

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Barker, Jessica L.; Power, Eleanor A.; Heap, Stephen; Puurtinen, Mikael; Sosis, Richard

Title: Content, cost, and context : A framework for understanding human signaling systems

Year: 2019

Version: Accepted version (Final draft)

Copyright: © 2019 Wiley Periodicals, Inc.

Rights: In Copyright

Rights url: <http://rightsstatements.org/page/InC/1.0/?language=en>

Please cite the original version:

Barker, J. L., Power, E. A., Heap, S., Puurtinen, M., & Sosis, R. (2019). Content, cost, and context : A framework for understanding human signaling systems. *Evolutionary Anthropology*, 28(2), 86-99. <https://doi.org/10.1002/evan.21768>

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

2

3 Jessica L. Barker*^{1,2}

4 Eleanor A. Power*^{3,4}

5 Stephen Heap⁵

6 Mikael Puurtinen⁵

7 Richard Sosis⁶

8

9 *Joint first authors and corresponding authors:

10 jessica.barker@bi.team, +44 7780 752 614; e.a.power@lse.ac.uk, +44 207 955 7997

11 ¹Aarhus Institute of Advanced Studies, Aarhus University, Denmark

12 ²Current address: The Behavioural Insights Team, London, UK

13 ³Santa Fe Institute, New Mexico, USA

14 ⁴Current address: Department of Methodology, London School of Economics and Political
15 Science, UK

16 ⁵Department of Biological and Environmental Science, University of Jyväskylä, Finland

17 ⁶Department of Anthropology, University of Connecticut, USA

18

19 Number of text pages: 28

20 Number of figures: 2

21

22 **Keywords:** communication, signaling theory, honest signaling, sender and receiver, audience
23 independent and dependent costs

24 **Author biographies**

25

26 Jessica L. Barker is an Associate Research Advisor at The Behavioural Insights Team, and was
27 formerly a Junior Fellow at the Aarhus Institute of Advanced Studies. She is interested the
28 evolution of cooperation in humans and other animals, focusing on cooperation and competition
29 within and among groups.

30

31 Eleanor A. Power is Assistant Professor in the Department of Methodology at the London
32 School of Economics and Political Science. She studies the reputational and social capital
33 consequences of religious action through fieldwork in Tamil Nadu, India.

34

35 Stephen Heap is a post-doctoral researcher in the Department of Biological and Environmental
36 Science at the University of Jyväskylä. He is interested in social systems and the interactions that
37 generate them.

38

39 Mikael Puurtinen is a University Researcher in the Department of Biological and Environmental
40 Science at the University of Jyväskylä. He is interested in the evolution of social systems,
41 especially cooperative and competitive interactions in human groups.

42

43 Richard Sosis is the James Barnett Professor of Humanistic Anthropology at the University of
44 Connecticut. His work focuses on the evolution of religion and he is co-founder and co-editor of
45 the journal *Religion, Brain & Behavior*, which publishes research on the bio-cultural study of
46 religion.

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 displays¹⁻⁴, drawing inspiration from behavioral ecology³⁻⁵,
51 economics,⁶ and the social sciences^{7,8}. While signaling theory is broadly aimed at explaining
52 honest communication, it has come to be strongly associated with the handicap principle⁹, which
53 proposes that such costly extravagance is in fact an adaptation for signal reliability³⁻⁵. 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 communication¹⁰. 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 signaling³⁻⁶, 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 expertise¹¹. 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 status¹². 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^{10,13}. For example, anthropologists found evidence suggesting that signal
82 senders convey information about their strength¹¹, skill¹⁴, prosociality^{15,16}, commitments^{17–19}, and
83 social status^{2,20}, 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^{11,12,14,21–23} (Box 2A); ii) contribution to a public good, as with blood donation^{24,25} (Box
87 2B); iii) religious behaviors that entail sizable investments of time, money, and energy in the
88 name of the divine^{17,19,26–30} (Box 2C). Empirical investigations have suggested that signals result
89 in improved status and reputational standing²⁷, leading to increased social support and well-
90 being^{16,19,23,29,31}, and ultimately reproductive success^{32–34}.

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 individuals³⁵⁻⁴¹. 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^{11,13,21,42}, 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 signaling⁴³ or what (if any) costs signaling may entail.

114

115 Consider a female sedge warbler hearing the song of a male⁴⁴. 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 response⁴⁵. 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^{9,38,45-49}.

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 song⁵⁰.

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"^{5,6}, 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^{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 contacts⁷. 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 songs⁵⁰), 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 character²⁷ (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"⁴¹. 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)⁴¹.

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^{38,47,53}, 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 misunderstanding⁹.

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 individual³⁻⁶. 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 matrilines²².

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^{49,54}. 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 scarification⁵⁵). 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^{9,38,47,48}—we suggest that such costs
246 are in fact compatible with signaling theory^{46,54} 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)^{36,38,53,56–58}. 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 warfare⁵⁹. 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^{53,60}. 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 setting⁶¹. The large literature on
273 monitoring and punishment makes clear the power of audience-dependent costs to drive
274 behavior⁶². 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”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 territory⁴⁴. 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 members⁷²) 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

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 economy⁷⁴. 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 assumed⁴³. 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 spend⁷⁵. 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 raid⁵⁵ 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

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 members⁷⁷. 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 above⁷⁴. 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^{43,53}. 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 matriline 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 strength²², 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^{78,79}. 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 inseparably⁴⁹. 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 change²⁷. 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^{48,80}. 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 challenging⁹. 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 culturally⁵¹. 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^{55,81}. 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 livelihood⁵¹. 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 influential⁹. 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 behavior⁴⁷. However, if the sender benefits,
486 cues can evolve into signals, making the boundary between signals and cues sometimes fuzzy⁸².

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^{9,10,13,46,49,80,83}.

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” signals⁵⁶ 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 bluff⁸⁴.

499

500 *Differential benefits*

501 Honesty can be maintained by differential benefits, rather than differential costs⁸⁵. For example,
502 a need can be honestly signaled when those most lacking benefit more, such as when chicks beg
503 for food⁸⁶.

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)^{47,65,87,46,88}. There is some debate among biologists concerning the boundary between indices
509 and costly signals⁸⁹, 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^{90,91}, 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 colleagues⁹² 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 others¹⁴. This interpretation of men's hunting has been
529 critiqued⁹³⁻⁹⁵, including recent concerns that hunting is too noisy to serve as an honest signal of
530 quality⁷⁹. Wood and Marlowe⁹⁶, 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 signal⁴⁷, 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 moiety⁹⁸.

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 guests⁹⁷⁻⁹⁹. 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 crests⁹⁹. That is,
588 such signals may be multiplex.

589
590 While these dramatic signals of spent capital are the main event of the potlatch⁹⁸, 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 Kan⁹⁸ 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. Ringel¹⁰⁰ 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 status⁹⁷. Boone² 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

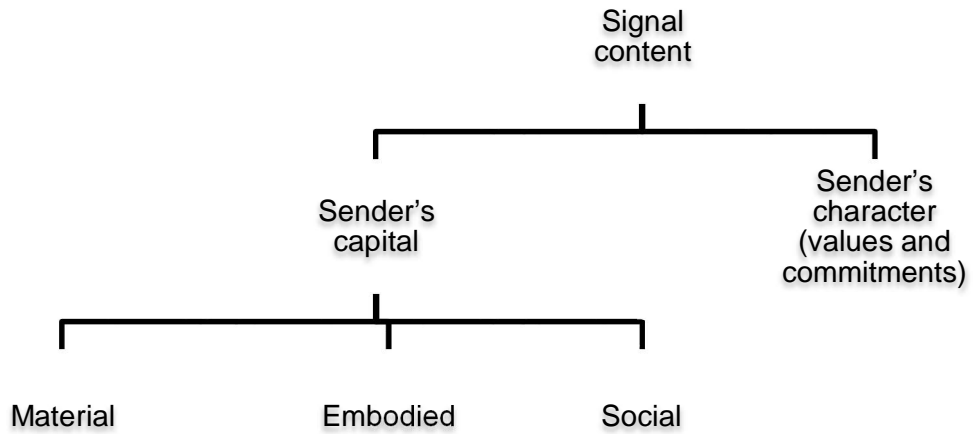
639 These various displays of religious devotion are not only seen as evidence of a person's
640 devotion; much more is inferred about a person from the sum total of her religious displays
641 (Figure 1). Villagers appear to be using these displays to discern something about the capital and
642 character of the individual²⁷. 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 relationships²⁹.

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)
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

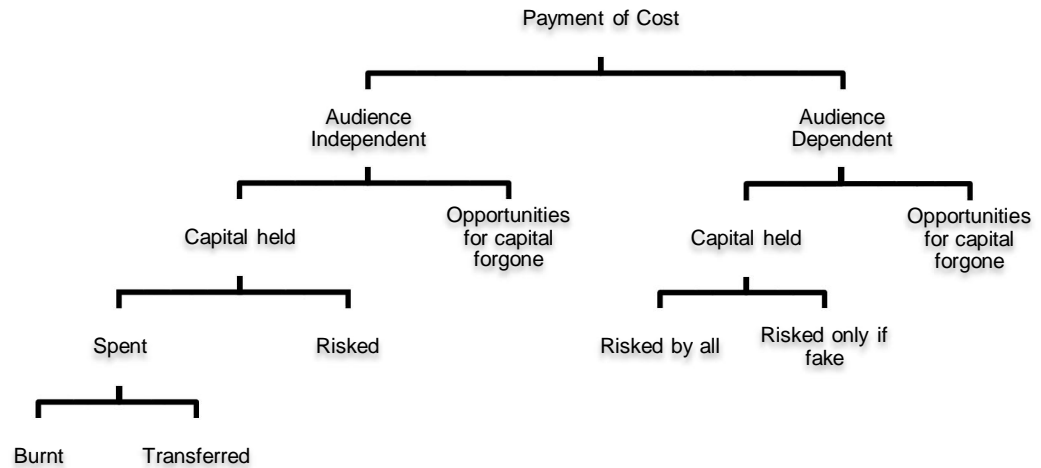
Tubers	-	Strength, stamina, skill	-	Commitment to supporting your family (and friends)
Honey	-	Strength, stamina, skill	-	Commitment to supporting your family (and friends)
Tlingit Potlatch				
	Material capital	Embodied capital	Social capital	Character (values and commitments)
Mock battles	Time and 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, risky	Audience independent, forgone	Audience dependent, risky by all	Audience dependent, risky if fake	Audience dependent, forgone
Vow fulfillment (e.g., firewalking)	<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
Attending monthly puja	<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	-	-	-

<p>Wearing tilaka</p>	<p><i>Material:</i> minor costs of mark</p>	<p>-</p>	<p>-</p>	<p>-</p>	<p><i>Social, embodied:</i> risk of discrimination (and violence) because of membership</p>	<p><i>Embodied, material:</i> risk of physical or financial punishment <i>Social:</i> risk of reputation loss, ostracism</p>	<p><i>Social:</i> forgone socializing with those of other religions</p>
<p>Hadza Foraging</p>							
	<p>Audience independent, burnt</p>	<p>Audience independent, transferred</p>	<p>Audience independent, risked</p>	<p>Audience independent, forgone</p>	<p>Audience dependent, risked by all</p>	<p>Audience dependent, risked if fake</p>	<p>Audience dependent, forgone</p>
<p>Big game hunting & sharing</p>	<p><i>Embodied:</i> energy expended in pursuit</p>	<p><i>Material:</i> meat given to/taken by others, often without the control of the hunter (tolerated scrounging)</p>	<p><i>Embodied:</i> risk of physical harm</p>	<p><i>Material:</i> opportunity cost of time spent in pursuit (though paper showing they eat plenty on the way)</p>	<p>-</p>	<p><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</p>	<p>-</p>
<p>Tuber digging & sharing</p>	<p><i>Embodied:</i> energy</p>	<p>-</p>	<p>-</p>	<p><i>Material:</i> opportunity cost of time</p>	<p>-</p>	<p>-</p>	<p>-</p>

	expended in pursuit			spent in pursuit			
Honey collection & sharing	<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	-
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	<i>Material:</i> may involve some destruction of own property	-	-	<i>Material:</i> minor opportunity cost of time	-	-	-
Dancing, songs & oratory	<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
Feasting & distribution of gifts	<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.

687 **ACKNOWLEDGEMENTS**

688 JLB was supported by an Aarhus Institute of Advanced Studies - Marie Curie COFUND
689 Fellowship, EAP by an Omidyar Fellowship at the Santa Fe Institute, SH by Academy of Finland
690 grant 292786, MP by Academy of Finland grant 258385, and RS by the James Barnett
691 Endowment. We thank the Aarhus Institute of Advanced Studies for hosting a meeting of the
692 authors, and Eric Smith, Szabolcs Számádó, and two anonymous reviewers for valuable
693 comments on the manuscript.

694

695 **BIBLIOGRAPHY**

- 696 **1** Cronk L. 1994. Evolutionary theories of morality and the manipulative use of signals. *Zygon*
697 29:81–101.
- 698 **2** Boone JL. 1998. The evolution of magnanimity. *Hum Nat* 9:1–21.
- 699 **3** Zahavi A. 1975. Mate selection - a selection for a handicap. *J Theor Biol* 53:205–214.
- 700 **4** Zahavi A. 1977. The cost of honesty (further remarks on the handicap principle). *J Theor Biol*
701 67:603–605.
- 702 **5** Grafen A. 1990. Biological signals as handicaps. *J Theor Biol* 144:517–546.
- 703 **6** Spence M. 1973. Job market signaling. *Q J Econ* 87:355–374.
- 704 **7** Bourdieu P. 1986. The forms of capital. In: Richardson JG, editor. *Handb. Theory Res. Sociol.*
705 *Educ.* New York: Greenwood. p 239–258.
- 706 **8** Veblen T. 1899. *The theory of the leisure class: An economic study in the evolution of*
707 *institutions.* New York: Macmillan.
- 708 **9** Grose J. 2011. Modelling and the fall and rise of the handicap principle. *Biol Philos* 26:677–
709 696.

- 710 **10** Cronk L. 2005. The application of animal signaling theory to human phenomena: some
711 thoughts and clarifications. *Soc Sci Inf* 44:603–620.
- 712 **11** Bliege Bird R et al. 2001. The hunting handicap: costly signaling in human foraging
713 strategies. *Behav Ecol Sociobiol* 50:9–19.
- 714 **12** Smith EA, Bliege Bird RL. 2000. Turtle hunting and tombstone opening: public generosity as
715 costly signaling. *Evol Hum Behav* 21:245–261.
- 716 **13** Bliege Bird R, Smith EA. 2005. Signaling theory, strategic interaction, and symbolic capital.
717 *Curr Anthropol* 46:221–248.
- 718 **14** Hawkes K, Bliege Bird R. 2002. Showing off, handicap signaling, and the evolution of men’s
719 work. *Evol Anthropol* 11:58–67.
- 720 **15** Bliege Bird R, Power EA. 2015. Prosocial signaling and cooperation among Martu hunters.
721 *Evol Hum Behav* 36:389–397.
- 722 **16** Bliege Bird R et al. 2012. The hierarchy of virtue: mutualism, altruism and signaling in Martu
723 women’s cooperative hunting. *Evol Hum Behav* 33:64–78.
- 724 **17** Bulbulia J, Sosis R. 2011. Signalling theory and the evolution of religious cooperation.
725 *Religion* 41:363–388.
- 726 **18** Hagen E, Bryant G. 2003. Music and dance as a coalition signaling system. *Hum Nat* 14:21–
727 51.
- 728 **19** Soler M. 2012. Costly signaling, ritual and cooperation: evidence from Candomblé, an Afro-
729 Brazilian religion. *Evol Hum Behav* 33:346–356.
- 730 **20** Munson J et al. 2014. Classic Maya bloodletting and the cultural evolution of religious rituals:
731 quantifying patterns of variation in hieroglyphic texts. *PLoS One* 9:e107982.
- 732 **21** Smith EA et al. 2003. The benefits of costly signaling: Meriam turtle hunters. *Behav Ecol*

- 733 14:116–126.
- 734 **22** Sosis R. 2000. Costly signaling and torch fishing on Ifaluk atoll. *Evol Hum Behav* 21:223–
- 735 244.
- 736 **23** Gurven M et al. 2000. “It’s a Wonderful Life”: signaling generosity among the Ache of
- 737 Paraguay. *Evol Hum Behav* 21:263–282.
- 738 **24** Gintis H et al. 2001. Costly signaling and cooperation. *J Theor Biol* 213:103–119.
- 739 **25** Lyle HFI, Smith EA. 2014. The reputational and social network benefits of prosociality in an
- 740 Andean community. *Proc Natl Acad Sci U S A* 111:4820–4825.
- 741 **26** Sosis R, Alcorta C. 2003. Signaling, solidarity, and the sacred: the evolution of religious
- 742 behavior. *Evol Anthropol* 12:264–274.
- 743 **27** Power EA. 2017. Discerning devotion: testing the signaling theory of religion. *Evol Hum*
- 744 *Behav* 38:82–91.
- 745 **28** Irons W. 2001. Religion as a hard-to-fake sign of commitment. In: Nesse RM, editor. *Evol.*
- 746 *Capacit. Commit.* New York: Russell Sage Foundation. p 290–309.
- 747 **29** Power EA. 2017. Social support networks and religiosity in rural South India. *Nat Hum*
- 748 *Behav* 1:0057.
- 749 **30** Henrich J. 2009. The evolution of costly displays, cooperation and religion: credibility
- 750 enhancing displays and their implications for cultural evolution. *Evol Hum Behav* 30:244–260.
- 751 **31** Lyle HFI, Smith EA. 2014. The reputational and social network benefits of prosociality in an
- 752 Andean community. *Proc Natl Acad Sci U S A* 111:4820–4825.
- 753 **32** von Rueden C et al. 2010. Why do men seek status? Fitness payoffs to dominance and
- 754 prestige. *Proc R Soc B* 278:2223–2232.
- 755 **33** Smith EA. 2004. Why do good hunters have higher reproductive success? *Hum Nat* 15:343–

- 756 364.
- 757 **34** von Rueden CR, Jaeggi A V. 2016. Men's status and reproductive success in 33 nonindustrial
758 societies: Effects of subsistence, marriage system, and reproductive strategy. *Proc Natl Acad Sci*
759 *U S A* 113:10824–10829.
- 760 **35** Hebets EA, Papaj DR. 2005. Complex signal function: developing a framework of testable
761 hypotheses. *Behav Ecol Sociobiol* 57:197–214.
- 762 **36** Hurd PL, Enquist M. 2005. A strategic taxonomy of biological communication. *Anim Behav*
763 70:1155–1170.
- 764 **37** McGregor PK. 2005. *Animal Communication Networks*. Cambridge: Cambridge University
765 Press.
- 766 **38** Searcy WA, Nowicki S. 2005. *The Evolution of Animal Communication*. Princeton, NJ:
767 Princeton University Press.
- 768 **39** Rendall D et al. 2009. What do animal signals mean? *Anim Behav* 78:233–240.
- 769 **40** Ruxton GD, Schaefer HM. 2011. Resolving current disagreements and ambiguities in the
770 terminology of animal communication. *J Evol Biol* 24:2574–2585.
- 771 **41** Hebets EA et al. 2016. A systems approach to animal communication. *Proc R Soc London B*
772 *Biol Sci* 283:20152889.
- 773 **42** Soler M et al. 2014. In the eye (and ears) of the beholder: Receiver psychology and human
774 signal design. *Evol Anthropol* 23:136–145.
- 775 **43** Lachmann M, Bergstrom CT. 1998. Signalling among relatives. II. Beyond the Tower of
776 Babel. *Theor Popul Biol* 54:146–160.
- 777 **44** Buchanan KL, Catchpole CK. 1997. Female choice in the sedge warbler *Acrocephalus*
778 *schoenobaenus*: multiple cues from song and territory quality. *Proc R Soc B* 264:521–526.

- 779 **45** Bradbury JW, Vehrencamp SL. 1998. Principles of Animal Communication. 1st ed.
780 Sunderland, MA: Sinauer Associates.
- 781 **46** Fraser B. 2012. Costly signalling theories: beyond the handicap principle. *Biol Philos* 27:263–
782 278.
- 783 **47** Maynard Smith J, Harper D. 2003. Animal Signals. Oxford: Oxford University Press.
- 784 **48** Számadó S. 2011. The cost of honesty and the fallacy of the handicap principle. *Anim Behav*
785 Elsevier Ltd. 81:3–10.
- 786 **49** Számadó S. 2012. The rise and fall of handicap principle: a commentary on the “Modelling
787 and the fall and rise of the handicap principle.” *Biol Philos* 27:279–286.
- 788 **50** Buchanan KL et al. 1999. Song as an indicator of parasitism in the sedge warbler. *Anim*
789 *Behav* 57:307–314.
- 790 **51** Borgerhoff Mulder M et al. 2009. Intergenerational wealth transmission and the dynamics of
791 inequality in small-scale societies. *Science* 326:682–688.
- 792 **52** Kaplan H. 1996. A theory of fertility and parental investment in traditional and modern
793 human societies. *Am J Phys Anthropol* 101:91–135.
- 794 **53** Lachmann M et al. 2001. Cost and conflict in animal signals and human language. *Proc Natl*
795 *Acad Sci U S A* 98:13189–13194.
- 796 **54** Polnaszek TJ, Stephens DW. 2015. Why are signals reliable? Honesty depends on costs,
797 sometimes. *Anim Behav* 110:e13–e16.
- 798 **55** Sosis R et al. 2007. Scars for war: evaluating alternative signaling explanations for cross-
799 cultural variance in ritual costs. *Evol Hum Behav* 28:234–247.
- 800 **56** Guilford T, Dawkins MS. 1995. What are conventional signals? *Anim Behav* 49:1689–1695.
- 801 **57** Dawkins MS. 1993. Are there general principles of signal design? *Philos Trans R Soc B*

- 802 340:251–255.
- 803 **58** Vehrencamp SL. 2000. Handicap, index, and conventional signal elements of bird song. In:
804 Espmark Y et al., editors. *Anim. Signals Signal. Signal Des. Anim. Commun.* Trondheim,
805 Norway: Tapir Academic Press. p 277–300.
- 806 **59** Rappaport RA. 1999. *Ritual and Religion in the Making of Humanity.* Cambridge: Cambridge
807 University Press.
- 808 **60** Smith EA. 2010. Communication and collective action: language and the evolution of human
809 cooperation. *Evol Hum Behav* 31:231–245.
- 810 **61** Sosis R. 2003. Why aren't we all Hutterites? *Hum Nat* 14:91–127.
- 811 **62** Boyd R, Richerson PJ. 1992. Punishment allows the evolution of cooperation (or anything
812 else) in sizable groups. *Ethol Sociobiol* 13:171–195.
- 813 **63** Boyd R, Mathew S. 2015. Third-party monitoring and sanctions aid the evolution of
814 language. *Evol Hum Behav* 36:475–479.
- 815 **64** Guilford T, Dawkins MS. 1991. Receiver psychology and the evolution of animal signals.
816 *Anim Behav* 42:1–14.
- 817 **65** Maynard Smith J, Harper D. 1995. Animal signals: models and terminology. *J Theor Biol*
818 177:305–311.
- 819 **66** Rowe C. 1999. Receiver psychology and the evolution of multicomponent signals. *Anim*
820 *Behav* 58:921–931.
- 821 **67** Candolin U. 2003. The use of multiple cues in mate choice. *Biol Rev* 78:575–595.
- 822 **68** Partan SR, Marler P. 2005. Issues in the classification of multimodal communication signals.
823 *Am Nat* 166:231–245.
- 824 **69** Bro-Jørgensen J. 2010. Dynamics of multiple signalling systems: animal communication in a

- 825 world in flux. *Trends Ecol Evol* 25:292–300.
- 826 **70** Higham JP, Hebets EA. 2013. An introduction to multimodal communication. *Behav Ecol*
827 *Sociobiol* 67:1381–1388.
- 828 **71** Johnstone RA. 1996. Multiple displays in animal communication: “backup signals” and
829 “multiple messages.” *Philos Trans R Soc B* 351.
- 830 **72** McCullough ME et al. 2016. Christian religious badges instill trust in Christian and non-
831 Christian perceivers. *Psycholog Relig Spiritual* 8:149–163.
- 832 **73** Reichard DG, Anderson RC. 2015. Why signal softly? The structure, function and
833 evolutionary significance of low-amplitude signals. *Anim Behav* 105:253–265.
- 834 **74** Berman E. 2000. Sect, subsidy, and sacrifice: an economist’s view of ultra-orthodox Jews. *Q*
835 *J Econ* 115:905–953.
- 836 **75** Mishra S et al. 2017. The relative state model: integrating need-based and ability-based
837 pathways to risk-taking. *Personal Soc Psychol Rev* 21:176–198.
- 838 **76** Rich P, Zollman KJS. 2016. Honesty through repeated interactions. *J Theor Biol* 395:238–
839 244.
- 840 **77** Gavrilets S, Fortunato L. 2014. A solution to the collective action problem in between-group
841 conflict with within-group inequality. *Nat Commun* 5:3526.
- 842 **78** Wilkins MR et al. 2015. Multimodal signalling in the North American barn swallow: a
843 phenotype network approach. *Proc R Soc London B The Royal Society*. 282:20151574.
- 844 **79** Stibbard-Hawkes DNE et al. 2018. A noisy signal: to what extent are Hadza hunting
845 reputations predictive of actual hunting skills? *Evol Hum Behav* in press.
- 846 **80** Higham JP. 2014. How does honest costly signaling work? *Behav Ecol* 25:8–11.
- 847 **81** Sosis R, Bressler ER. 2003. Cooperation and commune longevity: a test of the costly

- 848 signaling theory of religion. *Cross-Cultural Res* 37:211–239.
- 849 **82** Biernaskie JM et al. 2018. A general model of biological signals, from cues to handicaps.
850 *Evol Lett*.
- 851 **83** Zollman KJS. 2013. Finding alternatives to handicap theory. *Biol Theory* 8:127–132.
- 852 **84** Silk JB et al. 2000. Cheap talk when interests conflict. *Anim Behav* 59:423–432.
- 853 **85** Johnstone RA. 1997. The evolution of animal signals. In: Krebs JR, Davies NB, editors.
854 *Behav. Ecol. An Evol. Approach*. Oxford: Oxford University Press. p 155–178.
- 855 **86** Kilner R, Johnstone RA. 1997. Begging the question: are offspring solicitation behaviours
856 signals of need? *Trends Ecol Evol* 12:11–15.
- 857 **87** Frank RH. 1988. *Passions Within Reason*. New York: Norton.
- 858 **88** Reby D, McComb K. 2003. Anatomical constraints generate honesty: acoustic cues to age
859 and weight in the roars of red deer stags. *Anim Behav* 65:519–530.
- 860 **89** Biernaskie JM et al. 2014. The evolution of index signals to avoid the cost of dishonesty. *Proc*
861 *R Soc London B Biol Sci* 281.
- 862 **90** Marlowe F. 2010. *The Hadza: hunter-gatherers of Tanzania*. Berkeley, CA: University of
863 California Press.
- 864 **91** Blurton Jones NG. 2016. *Demography and evolutionary ecology of Hadza hunter-gatherers*.
865 Cambridge: Cambridge University Press.
- 866 **92** Hawkes K et al. 2001. Hunting and nuclear families: some lessons from the Hadza about
867 men's work. *Curr Anthropol* 42:681–709.
- 868 **93** Hill K et al. 1993. On why male foragers hunt and share food. *Curr Anthropol* University of
869 Chicago Press. 34:701–710.
- 870 **94** Wood B, Hill K. 2000. A test of the “showing-off” hypothesis with Ache hunters. *Curr*

- 871 Anthropol 41:124–125.
- 872 **95** Hill K, Kintigh K. 2009. Can anthropologists distinguish good and poor hunters? Implications
873 for hunting hypotheses, sharing conventions, and cultural transmission. *Curr Anthropol* 50:369–
874 378.
- 875 **96** Wood BM, Marlowe FW. 2014. Toward a reality-based understanding of Hadza men’s work.
876 *Hum Nat* 25:620–630.
- 877 **97** Barnett HG. 1938. The nature of the potlatch. *Am Anthropol* 6:145–238.
- 878 **98** Kan S. 1986. The 19th-century Tlingit potlatch: a new perspective. *Am Ethnol* 13:191–212.
- 879 **99** Kan S. 2015. *Symbolic Immortality: The Tlingit Potlatch of the Nineteenth Century*. 2nd ed.
880 Seattle: University of Washington Press.
- 881 **100** Ringel G. 1979. The Kwakiutl potlatch: history, economics, and symbols. *Ethnohistory*
882 26:347–362.
- 883