

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

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

61

## 62 INTRODUCTION

63

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

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

78  
79 Within evolutionary anthropology, early applications of signaling theory extended narrow  
80 ecological models of decision-making to include the pursuit of symbolic and culturally specific  
81 measures of status<sup>10,13</sup>. For example, anthropologists found evidence suggesting that signal  
82 senders convey information about their strength<sup>11</sup>, skill<sup>14</sup>, prosociality<sup>15,16</sup>, commitments<sup>17–19</sup>, and  
83 social status<sup>2,20</sup>, with one signal potentially conveying information about multiple attributes  
84 simultaneously. In this work, signaling theory has largely been used to explain three broad types  
85 of behavior: i) the pursuit of risky resources, especially when the resources are widely  
86 shared<sup>11,12,14,21–23</sup> (Box 2A); ii) contribution to a public good, as with blood donation<sup>24,25</sup> (Box  
87 2B); iii) religious behaviors that entail sizable investments of time, money, and energy in the  
88 name of the divine<sup>17,19,26–30</sup> (Box 2C). Empirical investigations have suggested that signals result  
89 in improved status and reputational standing<sup>27</sup>, leading to increased social support and well-  
90 being<sup>16,19,23,29,31</sup>, and ultimately reproductive success<sup>32–34</sup>.

91  
92 Behavioral ecologists have continued to develop and refine signaling theory since its initial

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

103

#### 104 **SIGNALING FRAMEWORK**

105

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

114

115 Consider a female sedge warbler hearing the song of a male<sup>44</sup>. In this example the male is the  
116 *sender*, who produces a *signal* (the song). The signal is then transmitted through the environment  
117 to a *receiver* (the female), prompting a possible response<sup>45</sup>. The signal is part of a *system* that  
118 includes multiple signalers (e.g., competing males), multiple signals (e.g., elaborate displays  
119 combining flight with song), and multiple receivers (e.g., females and predators who use the  
120 song as a cue to locate prey), operating within a particular socioecological context.

121 Understanding how a particular signal functions requires attention to all these elements.

122

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

130

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

138

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

150

### 151 **Signal content**

152

153 What is it that might comprise signal content? What is, for example, the signal content of the  
154 male sedge warbler's song? Turning to humans, what of a Tlingit chief carrying out a potlatch, a  
155 Tamil devotee participating in the monthly worship at the temple, or a Hadza forager sharing  
156 collected honey (Box 2)? By signal content, we refer to the attributes of the sender or the  
157 environment that the receiver(s) assess from the signal. Content is typically considered as an  
158 advertisement of the sender's "quality"<sup>5,6</sup>, which can denote a range of attributes including  
159 wealth, skills, status, and social commitments, or reveals information about the environment,  
160 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<sup>7,51</sup>. 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<sup>51,52</sup>. 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<sup>7</sup>. 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



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

190

191 *Receivers' interpretations and responses*

192

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

201

202 **Signal costs**

203

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

207 There are multiple ways in which signals may be kept reliable<sup>38,47,53</sup>, which we discuss further in  
208 Box 1. Here, however, we focus on signal costs, because they have received considerable  
209 attention in the anthropological literature and have also been a source of misunderstanding<sup>9</sup>.  
210  
211 Models of costly signaling have shown that signal costs function to maintain reliability when  
212 signaling at the same level is more costly to a lower quality individual than it is to a higher  
213 quality individual<sup>3-6</sup>. Strictly, what is important are the differential *marginal* costs: for example,  
214 the marginal cost of donating \$100 to charity would be extremely high for a donor with little  
215 material capital, but relatively low for a rich philanthropist. As anthropologists applying  
216 signaling theory have long recognized, these costs can be paid in many different currencies (e.g.,  
217 calories, time, money), which we again categorize in terms of capital. As an individual's capital  
218 determines her productive capacity, delineating costs in terms of capital explicitly draws the  
219 connection between the costs associated with a signal and its ultimate fitness consequences. Just  
220 as there are three forms of capital conveyed in signal content, signal costs are likewise composed  
221 of these same three forms: material capital (e.g., gift-giving displays), embodied capital (e.g.,  
222 competitive physical performances), and social capital (e.g., pledges not to associate with out-  
223 group members). Importantly, signals often entail costs across multiple capitals simultaneously  
224 (Figure 2). For example, torch fishing on Ifaluk, which has been analyzed as a costly signal of  
225 male fishers' matriline investments, entails the material capital costs of the required technology,  
226 including torches, hooks, and nets; the embodied capital costs of time and energy expenditure;  
227 and the social capital costs of forgoing investments in other matrilines<sup>22</sup>.

228

229 *How and when costs can be paid*

230

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

243

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

253

254 *Audience independent and dependent costs*

255

256 Costs also differ in whether they are paid without the involvement of others (audience  
257 independent) or are socially imposed (audience dependent)<sup>36,38,53,56–58</sup>. In this regard, spent costs  
258 are paid in the production of the signal and are thus necessarily independent of the audience.

259 Risked and forgone costs, however, may or may not be shaped by the audience. For example,  
260 risked embodied capital may be audience independent, as when a Tamil villager walks across a  
261 bed of hot coals (Box 2C), or audience dependent, as when a Maring man dances at a kaiko,  
262 publicly committing himself to participate in the next round of inter-tribal warfare<sup>59</sup>. Forgone  
263 costs can similarly be audience independent, such as fasting as part of a religious vow, or  
264 audience dependent, such as wearing markers of devotion that lead members of the religious out-  
265 group to distance themselves.

266

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

276 talk”<sup>63</sup>.

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<sup>44</sup>. 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)<sup>42,64,65</sup>.

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)<sup>66-70</sup>, at least in part to ensure a  
310 signal's observability, robustness, and memorability<sup>64,66,67,71</sup>. 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<sup>72</sup>) and the proportion  
315 of receivers who are unintended, i.e. “eavesdroppers”<sup>37,73</sup>. 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

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

330

## 331 **FUTURE DIRECTIONS**

332

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

335

### 336 **Theoretical issues**

337

#### 338 *Signal cost and content*

339

340 Our inclusive view of costs reveals ways in which cost may have a more complex relationship to  
341 content than is often assumed<sup>43</sup>. It is not always as straightforward as recognizing the  
342 physiological and cognitive effort (spent embodied capital), as is the case for the male sedge  
343 warbler's song. While spent costs such as these are dependent on the sender's capital, risked and  
344 forgone costs may not be so tightly constrained. Future modeling work should help clarify the  
345 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<sup>75</sup>. 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<sup>53,56</sup>. 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<sup>53,63,76</sup>. 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<sup>55</sup> or academics who  
363 falsify their curriculum vitae, rather than those who are revealed to be honest<sup>9,46,48,49</sup>. 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



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

374

### 375 *Context and signal evolution*

376

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

387

### 388 **Methodological issues**

389

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

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

394

395 *Context*

396

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

409

410 *Content*

411

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

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

425

426 *Costs*

427

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

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

445

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

461 livelihood<sup>51</sup>. 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<sup>3,4</sup> is a compelling idea and its application to explain extravagant behavior  
467 in humans and other animals has been influential<sup>9</sup>. 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.

477 **BOXES AND FIGURES**

478

479 **Box 1: Evolution of reliable communication**

480

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

487

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

491

492 *Relationship between sender and receiver*

493 Alignment of interests: when sender and receiver interests are aligned, there is no incentive for  
494 dishonesty and thus no need for an honesty enforcing mechanism. This results in low-cost  
495 “conventional” signals<sup>56</sup> that can be used to coordinate actions (e.g., similar jerseys on a sports  
496 team).

497 Repeated interactions: honesty can be maintained without high cost when senders and receivers  
498 interact repeatedly because receivers can call the sender’s bluff<sup>84</sup>.

499

500 *Differential benefits*

501 Honesty can be maintained by differential benefits, rather than differential costs<sup>85</sup>. For example,  
502 a need can be honestly signaled when those most lacking benefit more, such as when chicks beg  
503 for food<sup>86</sup>.

504

505 *Intrinsic properties of the display*

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

511

512 **Box 2: Signaling case studies**

513

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

518

519 *A: Hadza foraging*

520

521 Among the Hadza, a group of mobile hunter-gatherers living in northern Tanzania<sup>90,91</sup>, there is a  
522 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<sup>92</sup> 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<sup>14</sup>. This interpretation of men's hunting has been  
529 critiqued<sup>93-95</sup>, including recent concerns that hunting is too noisy to serve as an honest signal of  
530 quality<sup>79</sup>. Wood and Marlowe<sup>96</sup>, 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<sup>47</sup>, 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"<sup>90</sup>. 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"<sup>97</sup>—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<sup>98</sup>.

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<sup>97-99</sup>. 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<sup>99</sup>. That is,  
588 such signals may be multiplex.

589  
590 While these dramatic signals of spent capital are the main event of the potlatch<sup>98</sup>, 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<sup>98</sup> 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<sup>98,99</sup>. 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<sup>100</sup> 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<sup>97</sup>. Boone<sup>2</sup> 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

615 so in part because of beliefs about how a person's actions reflect her nature and character.  
616

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

638

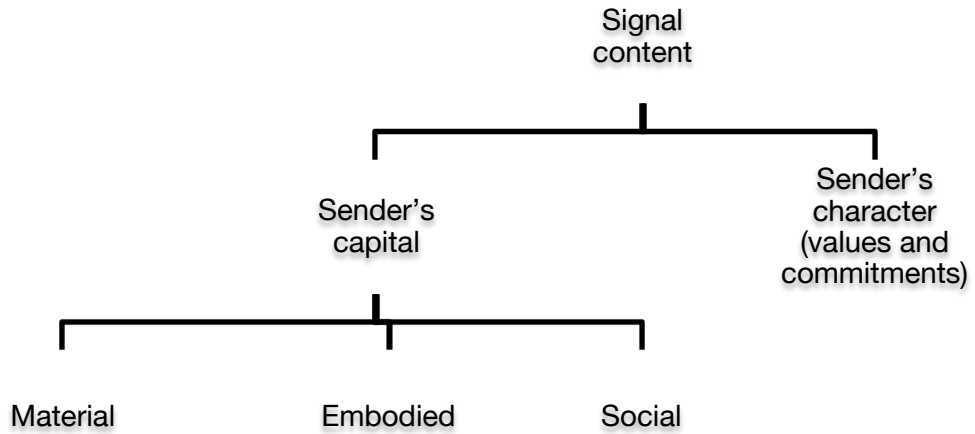
639 These various displays of religious devotion are not only seen as evidence of a person's  
640 devotion; much more is inferred about a person from the sum total of her religious displays  
641 (Figure 1). Villagers appear to be using these displays to discern something about the capital and  
642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

648

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

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

667 **Figure 1. Signal content**



668

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

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

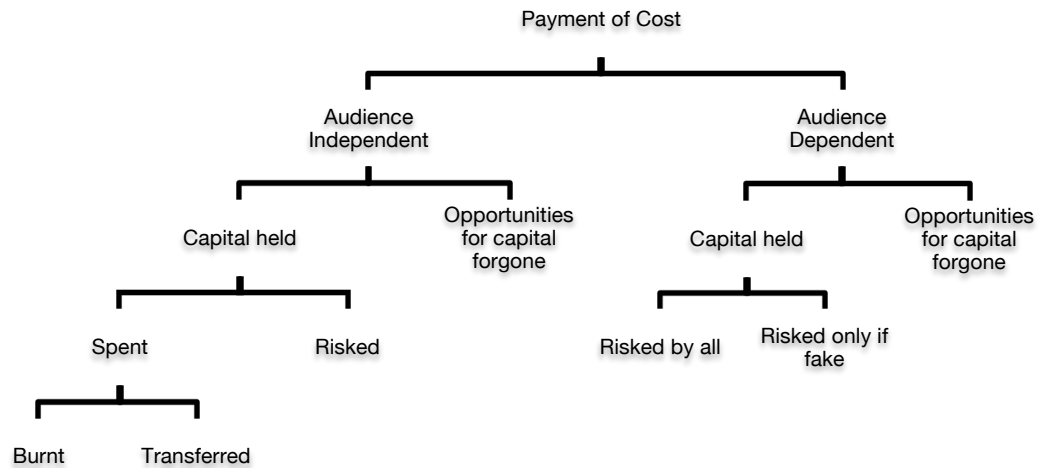
669

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

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

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