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

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Zahavi’s\textsuperscript{1,2} 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\textit{addition} to information about the show-off. Zahavi\textsuperscript{3} 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,\textsuperscript{1,2,4–6} 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.\textsuperscript{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 anthropological puzzles, including seemingly maladaptive cultural practices, monumental architecture, relatively inefficient foraging behaviors, and generosity.\textsuperscript{8–13} Bliege Bird\textsuperscript{14–16} 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\textsuperscript{1,2,3,17,18} 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, \textit{Turdoides squamiceps}), dominants display their quality by standing sentinel duty, distracting or fending off predators, and presenting...
food to subordinates. Displays that supply such benefits are readily noted by other bidders. 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 in his classic 1899 analysis, the similarity between public generosity and “conspicuous consumption.”

**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. 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, 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. The interest all have in the meat acquired by hunters makes hunting a central arena for social competition among

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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. Olson28 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, Hawkes35 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.23,34 However, some still see a second-order collective-action problem lurking here.12,35,36 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 Bird12,37 and Bliege Bird, Smith, and Bird15 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

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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 Jones32,33 noted that food sharing need not imply owners paying a cost to give up shares. Instead of ownership rights falling automatically on the acquire, 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 big-game 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.48,51,56,67,94 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.87 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,27,95,96 it would conform to Trivers’86 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.8,16,63,97–102
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-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.

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. 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.”

In the human case, a reputation for good hunting generally affects a man’s social standing relative to other men in foraging communities. In the northern Kalahari, traditional hunters usually bagged no more than two or three large antelope in a year. Thomas 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. When living in the forest, Ache men spend nearly fifty hours a week in food acquisition, supplying a very large fraction of a diet that is uncommonly ample among modern hunter-gatherers. The generous nutrient averages result not from high hourly foraging return rates but from these long hours, with better hunters spending the most time hunting (see Box 3). Wide sharing is especially well documented in this case. While other Hadza hunters have younger wives, better Hadza hunters tend to be married to harder-working wives. Older men who are better hunters have younger wives, 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.

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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. Stanford and coworkers 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. Sometimes this applies to certain kinds of food and not others. For example, Gurven and co-workers, analysis of Hiwi sharing patterns suggests that reciprocity-based 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. 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.
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. Teleki\textsuperscript{67} found that Gombe females were both more likely to beg meat from males and more likely to get meat when in estrus. Stanford\textsuperscript{68} observed “meat for sex” exchanges. But at other times and at other sites this is less common.\textsuperscript{65,69,70} During Mitani and Watts\textsuperscript{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.\textsuperscript{65,68–71}

At Ngogo,\textsuperscript{64} males who shared meat with each other also shared coalitionary support. Mitani and Watts\textsuperscript{64} concluded that Ngogo males hunt to obtain meat they then use to develop and maintain social relationships with other males.

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

Box 2. (Continued)

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 ($R = -0.243$) and the frequency of sharing and receiving ($R = -0.194$). Indeed, among both the Hadza and Meriam, those who never supplied meat received 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 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.

![Figure 1](https://example.com/figure1.png) 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\textsuperscript{57} (see Box 2) back to the residential base. (Photograph courtesy of J. F. O’Connell.)
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Box 3. Competition Intensifies Work Effort

Kaplan and coworkers have recently interpreted age-related 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. Ache men hunt very long hours, and better Ache hunters spend even more time hunting. The same appears to be true for the !Kung and Hadza as well, with better hunters spending more time hunting. Better Meriam spear fishers also spend more time out on the reef. 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.

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 famous anecdote about the properly self-effacing behavior of !Kung hunters captures the common pattern. But !Kung men talk end-

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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, 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, because they provide different sorts of information, or both. Peacock tails, conspicuous leisure, or spear-throwing accuracy 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. 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. 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. Signals 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. The provisioning of collective goods may serve the purpose of reaching a wide audience better. Both competition among signalers and audience preference for particular signals can play a role in shaping the display.

CONCLUSIONS

Darwin 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 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 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.

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