer's lineage and its claims to the clan's crests; love songs, which carried a meaning of
596 appeasement between potential rivals; and riddles, where rival would attempt to outwit each
597 other[98,99]. Here, the hosts are not the only signal senders: the guests also signal to the hosts, and
598 rival groups of guests signal to each other, creating an arena in which valuable social information
599 about relative status is exchanged and evaluated.
600
601 The potlatch offers two additional points of interest from a signaling perspective. First, the
602 signals have likely been affected by changes in socioeconomic context, namely the arrival of
603 white settlers. Ringel[100] suggests that the concomitant increase in material wealth and decrease in
604 other means to gain social status (e.g. due to banning of warfare) shifted the function of Kwakiutl
605 potlatches from signaling group membership to signaling personal status. Second, while some
606 authors see the potlatch simply as an expression of status, others suggest that in fact it functions
607 to raise status[97]. Boone[2] argues that the latter is not a true signal, as a signal should inform the
608 receiver of the attribute being signaled, but not change that attribute. How signals may evolve
609 into behaviors that do function to affect the attribute being signaled is a promising avenue for
610 future research.
611
612 *C: South Indian religious displays*
613
614 In Tamil Nadu, South India, people carefully observe the religious actions of their peers. They do

so in part because of beliefs about how a person's actions reflect her nature and character.

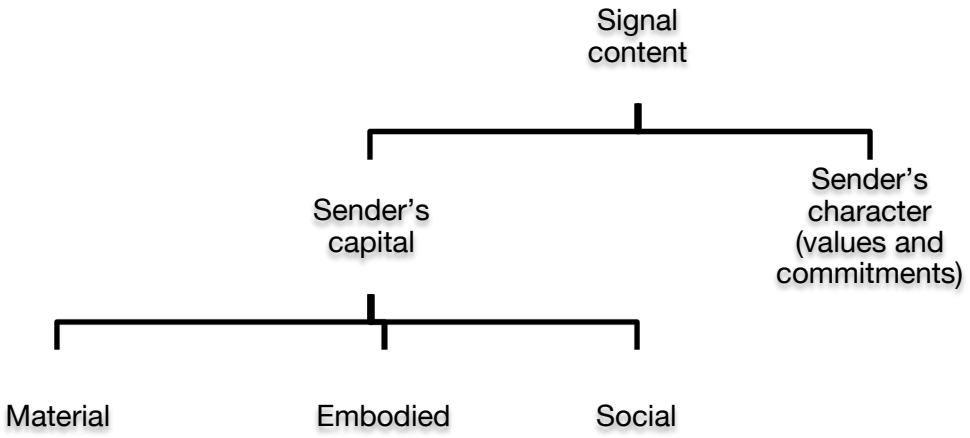
A person's religious adherence is often clearly marked in South India, as elsewhere. After worshipping at home or at a temple, Hindus mark their foreheads with powder or ash, with particular markings (*tilaka*) associated with specific deities and sects. Hindu women place a small dot (*poṭṭu, bindi)* on their forehead as a sign of modesty, and Christian women are consequently identifiable by their bare foreheads. When devotees are preparing to perform a religious act, they will often wear clothes of a particular color, with that color being associated with a particular deity (red or yellow for the goddess, black for Ayyappan, light blue or khaki for Jesus, etc.). The acts of devotion that individuals carry out are their most conspicuous demonstrations of faith. Many Christians attend Sunday services, while Hindus visit temples each week to take *darshan*, the auspicious mutual viewing of the deity, and participate in monthly *pujas*. Festivals are opportunities for further enactments of faith. Often, devotees fulfill vows made in gratitude for divine assistance (help conceiving a child, getting a job, overcoming an illness, etc.). These acts of vow fulfillment (*nērttikkaṭaṉ*) can take many different forms, at the discretion of the fulfiller: making a simple offering to the deity, going on pilgrimage to the deity's church or temple, walking across a bed of hot coals, sacrificing a goat, or piercing one's body with hooks or spears. Some Hindus also become possessed, their eyes bulging and arms flailing. Often, the fulfillment of religious vows entails a period of fasting (*viratam*), during which time devotees follow a variety of requirements and prohibitions. They are limited to one meal a day, are barred from drinking alcohol or smoking, must bathe daily, are prohibited from fighting with others, cannot eat particular foods, must abstain from sex, have to avoid the houses of pregnant and menstruating women, can only eat at homes where others are fasting, etc.

These various displays of religious devotion are not only seen as evidence of a person's devotion; much more is inferred about a person from the sum total of her religious displays (Figure 1). Villagers appear to be using these displays to discern something about the capital and character of the individual[27]. For example, they are more likely to see those performing all religious acts as more devout (character), those who perform physically demanding acts as strong (embodied capital), and those who attend regular worship and undertake public ritual acts as generous and of good character (social capital). Consequently, villagers are more likely to turn to such individuals when they are in need of support, ultimately conferring benefits to both senders and receivers, as they are more likely to have enduring, reciprocal relationships[29].

There are multiple ways in which these religious displays are kept reliable (Figure 2). Possession may be such a convincing demonstration of devotion because it is physiologically and emotionally hard to fake. The dramatic acts of vow fulfillment are often monetarily costly (burnt material capital), entail immediate strain and stress (burnt embodied capital), and risk serious bodily harm (audience-independent risked embodied capital). Consistently attending weekly and monthly services involves the cumulative commitment of many hours that could otherwise have been used for other ends (audience-independent forgone capital). The prohibitions associated with fasting entail serious opportunity costs, whether in terms of forgone calories (audience-independent forgone capital) or forgone socializing (audience-dependent forgone capital). While some religious displays such as the various bodily adornments that mark a person as a devotee are certainly materially cheap, the diligent policing of those markers by others mean that those who are found to be faking can face serious punishment in the form of social ostracism

(audience-dependent risked capital). Any one individual will be performing multiple types of religious displays, across multiple modalities and entailing multiple types of costs across multiple forms of capital. Although these varied potential costs have been recognized, their commensurability remains an open question. Further research should also identify how the *differential* costs associated with these signaling acts shape individuals' ability to undertake them.

667 **Figure 1. Signal content**



668

Tamil Religious Practice				
	Material capital	**Embodied capital**	**Social capital**	**Character (values and commitments)**
Vow fulfillment (e.g., firewalking)	Resources to commit to the task	Strength	Some social support	Bhakti (devotion to god), commitment to religious group, its tenets and its members
Attending monthly *puja*	Time to commit to the task	-	-	Bhakti (devotion to god), commitment to religious group, its tenets and its members
Wearing *tilaka*	-	-	Group membership	Bhakti (devotion to god), commitment to religious group, its tenets and its members
Hadza Foraging				
	Material capital	**Embodied capital**	**Social capital**	**Character (values and commitments)**
Big game	-	Strength, stamina, skill	-	Hunting epeme game is valued; Generosity is valued

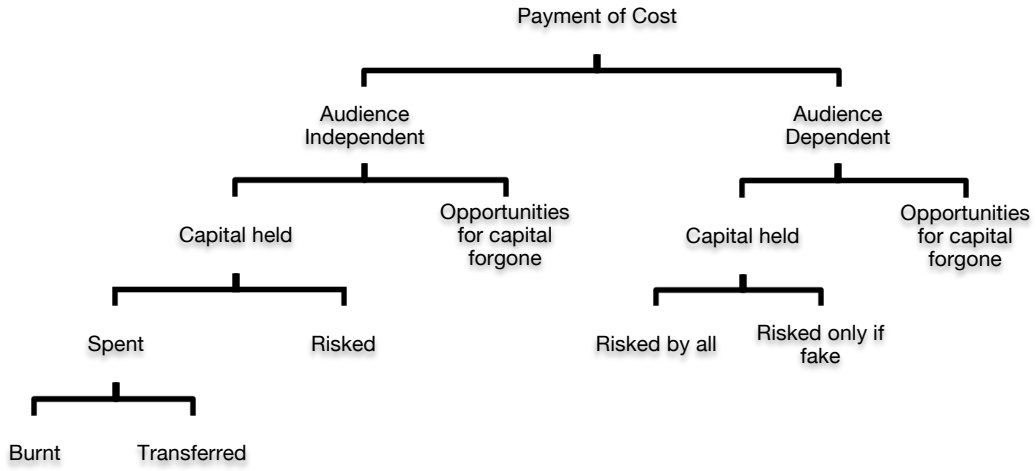
Tubers	-	Strength, stamina, skill	-	Commitment to supporting your family (and friends)
Honey	-	Strength, stamina, skill	-	Commitment to supporting your family (and friends)
Tlingit Potlatch				
	Material capital	**Embodied capital**	**Social capital**	**Character (values and commitments)**
Mock battles	Time and material investment in regalia	-	Clan size	Reciprocity is valued
Dancing, songs & oratory	Clan's property	Individual skill, knowledge	Individual rank/status	Clan's commitment to defending its property
Feasting & distribution of gifts	Clan's property	-	Individual and clan rank/status	Host's commitment to relationship with recipients Clan's commitment to defending its property

669

670

671 **Figure 1.** The content of a signal -- including the message sent by the sender as well as the
672 meaning inferred by a receiver -- comprises information about the sender's capital (embodied,
673 material and/or social capital) and/or the sender's character (values and commitments). Three
674 case studies (Box 2) illustrate how a single signal may have manifold content of any single
675 signal. It is important to note that these are postulated examples of signal content, and all
676 categories of signal content need not be simultaneously present.

677 **Figure 2. Signal cost**



678

Tamil Religious Practice							
	Audience independent, burnt	**Audience independent, transferred**	**Audience independent, risked**	**Audience independent, forgone**	**Audience dependent, risked by all**	**Audience dependent, risked if fake**	**Audience dependent, forgone**
Vow fulfillment (e.g., firewalking)	*Embodied:* energy expended in act *Material:* money spent on equipment, clothes, fee for special priests	*Material:* some vows entail providing food to others	*Embodied:* risk of physical harm	*Embodied:* fasting entails forgoing particular foods, etc. *Material:* opportunity cost of time spent at event	*Social, embodied:* risk of discrimination (and violence) because of membership	*Embodied, material*: risk of physical or financial punishment *Social:* risk of reputation loss, ostracism	*Social:* fasting entails forgoing certain social relationships
Attending monthly *puja*	*Material:* time committed to act, cost of offerings made	*Material:* some offerings redistributed to attendees	-	*Material:* opportunity cost of time spent at event	-	-	-

Wearing *tilaka*	*Material*: minor costs of mark	-	-	-	*Social, embodied:* risk of discrimination (and violence) because of membership	*Embodied, material*: risk of physical or financial punishment *Social:* risk of reputation loss, ostracism	*Social:* forgone socializing with those of other religions
Hadza Foraging							
	Audience independent, burnt	**Audience independent, transferred**	**Audience independent, risked**	**Audience independent, forgone**	**Audience dependent, risked by all**	**Audience dependent, risked if fake**	**Audience dependent, forgone**
Big game hunting & sharing	*Embodied:* energy expended in pursuit	*Material:* meat given to/taken by others, often without the control of the hunter (tolerated scrounging)	*Embodied:* risk of physical harm	*Material:* opportunity cost of time spent in pursuit (though paper showing they eat plenty on the way)	-	*Social:* risk of shame & misfortune if eat *epeme* meat (eaten by women, eaten by *epeme* men alone); risk of being called stingy & being abandoned if don't share	-
Tuber digging & sharing	*Embodied:* energy	-	-	*Material:* opportunity cost of time	-	-	-

	expended in pursuit			spent in pursuit			
Honey collection & sharing	*Embodied:* energy expended in pursuit	*Material:* honey given to/taken by others	-	*Material:* opportunity cost of time spent in pursuit	-	*Social:* risk of being called stingy if don't share	-
Tlingit Potlatch							
	Audience independent, burnt	**Audience independent, transferred**	**Audience independent, risked**	**Audience independent, forgone**	**Audience dependent, risked by all**	**Audience dependent, risked if fake**	**Audience dependent, forgone**
Mock battles	*Material:* may involve some destruction of own property	-	-	*Material:* minor opportunity cost of time	-	-	-
Dancing, songs & oratory	*Embodied:* energy expended	-	-	*Embodied, material:* cognitive and time costs in learning material to be performed	-	*Social, embodied:* risk of violence if anger audience with sung challenges	*Social*: forgoing relationships with other clans
Feasting & distribution of gifts	*Material:* valuable property literally burnt or otherwise destroyed	*Material:* food and gifts given to guests	-	*Material:* opportunity cost of time spent at event	-	*Social:* potential to insult guests by giving insufficiently	*Social*: forgoing relationships with other clans

679

680

681 **Figure 2.** Signal costs may be paid in three forms of capital (embodied, material and/or social).

682 Costs may be paid by forgoing opportunities to acquire more capital; otherwise, costs are paid by
683 risking or spending capital already held. Capital that is spent may be used up in the signal (burnt)
684 or transferred to the receiver. Case studies from Box 2 illustrate how any given signal can
685 include multiple costs paid in different ways. These are postulated examples of signal cost, and
686 all categories of signal cost need not be simultaneously present.

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