# Showing Off, Handicap Signaling, and the Evolution of Men's Work

KRISTEN HAWKES AND REBECCA BLIEGE BIRD

Zahavi's<sup>1,2</sup> handicap principle makes "waste" a common outcome of signal selection because the cost of a signal guarantees its honesty. The capacity to bear the cost reveals the show-off's hidden qualities. While displays take many forms, some also provide fitness-related benefits to the audience *in addition* to information about the show-off. Zahavi<sup>3</sup> has used the handicap principle to explain both merely wasteful displays and altruistic behavior. Here we focus on the distinction between these two kinds of display and the importance of benefits other than information in show-off explanations of a particular puzzle in human evolution: men's work. Males of other primate species do not contribute any significant fraction of the food consumed by females and juveniles. Our own species is different. When people live on wild foods, hunting is usually a specialty of men, and meat is commonly a substantial component of everyone's diet. Here we explore the hypothesis that this unique male subsistence contribution may have evolved as hunting large animals became a focus of competitive display.

Displays are a form of communication, providing information about an individual, often in a widely observable forum. In order for a display to be worth performing, there must be an audience. In order for observers to bother paying attention, it must benefit them to do so. According to costly signaling theory,<sup>1,2,4–6</sup> the observer benefit for paying attention is the information about an otherwise hidden quality that is conveyed by the display. The information is kept honest through intrinsic links between the

production of the display and the quality being advertised. Honesty is ensured when individuals of higher quality can pay highest costs to produce a more elaborate display or when individuals gain higher benefits for producing a display of given cost.7 The differential costs or benefits of signal production make it highly unlikely that lower-quality individuals will be able to fake the signal: they cannot afford to. The honesty of the information provided in a display gives an immediate benefit to observers because they can use the information to adjust their own behavior toward the show-off to benefit themselves. Show-offs benefit from the treatment that follows. Bluffs about the show-off's quality would not inform the audience, so only signals that are too costly to fake are reliable. Zahavi's label, "the handicap principle," underlines the paradox that it is cost to the signaler that makes displays honest enough to be worthy of audience attention.

Costly signaling models are proving useful for unraveling an array of an-

thropological puzzles, including seemingly maladaptive cultural practices, monumental architecture, relatively inefficient foraging behaviors, and generosity.8-13 Bliege Bird14-16 has shown that attention to the signaling content of foraging strategies can help explain differences between the efforts that men and women devote to them. Among the Meriam Islanders of the Torres Strait, turtle hunters supply meat that is widely shared at feasts, while spearfishers target prey that are too small to be widely shared but are especially difficult to capture. Signal content can help explain why men forego sardine fishing or shell-fish collecting which could earn them a higher rate of nutrient acquisition than the activities they do choose.

Costly signals are enormously variable. One important dimension of variation is between signals that provide little but information and those that provide benefits to the audience in addition to information. For example, when a display consists of providing feasts, others gain from participating in the feast. By signaling in this way, the show-off provides something *besides information about a hidden quality* to the audience.

Zahavi<sup>1,2,3,17,18</sup> has applied his handicap principle to both kinds of display, proposing that the "altruism" of the second kind, in which the fitness-related benefits other than information are supplied to audiences, can be explained by its contribution to the effectiveness of the signal. For example, among the cooperatively breeding birds he has studied for decades (Arabian babblers, *Turdoides squamiceps*), dominants display their quality by standing sentinel duty, distracting or fending off predators, and presenting

Kristen Hawkes, Professor of Anthropology at the University of Utah, uses evolutionary ecology to investigate age and sex differences in human foraging strategies, with special emphasis on problems in human evolution.

Rebecca Bliege Bird, Research Assistant Professor in the same department, uses behavioral ecology to investigate age and sex differences in human foraging strategies, with special emphasis on explaining ethnographic variation.

food to subordinates. Displays that supply such benefits are readily noted by other babblers. Demonstration of the capacity to bear the cost of these displays substitutes for overt threats, which potentially lead to fights that could be even more costly for the signaler and at least some of the audience. Using the label "conspicuous donations," Zahavi underlines, as did Veblen<sup>19</sup> in his classic 1899 analysis, the similarity between public generosity and "conspicuous consumption."<sup>12</sup>

# HUNTING AS DISPLAY

Recognition that signal content may play a role in the evolution of socially productive behaviors has implications with respect to variability in the relative subsistence contributions of males and females. Among foragers, men produce, on average, from 30% of all calories to nearly 100%, if one does not count a woman's processing and tool preparation as contributing to production.<sup>20</sup> These long-term averages often include extremely high short-term variation, including periods when men provide little or nothing. Where men's average caloric production is disproportionately greater than women's, men almost always spend most of their foraging time hunting large game animals and then sharing them widely, producing more calories for the group than for their own households. The traditional explanation for this pattern relies on two often untested and somewhat paradoxical assumptions: that such hunting is part of the most efficient energy or protein maximization strategy and that such hunting is inefficient when attempted by women. Because these two assumptions may not always hold,14 some other explanation is warranted.

Men's contribution to subsistence may have evolved and may persist because men establish and maintain their relative social standing by showing off their hunting prowess. Various versions of that show-off hypothesis propose that hunters attract the favorable attention of many potential consumers by acquiring foods that are widely consumed.<sup>12,15,16,21–23</sup> The interest all have in the meat acquired by hunters makes hunting a central arena for social competition among men. When hunters target large prey, and when others can learn about and compare their successes, hunting reputation becomes a prominent determinant of how desirable a neighbor and ally, and how dangerous a rival, a man might be.<sup>24,25</sup>

One treatment of the show-off hypothesis for men's work emphasizes the value the audience places on meat and the nutritional gains they realize from preferential association with show-offs, both of which give successful hunters latitude in pressing their own interests.<sup>23</sup> It is proposed that a man's reputation as a hunter affects the way that others treat him because of the nutritional benefits they expect from living in the same group with him.

This argument depends on an important inference about the wide shar-

Recognition that signal content may play a role in the evolution of socially productive behaviors has implications with respect to variability in the relative subsistence contributions of males and females.

ing of meat. Ethnographers have long noted that people in small face-to-face communities share food readily.26,27 Anthropologists from diverse theoretical traditions have favored explanations for this sharing that focus on reducing the nutritional income variability of unpredictable resources (see Box 1). This explanation has been especially favored for meat sharing. Game animals are large enough, and hunting is risky enough, that if hunters owned the meat of the prey they killed they would increase the average nutritional utility they derive from it by giving shares they value little when they have a lot in exchange for the larger benefit of shares to be repaid later when they have little. The stability of this sharing strategy depends on the exclusion of nonreciprocators. However, no quantitative studies of food sharing have found consumers repaying the hunter by returning shares of meat to him (see Box 2). Without strictly contingent sharing, in which providing meat at one time is the necessary price for claiming meat at another, those who free-ride on the work of others net greater nutritional gains than do the workers.

If meat distributions do not exclude free-riders, then the meat of large animals can be rather like a public good. If supplied by one, consumption benefits will be claimed by many. When individual effort supplies goods that also benefit others, individual and collective interests in those goods can be at odds, resulting in collective-action problems.<sup>28</sup> Because consumers can benefit whether or not they themselves are providers, public goods are often under-supplied.29 As with community defense or public radio, nonproviders can free-ride, so that a provider's own expected consumption gain from such goods is not enough incentive to supply them. Why pay for what you can get for free?30 This problem arises with any good that is not the private property of the producer. The distinction between private and public goods turns on whether or not users can exclude other claimants and whether anyone's consumption of the good affects the consumption benefits available to others. A perfectly public good cannot be used exclusively by anyone. Also, consumers can use it concurrently; that is, consumption by one does not reduce what is available to others. Ostrom and Ostrom<sup>31</sup> usefully distinguished these two independent dimensions, labeling them "exclusion" and "subtractability." Because both excludability and subtractability are more continuous than discrete, few goods are perfectly private or perfectly public. But some goods allow more concurrent consumption; and sometimes exclusion is impossible, or its costs are too high to pay.32,33

Because hunting successes can be so unpredictable and the meat then go mostly to others, whether by demand sharing, tolerated theft, or normative rules of distribution, the nutritional benefits a hunter can expect for him-

#### Box 1. Reciprocity in the Sharing of Display Game

Models of sharing used by behavioral ecologists typically incorporate Trivers'86 model of reciprocal altruism in which an individual pays a short-term cost that benefits someone else but nets an overall profit when the beneficiary later returns the favor. Trivers highlighted the substantial benefits that reciprocal altruists would accumulate as compared to nonsharers if they could somehow overcome their vulnerability to exploitation by recipients who did not repay. His ideas were supported by formal modeling and computer simulations designed to tease out the precise conditions that allow reciprocal altruism to be evolutionarily stable. That work showed that reciprocators could do well if they clustered together and if the range of alternative strategies was sharply limited. In the case of humans, Trivers suggested that features of our emotional architecture such as guilt and moralistic aggression indicate an evolutionary design for reciprocal altruism. Pairwise exchanges of private goods among humans can be highly reciprocal and subject not only to stringent control, but also conventions about valuation and expectations regarding the timing and quantity of returns (for example, Hxaro gift exchange,87 Kula88).

But human sharing can also involve multiple recipients and have few, if any, of these features. In cases where food flows to multiple recipients and few are excluded, sharing may not be exchange at all. Instead of trading shares with each other, claimants may be appropriating shares from the "public domain." Blurton Jones<sup>32,33</sup> noted that food sharing need not imply owners paying a cost to give up shares. Instead of ownership rights falling automatically on the acquirer, there could be a cost for defending shares from the claims of other users. The costs of not sharing could sometimes be too high to be worth paying.89 The Blurton Jones "tolerated-theft" model showed that sharing could result if resources came in large but divisible lumps, but not to everyone at once, and if consumers were prepared to press claims for a share according to the nutritional value of the resource to them. As he noted, this need not mean incessant squabbling, since potential claimants

gauging the interest and appetite of others would do better not to start fights they would be likely to lose.

The exchange model, in contrast, assumes that suppliers own whatever they acquire. They thus incur a cost when giving up shares, but net a compensating benefit from subsequent repayment. The repayment is necessary for reciprocal altruism to be stable. Nonreciprocators must be excluded, something that becomes increasingly difficult when strategies are more variable and groups include more than a few individuals.90-93 Repayment can be especially difficult to enforce when sharing is highly visible, as when very large game animals are acquired and successes are unpredictable, with the hunter's daily risk of failure generally increasing with prey size.24,25,54 When a biggame hunter is successful, there is a great deal of meat and many who are hungry for it, and many of them are armed with lethal weapons.33 Hunters themselves often do not control the distribution, so they cannot direct shares to or away from particular individuals based on either debts or prospects.25,40,50,55-57 Quantitative records of meat distributions over time often find claimants continuing to get shares whether or not they ever supply them, and hunters continuing to supply more meat even when others are deeply in their debt.48,51,56,57,94 When this is so, the question is why hunters continue to expend their effort supplying goods that go mostly to others.

It could be that in spite of the evidence that they do not control distributions of their prey, hunters are repaid by recipients in some other currency.<sup>47</sup> This would mean that the meat is not like a public good after all, but instead that consumers are, in some undetermined way, paying every hunter for each share. While this would not conform to the nutritional variability reduction models of sharing,<sup>27,95,96</sup> it would conform to Trivers'<sup>86</sup> model. Although the search for the currency in which to find repayments continues, both theoretical and empirical work has increasingly stimulated researchers from many fields to consider other explanatory pathways to the evolution of cooperation, sharing, and the provisioning of public goods.<sup>8,18,83,97–102</sup>

self and his family are not great enough to make hunting an effective provisioning strategy. This is strong provocation to look for other reasons why men hunt. Olson<sup>28</sup> noted that selective incentives, benefits that went only to suppliers, could motivate a supply of collective goods. Selective incentives could draw men into hunting. Men may be enticed to hunt because doing so earns them differential social attention. Rather than because of the nutritional value meat has for them or their families. This *could* pose another collective-action problem. If some paid special attention to a hunter, others might be able to freeride, consuming meat brought down by a hunter without paying special attention to him. In hypothesizing that preferential attention is the selective incentive motivating hunters, Hawkes<sup>23</sup> defined that problem away. Like the attention foragers pay to more productive patches by monitoring them more closely, preferential attention to better hunters was assumed to increase the chances for consuming meat.<sup>23,34</sup> However, some still see a secondorder collective-action problem lurking here.<sup>12,35,36</sup> If audience members can pay attention to the hunter and thus eat more of his meat without doing anything that benefits him, the hunter's selective incentive will disappear.

Smith and Bliege Bird<sup>12,37</sup> and Bliege Bird, Smith, and Bird<sup>15</sup> addressed these issues by using costly signaling as a model for the payoffs to hunters and observers. These models stress the *information* that others gain as the key to evolutionary stability. More than its value as a source of nutrition, meat is a medium of communication through which the hunter transmits information to potential mates, allies, and competitors. Collective-action problems do not arise in handicap models because it is mutually beneficial to both show-off and audience to have the information about the show-off's qualities revealed. Show-off's obtain differential treatment only by paying the signal cost; signal recipients obtain information about a signaler's quality only by attending to the signal.

If men hunt to display their relative quality, then the benefits they earn for that effort come not from exchanges of meat for other goods and services, but from the different ways that others treat them in light of the quality they reveal. Others use the information of hunting reputations to their own advantage in the numerous decisions of social life.

# THE HUNTER'S INCENTIVES

If hunting is a signal of quality, then the hunter's benefit does not depend on collecting repayments from each recipient of meat. Rather, hunters increase their prestige by contributing more than others do (See Box 3). Zahavi has observed babblers demonstrating superior stamina by competing to invest more in costly sentinel duty.<sup>3,17,18,38</sup> While others benefit from this public good, the providers earn prestige for their quality. "Social prestige functions like a peacock's tail or the song of a songbird. It attracts collaborators and deters rivals."<sup>3</sup>

In the human case, a reputation for good hunting generally affects a man's social standing relative to other men in foraging communities.<sup>20,39,40</sup> In the northern Kalahari, traditional hunters usually bagged no more than two or three large antelope in a year.<sup>41</sup> Thomas<sup>42</sup> reported the characterization of a famous man with the hyperbole that underlines the value placed on hunting success:

> It was said of him that he never returned from a hunt without having killed at least a wildebeest, if not something larger. Hence the people connected with him ate a great deal of meat and his popularity grew.

There is increasing evidence that good hunters in many societies enjoy

greater social, political, and reproductive success than do poorer competitors. Ache foragers of eastern Paraguay are an especially well-studied case.43 When living in the forest, Ache men spend nearly fifty hours a week in food acquisition,<sup>44</sup> supplying a very large fraction of a diet that is uncommonly ample among modern huntergatherers.45 The generous nutrient averages result not from high hourly foraging return rates but from these long hours,46,47 with better hunters spending the most time hunting<sup>48</sup> (see Box 3). Wide sharing is especially well documented in this case.49,27 While

Collective-action problems do not arise in handicap models because it is mutually beneficial to both showoff and audience to have the information about the show-off's qualities revealed. Show-offs obtain differential treatment only by paying the signal cost; signal recipients obtain information about a signaler's quality only by attending to the signal.

the Ache are on forest treks, any hunter's prey is distributed to all. The hunter himself has no hand in this distribution, and so does not direct shares preferentially to particular recipients.<sup>50</sup> The families of better hunters end up with no more meat than other families.<sup>27</sup> Hill and Hurtado's<sup>43</sup> demographic data show little difference in survival risk for the children of better hunters. But men rated as better hunters had much higher fertility. In a smaller data set,<sup>51</sup> better Ache hunters were more often named by women as lovers and as secondary fathers of more children. (Secondary fathers are men other than a mother's husband who were sexually involved with her at the time of her pregnancy). Ache women did not nominate hunting skill as a criterion for choosing a mate, but men emphasized its importance for success with women.<sup>43</sup>

In other ethnographic cases, hunting success is also associated with advantages in male competition. Hadza men foraging in northern Tanzania are big game specialists<sup>52–54</sup> (Fig. 1). As among the Ache, hunters do not control the distribution of meat.55-57 In this case, the wives and children of better hunters do have more positive weight gains,<sup>58</sup> and those wives have surviving children faster.59 But these differences are directly associated with the foraging effort of the women themselves.<sup>60,61</sup> As with the Ache, the wide sharing of meat means that Hadza women and children receive little of their meat from kills by their husband and father. Consistent with this, a father's death or parental divorce has no effect on child survival.62 However, better Hadza hunters tend to be married to harder-working wives.61 Older men who are better hunters have younger wives,59 suggesting they are more likely to leave an older wife to raise a second family-another way they have increased success in competing for paternity. Meriam turtle hunters also have higher age-specific reproductive success than do nonhunters and, as with the Hadza, this seems due to assortative mating: hunters claim more fertile wives than do nonhunters.63

# COMPARISONS WITH CHIMPANZEE HUNTING

Studies of the benefits chimpanzees obtain by hunting red colobus monkeys suggest some parallels with human hunting. In that species, hunting is also a male specialty, and meat is more widely shared than are other foods. Accumulating evidence suggests that chimpanzee hunting is best explained as a male strategy for gaining and maintaining higher status.<sup>64,65</sup> Stanford and coworkers<sup>66</sup> found that the three variables most strongly associated with the likeli-



# Box 2. Sharing Among the Hadza and the Meriam: Do Those Who Supply More Meat Receive More Meat From Others?

When sharing is exchange, someone is giving up a share, and so incurring a cost to get a repayment in return. What people say about their "rights" as claimants is relevant to this question, but it is also of interest to see, whatever the stated rules of ownership, whether there is a "quid pro quo" pattern in the actual flow of shares. Tests of reciprocal altruism in human food-sharing patterns sometimes show that recipients do repay suppliers.<sup>103</sup> Sometimes this applies to certain kinds of food and not others. For example, Gurven and coworkers,104 analysis of Hiwi sharing

patterns suggests that reciprocitybased explanations are more likely to apply to the sharing of nongame or nonforest resources. Game, especially large game, which often is shared in public, seems not to follow the same sharing rules as do other resources.

Are sharers rewarded for the shares they supply with future shares of the same high-variability resource? This is the central assumption of the "risk-reduction reciprocity" hypothesis that hunters exchange meat to reduce the variability in their nutritional income. Among both the Hadza and the Meriam, those households who supply meat in greater quantities (A and B) or who supply it more frequently (C and D) do not seem to be rewarded for their generosity with more meat supplied by others or more frequent receipts.57,94 The Meriam data come from a systematic survey of the distribution patterns of all turtles acquired by island households during one year. The Hadza meat-sharing data come from a sample of shares from large game (Fig. 1) carried to households in a study camp that moved its location and changed in membership over time.

Men could only be recorded as recipients or suppliers of shares while co-resident with the observers. Those who were in the sampling window longer were, other things the same, more likely to be caught doing both, which accounts for the slight but still insignificant positive trend. After accounting for the large variation among hunters in days resident, partial correlations actually indicate a slight negative trend between both Kg shared and received (R = -.243) and the frequency of sharing and receiving (R = -.194). Indeed, among both the Hadza and Meriam, those who never supplied meat received

hood of chimpanzee hunting over a ten-year period at Gombe were the number of males in a party, total party size, and the number of females with estrous swellings in the party. The last of these was the strongest predictor, suggesting that hunting is more likely when male mating competition is most immediate. Teleki67 found that Gombe females were both more likely to beg meat from males and more likely to get meat when in estrus. Stanford68 observed "meat for sex" exchanges. But at other times and at other sites this is less common.65,69,70 During Mitani and Watts'65 observations at Ngogo, estrous females received meat more often and anestrous females less often than expected by chance, but sharing did not affect the probability or frequency of mating. Overall, adult males consume most of the meat, little going to females and even less to juveniles.65,68-71

At Ngogo, hunting was not a strategy for meeting a nutritional shortfall. To the contrary, Mitani and Watts<sup>64</sup> found that hunting increased when there was more ripe fruit available. This is consistent with Stanford's<sup>72</sup> conclusion based on observations at Gombe:

> Most members of the hunting party receive very little meat for their effort, and the number of chimp-hours expended on the hunt plus the long begging and

### Box 2. (Continued)

just as much and just as frequently as those who supplied it most generously. Sharing turtle among the Meriam and sharing large game animals among the Hadza seems not to be conditional on getting portions from others. The benefits of supplying meat do not appear to come from getting more meat from others.

There is the possibility that shares of Hadza game and Meriam turtles are traded for other resources. For the Meriam, turtle makes up more than 80% of all calories of food transferred between households during the nesting season, with fish and other marine resources making up the remainder. For

sharing session that follows can be enormously costly relative to the quantity of meat that is usually available.

At Ngogo,<sup>64</sup> males who shared meat with each other also shared coalitionary support. Mitani and Watts<sup>64</sup> concluded that Ngogo males hunt to obtain meat they then use to develop and maintain social relationships with other males. the Hadza, we can immediately reject this possibility because the majority of calories that acquirers supply to other nuclear families are from large game animals, with only a small proportion coming from honey. Could Meriam households be trading turtle calories for fish? This does not seem likely: Meriam households who shared turtle during the nesting season were not preferentially given fish. Among eight households sampled, five never shared turtle, yet received an average of 50 grams of fish per capita per sample day, while the three households that shared turtle received an average of 4 grams of fish.

Chimpanzee males could be drawn into hunting because control of meat is an effective way to display relative quality. Unlike the human case where, as argued here, a hunter's own benefit depends on credit for the kill rather than on control of the meat, chimpanzee males compete for possession of the meat. Sometimes they rip the carcass apart in the process. Unlike other forms of display among male chimpanzees, however, hunting and meat



Figure 1. Hadza men women and children returning home from a death, butchery, and consumption site where all have been eating meat. They are carrying household meat shares<sup>57</sup> (see Box 2) back to the residential base. (Photograph courtesy of J. F. O'Connell.)

#### Box 3. Competition Intensifies Work Effort

Kaplan and coworkers<sup>47</sup> have recently interpreted agerelated changes in foraging productivity as evidence that foraging ability accumulates over the life span as a result of increased practice and experience. We emphasize an alternative and additional influence on productivity profiles: changes in the benefits for working longer hours or foraging with greater intensity. Sometimes working longer hours does not mean more food for one's own household but increased relative status among group members. Arabian babblers compete among themselves for the opportunity to spend time as group sentinels.<sup>38</sup> Ache men hunt very long hours,<sup>44,47</sup> and better Ache hunters spend even more time hunting.<sup>48</sup> The same appears to be true for the !Kung and Hadza as well, with better hunters spending more time hunting.<sup>41,57</sup> Better Meriam spear fishers also spend more time out on the reef.<sup>15</sup> When some individuals gain competitive advantages over others by engaging in activities with display value, and when productive activities are effective displays, increased productivity can be the outcome of status competition.

sharing result in more than information for the audience. At least some others get to eat meat as a consequence, a possible evolutionary foundation for the much greater benefits that flow to others from some kinds of human showing off.

The male competition for status seen in modern chimpanzee hunting provides a hominoid foundation for the evolution of human hunting. Modern human hunters often display in a way that provides more nutritional benefits to all. That difference can be related to other differences between us and our sister species. One of those differences is, of course, that human hunters have the technology to capture prey larger than themselves. Another may be the inability of chimpanzee hunting techniques to distinguish effectively among the varying skill levels of hunters. Another difference is especially relevant in the context of arguments here: We have language. Among people, the story of a hunter's success spreads to a wide audience, though few, if any, of its members actually saw him capture the prey. Human reputations can be built through storytelling, but chimpanzee reputations cannot: only those on the scene of hunting and meat sharing episodes can be signal recipients. Language broadens the audience to include all who hear the story and thus may vastly increase the signaling benefits of displaying skill through game acquisition.

Talk, however, is cheap. Tales of hunting might allow show-offs to bluff about their successes, or at least claim near misses, without paying real costs. Widespread ethnographic observation shows that this danger is minimized because it is not a hunter himself who touts his own exploits. Lee's<sup>73</sup> famous anecdote about the properly self-effacing behavior of !Kung hunters captures the common pattern.<sup>74</sup> But !Kung men talk end-

The male competition for status seen in modern chimpanzee hunting provides a hominoid foundation for the evolution of human hunting. Modern human hunters often display in a way that provides more nutritional benefits to all. That difference can be related to other differences between us and our sister species.

lessly about hunts and hunting, rehearsing the "minutest details."<sup>41,75,76</sup> All those who listen to the storytelling soon know which man it was that made every kill. The self-effacing style also characterizes Ache hunters, who arrive at the evening's forest camp without a word, whether they have taken any prey or not. Ten minutes or more may pass before the men begin to talk quietly of the day. Then, without fanfare, someone else, perhaps a boy, will step outside the circle of fires and drag in any prev left discretely at the margins of the camp. This absence of self-aggrandizement among hunters seems initially inconsistent with the proposition that hunting is display, but if the message is in the meat, it is the reliable links between a hunter and the prey that matters. The stories told by others, accumulating from the interwoven observations of many, make that link. As in other domains of male contest, "trash talk" may have its uses, but reputations for delivering the goods cannot be built upon it.

# WHY IS MEAT THE SIGNAL?

If it is merely information that is being transferred, does this mean that signal form is arbitrary (as in Fisherian runaway sexual selection) as long as information is transmitted honestly to the appropriate observers? There are good reasons to think not. While it is just as costly for signalers to give an altruistic signal as an equivalently wasteful display,18 it may not be equally beneficial. Some observers may be more interested in "altruistic" signals than "wasteful" ones because such signals provide more than simply information,<sup>25</sup> because they provide different sorts of information,37 or both. Peacock tails,77 conspicuous leisure,19 or spear-throwing accuracy15 give only information to signal recipients. Sentinel duty, hunting, feasting, political pork, and group defense send information but also benefit the audience in other ways. Benefits other

than information can play a role in the dynamics of selection for displays because it is audience attention that determines gains to the show-off.

Audience sensitivity (receiver bias) affects the nature of displays because signals must be detected effectively by appropriate recipients.78-82 Because public goods are consumed by many, identification with those goods reaches a wide audience of consumers. This "broadcast effectiveness" might help explain the recurrence of common goods provisioning among humans.<sup>12,83</sup> Signals designed to acquire or maintain higher social standing in a group should be directed to the group at large; other more specialized signals may be directed to smaller subsets of the population. Signalers competing for popular prestige should seek to gain a larger and larger share of the advertising market. They gain a larger share by providing more of what the viewers want to see or consume than the competition provides.<sup>25</sup> The provisioning of collective goods may serve the purpose of reaching a wide audience better.37 Both competition among signalers and audience preference for particular signals can play a role in shaping the display.

#### CONCLUSIONS

Darwin<sup>84</sup> developed the theory of sexual selection to explain the evolution of armaments and ornaments, which seemed so extravagantly costly and remarkably wasteful, given an expectation that natural selection would favor features that increased the probability of survival. Soon after, Thorstein Veblen<sup>19</sup> developed a costly signaling argument, recognizing that competition among closely matched individuals was a powerful influence on social behavior and could lead to enormous waste. Zahavi's handicap principle dissolves the riddle of waste by showing it to be the very thing that guarantees signal honesty and so makes signaling systems stable.

Paradoxically, honest signaling models can account for both wasteful "luxury fever" in the evolution of environmentally damaging sport utility vehicles<sup>85</sup> and socially beneficial provisioning of collective goods in the evolution of male foraging strategies. In the last few years, a combination of empirical and theoretical work has found costly displays to be much more widespread than was previously recognized. Darwin focused on mate choice and competition for mates, but if displays are signals, selection can favor wasteful expenditure on them in any kind of social interaction, including those between parents and offspring or predators and prey.

Our arguments seek to explain the evolution of men's subsistence work as a strategy to compete effectively for social advantage in a world where honesty is at a premium and political alliances substitute for body size and canine weaponry in gaining the advantages of status. We highlight the fact that, at least among humans, both signaler and audience preference for more effective and competitive signals can drive the evolution of displays toward increasing social benefits. The hypothesis that men's work evolved and often continues to be shaped by showing off does not imply that men contribute little to subsistence. On the contrary, the showoff hypothesis and costly signaling can help explain how individuals seeking competitive advantages can increase their own standing and so earn preferential treatment by acting in ways that supply highly valued benefits to others.

#### **ACKNOWLEDGMENTS**

We thank Helen Alvarez, Douglas Bird, Nicholas Blurton Jones, Jack Hirshleifer, James O'Connell, Mark Pagel, Lars Rodseth, Carel van Schaik, Eric Alden Smith, Craig Stanford, and Pauline Wiessner for helpful comments and advice.

#### REFERENCES

1 Zahavi A. 1975. Mate selection: selection for a handicap. J Theor Biol 53:205–14.

**2** Zahavi A. 1977. The cost of honesty (further remarks on the handicap principle). J Theor Biol 67:603–5.

**3** Zahavi A. 1995. Altruism as a handicap—the limitations of kin selection and reciprocity. Avian Biol 26:1–3.

**4** Grafen A. 1990. Biological signals as handicaps. J Theor Biol 144:517–46.

**5** Johnstone RA. 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. Biol Rev 70:1–65.

6 Johnstone RA. 1997. The evolution of animal signals. In: Krebs JR, Davies NB, editors. Behav-

ioral ecology: an evolutionary approach. Oxford: Blackwell Science. p 155–178.

**7** Getty T. 1998. Handicap signaling: when fecundity and viability do not add up. Anim Behav 56:127–130.

**8** Boone JL. 1998. The evolution of magnanimity: when is it better to give than to receive? Hum Nat 9:1–21.

**9** Neiman FD. 1998. Conspicuous consumption as wasteful advertising: a Darwinian perspective on spatial patterns in the Classic Maya terminal monument dates. In: Barton CM, Clark GA, editors. Rediscovering Darwin: evolutionary theory and archaeological explanation. Washington D. C.: Archaeological Papers of the American Anthropological Association, No. 7. p 267–290.

**10** Miller GF. 1999. Sexual selection for cultural displays. In: Dunbar R, editors. The evolution of culture. Edinburgh: Edinburgh University Press. p 71–91.

**11** Miller GF. 2000. The mating mind: how sexual choice shaped the evolution of human nature. New York: Doubleday.

**12** Smith EA, Bliege Bird R. 2000. Turtle hunting and tombstone opening: public generosity as costly signaling. Evol Hum Behav 21:245–261.

**13** Sosis R. 2000. Costly signaling and torch fishing on Ifaluk Atoll. Evol Hum Behav 21:223–244.

**14** Bliege Bird R. 1999. Cooperation and conflict: the behavioral ecology of the sexual division of labor. Evol Anthropol 8:65–75.

**15** Bliege Bird R, Smith EA, Bird D. 2001. The hunting handicap: costly signaling in human foraging strategies. Behav Ecol Sociobiol, in press. **16** Bliege Bird R, Bird D. 2001. Gendered fishing among the Meriam: implications for sexual division of foraging labor, submitted.

**17** Zahavi A. 1990. Arabian babblers: the quest for social status in a cooperative breeder. In: Stacey PB, Koenig WD, editors. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge: Cambridge University Press. p 103–130.

**18** Zahavi A, Zahavi A. 1997. The handicap principle: a missing piece of Darwin's puzzle. Oxford: Oxford University Press.

**19** Veblen T. 1992. The Theory of the Leisure Class. Mills CW, editor. New Brunswick, NJ: Transaction Publishers.

**20** Kelly RL. 1995. The foraging spectrum: diversity in hunter-gatherer lifeways. Washington: Smithsonian Institution Press.

**21** Hawkes K. 1990. Why do men hunt? some benefits for risky strategies. In: Cashdan E, editor. Risk and uncertainty in tribal and peasant economies. Boulder: Westview Press. p 145–166.

**22** Hawkes K. 1991. Showing off: tests of an hypothesis about men's foraging goals. Ethol Sociobiol 12:29–54.

**23** Hawkes K. 1993. Why hunter-gatherers work: an ancient version of the problem of public goods. Curr Anthropol 34:341–361.

**24** Hawkes K. 2000. Big game hunting and the evolution of egalitarian societies. In: Deihl M, editor. Hierarchies in action: cui bono? Center for Archaeological Investigations, Occasional Paper No. 27:59–83. Southern Illinois University.

**25** Hawkes K. 2001. Is meat the hunter's property? Big-game, ownership and explanations of hunting and sharing. In: Stanford C, Bunn H, editors. Meat-eating and human evolution. Oxford: Oxford University Press. p 219–236.

**26** Sahlins M. 1972. Stone Age economics. Chicago: Aldine.

**27** Kaplan H, Hill K. 1985. Food sharing among Ache foragers: tests of explanatory hypotheses. Curr Anthropol 26:223–246.

**28** Olson M. 1965. The logic of collective action: public goods and the theory of groups. Cambridge: Harvard University Press.

**29** Samuelson PA. 1954. The pure theory of public expenditure. Rev Econ Statistics 36:387–389.

**30** Hawkes K. 1992. Sharing and collective action. In: Smith EA, Winterhalder B, editors. Evolutionary ecology and human behavior. New York: Aldine de Gruyter. p 269–300.

**31** Ostrom V, Ostrom F. 1977. Public goods and public choices. In: Savas ES, editor. Alternatives for delivering public services: toward improved performance. Boulder: Westview. p 7–49.

**32** Blurton Jones NG. 1984. A selfish origin for food sharing: tolerated theft. Ethol Sociobiol 5:1–3.

**33** Blurton Jones NG. 1987. Tolerated theft: suggestions about the ecology and evolution of sharing, hoarding and scrounging. Soc Sci Information 26:31–54.

**34** Hawkes K, Bliege Bird R, Bird D. 1998. Comment on Wilson DS: hunting, sharing, and multilevel selection: the tolerated theft model revisited. Curr Anthropol 39:89–90.

35 Smith EA. 1993. Comment on Hawkes K: why hunter-gatherers work: an ancient version of the problem of public goods. Curr Anthropol 34:356.36 Wilson DS. 1998. Hunting, sharing, and multilevel selection: the tolerated theft model revisited. Curr Anthropol 39:73–97.

**37** Smith EA, Bliege Bird R, (n.d.) Costly signaling and prosocial behavior. In: Bowles S, Boyd R, Fehr E, Gintis H, editors. Strong reciprocity: roots of cooperation and exchange.

**38** Carlisle TR, Zahavi A. 1986. Helping at the nest, allofeeding and social status in immature arabian babblers. Behav Ecol Sociobiol 18:339–351.

**39** Dowling JH. 1968. Individual ownership and the sharing of game in hunting societies. Am Anthropol 70:502–507.

**40** Wiessner P. 1996. Leveling the hunter: constraints on the status quest in foraging societies. In: Wiessner P, Schiefenhovel W, editors. Food and the status quest: an interdisciplinary perspective. Providence: Berghahn Books. p 171–191.

**41** Lee RB. 1979. The !Kung San: men, women and work in a foraging society. Cambridge: Cambridge University Press.

**42** Thomas EM. 1959. The harmless people. New York: Knopf.

**43** Hill K, Hurtado AM. 1996. Ache life history: the ecology and demography of a foraging people. New York: Aldine de Gruyter.

**44** Hill K, Kaplan H, Hawkes K, Hurtado AM. 1985. Men's time allocation to subsistence work among the Ache of eastern Paraguay. Hum Ecol 13:29–47.

**45** Hill K, Hawkes K, Hurtado AM, Kaplan H. 1984. Seasonal variance in the diet of Ache hunter-gatherers in eastern Paraguay. Hum Ecol 12: 145–180.

**46** Hawkes K. 1987. How much food do foragers need? In: Harris M, Ross E, editors. Food and evolution: toward a theory of human food habits. Philadelphia: Temple University Press. p 341–355.

**47** Kaplan H, Hill K, Lancaster J, Hurtado AM. 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol Anthropol 9:156–185.

**48** Hill K, Hawkes K. 1983. Neotropical hunting among the Ache of eastern Paraguay. In: Hames R, Vickers W, editors. Adaptations of native Amazonians. New York: Academic Press. p 139–188. **49** Kaplan H, Hill K, Hawkes K, Hurtado AM. 1984. Food sharing among Ache hunter-gather-

ers of eastern Paraguay. Curr Anthropol 25:113–115.

50 Hill K, Kaplan H. 1988. Tradeoffs in male and female reproductive strategies among Ache foragers. In: Betzig L, Borgerhoff Mulder M, Turke P, editors. Human reproductive effort. Cambridge: Cambridge University Press. p 277–306. 51 Kaplan H, Hill K. 1985. Hunting ability and reproductive success among male Ache foragers:

preliminary results. Curr Anthropol 26:131–133. 52 Woodburn J. 1968. An introduction to Hadza ecology. In: Lee RB, DeVore I, editors. Man the hunter. Chicago: Aldine de Gruyter. p 49–55.

**53** O'Connell JF, Hawkes K, Blurton Jones NG. 1988. Hadza scavenging: implications for Plio-Pleistocene hominid subsistence. Curr Anthropol 29:356–363.

**54** Hawkes K, O'Connell JF, Blurton Jones NG. 1991. Hunting income patterns among the Hadza: big game, common goods, foraging goals, and the evolution of the human diet. Philosophical Trans R Soc B 334:243–251.

**55** Barnard A, Woodburn J. 1988. Property power and ideology in hunting and gathering societies: an introduction. In: Ingold T, Riches D, Woodburn J, editors. Hunters and gatherers 2: property, power and ideology. New York: Berg. p 4–31.

**56** Woodburn J. 1998. Sharing is not a form of exchange: an analysis of property sharing in immediate return hunter-gatherer societies. In: Hann CM, editor. Property relations: renewing the anthropological tradition. Cambridge: Cambridge University Press. p 48–63.

**57** Hawkes K, O'Connell JF, Blurton Jones NG. 2001. Hadza meat sharing. Evol Human Behav 22:113–142.

58 Hawkes K. 1993b. On why male foragers hunt and share food: Reply to Hill and Kaplan. Curr Anthropol 34:706-710.

59 Blurton Jones NG, Hawkes K, O'Connell JF.
1997. Why do Hadza children forage? In: Segal N, Weisfeld GE, Weisfeld CC, editors. Uniting psychology and biology: integrative perspectives on human development. Washington, D.C.: American Psychological Association. p 279–313.
60 Hawkes K, O'Connell JF, Blurton Jones NG.

1997. Hadza women's time allocation, offspring production, and the evolution of long postmenopausal life spans. Curr Anthropol 38:551–577.

**61** Hawkes K, O'Connell JF, Blurton Jones NG (n.d.) Hadza hunting and the evolution of nuclear families. Curr Anthropol, in press.

**62** Blurton Jones NG, Marlowe F, Hawkes K, O'Connell JF. 2000. Hunter-gatherer divorce rates and the paternal provisioning theory of human monogamy. In: Cronk L, Chagnon N, Irons W, editors. Adaptation and human behavior: an anthropological perspective. New York: Aldine de Gruyter. p 65–84.

**63** Smith EA, Bliege Bird R. 2000. Benefits of costly signaling: Mariam turtle hunters and spear fishers. Anthropological Association Annual Meetings. San Francisco.

**64** Nishida T, Hasegawa T, Hayaki H, Takahata Y, Uehara S. 1992. Meat-sharing as a coalition strategy by an alpha male chimpanzee? In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors. Topics in primatology, Vol. I, Human origins. Tokyo: University of Tokyo Press. p 159–174.

**65** Mitani J, Watts D. 2001. Why do chimpanzees hunt and share meat? Anim Behav 61, in press. **66** Stanford CB, Wallis J, Mpongo E, Goodall I. 1994. Hunting decisions in wild chimpanzees. Behaviour 131:1–20.

67 Teleki G. 1973. The predatory behavior of

wild chimpanzees. Lewisburg: Bucknell University Press.

**68** Stanford CB. 1998. Chimpanzee and red colobus: the ecology of predator and prey. Cambridge: Harvard University Press.

**69** Goodall J. 1986. The chimpanzees of Gombe: patterns of behavior. Cambridge: Harvard University Press.

**70** Boesch C, Boesch H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. Am J Phys Anthropol 78:547–573.

**71** Wrangham RW, Riss E van ZB. 1990. Rates of predation on mammals by Gombe chimpanzees, 1972–1975. Primates 31:157–170.

**72** Stanford CB. 1999. The Hunting apes: meat eating and the origins of human behavior. Princeton: Princeton University Press.

**73** Lee RB. 1968. What hunters do for a living: how to make out on scarce resources. In: Lee RB, DeVore I, editors. Man the hunter. Chicago: Aldine de Gruyter. p 30–48.

**74** Hawkes K. 1992. On sharing and work (a comment on Bird-David). Curr Anthropol 33:404–407.

**75** Blurton Jones NG, Konner M. 1976. !Kung knowledge of animal behavior (or: the proper study of mankind is animals). In: Lee RB, DeVore I, editors. Kalahari hunters: studies of the !Kung San and their neighbors. Cambridge: Harvard University Press. p **325–348**.

**76** Marshall L. 1976. The !Kung of Nyae Nyae. Cambridge: Harvard University Press.

**77** Petrie M, Halliday T, Sanders C. 1991. Peahens prefer peacocks with elaborate trains. Anim Behav 41:323–31.

**78** Ryan MJ. 1990. Sensory systems, sexual selection, and sensory exploitation. Oxford Surveys Evol Biol 7:157–195.

**79** Endler JA. 1992. Signals, signal conditions and the direction of evolution. Am Nat 139:S125–S153.

**80** Endler JA. 1993. Some general comments on the design of animal signaling systems. Philos Trans R Soc London B 340:215–225.

**81** Guilford T, Dawkins MS. 1993. Receiver psychology and the design of animal signals. Trends Neurosci 16:430–436.

**82** Guilford T. 1997. The extravagance of animal signals. J Biol Educ 31:24–29.

**83** Roberts G. 1998. Competitive altruism: from reciprocity to the handicap principle. Proc R Soc London B 265:427–431.

**84** Darwin C. 1871. The descent of man, and selection in relation to sex. London: J. Murray.

**85** Frank R. 1999. Luxury fever: why money fails to satisfy in an era of excess. New York: The Free Press.

**86** Trivers RL. 1971. The evolution of reciprocal altruism. Q Rev Biol 46:35–57.

**87** Wiessner P. 1982. Risk, reciprocity, and social influences on !Kung San economics. In: Leacock E, Lee RB, editors. Politics and history in band societies. Cambridge: Cambridge University Press. p 61–84.

88 Malinowski B. 1922. Argonauts of the Western Pacific. New York: E. P. Dutton.

**89** Peterson N. 1993. Demand sharing: reciprocity and the pressure for generosity among foragers. Am Anthropol 95:860–74.

**90** Axelrod R, Hamilton WD. 1981. The evolution of cooperation. Science 211:1390–1396.

**91** Boyd R, Lorberbaum J. 1987. No pure strategy is evolutionarily stable in the repeated prisoner's dilemma game. Nature 327:58–59.

**92** Boyd R, Richerson P. 1988. The evolution of reciprocity in sizeable groups. J Theor Biol 132: 337–356.

**93** Hirshleifer J, Martinez-Coll JC. 1988. What strategies can support the evolutionary emergence of cooperation? J Conflict Resolution 32: 367–398.

**94** Bliege Bird R, Bird D. 1997. Delayed reciprocity and tolerated theft. Curr Anthropol 38:49–78. **95** Winterhalder B. 1986. Diet choice, risk, and food sharing in a stochastic environment. J Anthropol Archaeol 5:369–392.

**96** Smith EA. 1988. Risk and uncertainty in the "original affluent society": evolutionary ecology of resource sharing and land tenure. In: Ingold T, Riches D, Woodburn J, editors. Hunter gatherers 1: history, evolution, and social change. Oxford: Berg. p 222–252.

**97** Nowak MA, Sigmund K. 1998. Evolution of indirect reciprocity by image scoring. Nature 393:573–577.

98 Hirshleifer J. 1999. There are many evolutionary pathways to cooperation. J Bioecon 1:73–93.99 Dugatkin LA. 1997. Cooperation among ani-

mals. Oxford: Oxford University Press. **100** Connor RC. 1986. Pseudo-reciprocity: investing in mutualism. Anim Behav 34:1562–1584.

**101** Clements KC, Stephens DW. 1995. Testing models of animal cooperation: feeding bluejays cooperate mutualistically, but defect in a massively iterated Prisoner's Dilemma. Anim Behav 50:527–535.

102 Pusey AE, Packer C. 1997. The ecology of

relationships. In: Krebs JR, Davies NB, editors. Behavioral ecology: an evolutionary approach. Oxford: Blackwell Science. p 254–283.

**103** Hames R. 2000. Reciprocal altruism in Yanomamo food exchange. In: Cronk L, Chagnon N, Irons W, editors. Adaptation and human behavior: an anthropological perspective. New York: Aldine De Gruyter. p 397–416.

**104** Gurven M, Hill K, Hurtado A, Lyles R. 2000. Food transfers among Hiwi foragers of Venezuela: tests of reciprocity. Hum Ecol 28: 171–214.

© 2002 Wiley-Liss, Inc. Published online in Wiley InterScience (www.interscience.wiley.com). DOI 10.1002/evan.20005

