

Original Article

The hunting handicap: costly signaling in human foraging strategies

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Abstract. Humans sometimes forage or distribute the products of foraging in ways that do not maximize individual energetic return rates. As an alternative to hypotheses that rely on reciprocal altruism to counter the costs of inefficiency, we suggest that the cost itself could be recouped through signal benefit. Costly signaling theory predicts that signals can provide fitness benefits when costs are honestly linked to signaler quality, and this information is broadcast to potential mates and competitors. Here, we test some predictions of costly signaling theory against empirical data on human food acquisition and sharing patterns. We show that at least two types of marine foraging, turtle hunting and spearfishing, as practiced among the Meriam (a Melanesian people of Torres Strait, Australia) meet key criteria for costly signaling: signal traits are (1) differentially costly or beneficial in ways that are (2) honestly linked to signaler quality, and (3) designed to effectively broadcast the signal. We conclude that relatively inefficient hunting or sharing choices may be maintained in a population if they serve as costly and reliable signals designed to reveal the signaler's qualities to observers.

Keywords. Costly signaling - Human behavioral ecology - Hunting - Handicap models

Introduction

Human foragers often make decisions that lead them to bypass alternative activities with higher energy gain rates, provide widely shared goods without repayment, or incur an increased risk of injury. These decisions have often been explained by the benefits of a sexual division of labor in parental investment (e.g., Hurtado et al. 1992), the optimization of macronutrients (e.g., Hill 1988), or reduction of consumption variance (e.g., Smith 1988). In particular, the practice common to many hunter-gatherer societies of widespread or group-wide sharing of large prey captured by any subset of the group is conventionally explained as a form of risk reduction where all ultimately benefit from a reciprocal sharing of unpredictable harvests (reviews in Hawkes 1992; Winterhalder 1997).

While some types of food seem to be distributed in ways that conform to delayed reciprocity (Gurven et al. 2000), recent studies (Hawkes 1993; Bliege Bird and Bird 1997) have challenged its ability to explain the wide variety of sharing patterns to which it has been claimed to apply. The cases that seem least congruent with strategies of delayed reciprocity are those associated with public distributions of food in which the acquirer does not control access to the harvest or its distribution, and may not even reserve a portion for him- or herself (Wiessner 1996). Under these conditions, acquirers seem unlikely to be able to direct shares to reciprocators and withhold them from free-riders, as is required to solve the collective action problem (e.g., prisoner's dilemma) associated with enforcing delayed reciprocity. Similar challenges to the primacy of reciprocal altruism (RA) on both theoretical and empirical fronts are also found in recent literature on non-human behavior (reviews in Dugatkin 1997; Pusey and Packer 1997). Many theorists have suggested the paradigm may require extensive revisions (Clements and Stephens 1995; Connor 1996; Dugatkin 1997; Roberts 1998).

An alternative explanation for such "economically irrational" decisions is that under some circumstances they could serve as an honest signal of one or more dimensions of fitness-related quality (Neiman 1998; Boone 1998; Sosis 2000; Smith and Bliege Bird 2000). Costly signaling theory (CST) provides a powerful framework for explaining two paradoxical observations: the persistence of wasteful phenotypes when natural selection is assumed to create greater efficiency, and the evolution of honest communication despite the pervasive conflicts of interest underlying evolutionary processes (Zahavi 1975, 1977; Grafen 1990; Johnstone 1995, 1997; Getty 1998). CST proposes that communication between individuals with conflicting interests can be evolutionarily stable if the signal honestly advertises an underlying quality of interest to observers. Advertising is kept honest and thus mutually beneficial to both signaler and observer as long as the cost or benefit of advertisement is so closely tied to the quality of the signaler that faking it costs more than the signal is worth. If this holds, the correlation between the quality of a signaler and the quality or intensity of the signal will be maintained by differences in marginal cost or benefit, allowing recipients to reliably discriminate among competing signalers. When these conditions are met, honest signals and reliable communication will be evolutionarily stable, even when signaler and recipient are antagonists or competitors.

The hypothesis that hunting might serve as a form of status competition among men interested in "showing off" to a public audience is not new (Hawkes 1990, 1991). Here, we recast the "show-off" model using a payoff structure compatible with CST (Smith and Bliege Bird 2000). We propose that individuals of high phenotypic quality might reap higher benefits or pay lower costs to acquire skill-based resources or to unconditionally share their harvest. These benefits (material, political, and reproductive) flow from observers who find it in their interest to behave in ways that improve the relative advantage, status, or social dominance of signalers, ultimately enhancing signaler fitness. Analyzed according to CST, this is not delayed reciprocity involving an exchange of substance (to the observer) for social status (to the signaler), but rather a form of by-product mutualism. The payoff to the observer comes from the usefulness of the information inferred from the signal: he or she should

be able to evaluate the signaler's suitability as a competitor, mate, or ally by attending to the signal rather than through more costly or unreliable means of assessing the signaler's abilities or hidden qualities. The high cost or low benefit of faking the signal guarantees that signalers will not engage in false advertising, and that observers will pay attention. Costly signaling can thus spread (by natural selection or imitation) because of its mutual benefits to both signalers and observers.

Here, we test the costly signaling hypothesis among the Meriam (a Melanesian people of Torres Strait, Australia). We evaluate two candidate foraging activities (spearfishing on the reef at low tide, and hunting turtle for public feasts), to determine whether these hunt types meet key criteria for costly signaling in being (1) differentially costly or beneficial in ways that are (2) honestly linked to signaler quality, and (3) designed to effectively broadcast the signal to the intended audience. We propose that accomplished spearfishers signal such qualities as hand-eye coordination, stealth, and patience, while successful turtle hunters signal strength, risk-taking, and (in the case of hunt leaders) a variety of cognitive and leadership abilities to potential allies, mates, and competitors.

Methods

Mer (a.k.a. Murray Island) is a small (1.6 × 2.2 km) island on the northern end of the Great Barrier Reef, 140 km from New Guinea in Australia's Torres Strait. The island's current population is 430 individuals of Torres Strait Islander descent, scattered in approximately 85 households. The Torres Strait as a whole is administered by the State of Queensland and the Commonwealth of Australia.

Prior to about 1975, when Australian welfare payments were first made available to all indigenous Australians, the Meriam were nearly full-time subsistence horticulturalists and marine foragers planting tropical yams, bananas, sugar cane, and introduced new world crops such as manioc, sweet potatoes, and corn, and harvesting marine fish, shellfish, and sea turtles. Today, fishing and shellfish collecting remain a critical component of Meriam subsistence economy: mean per capita after-sharing consumption rates average 630 kcal of meat and 40 g of protein. More than 80% of these calories are supplied by turtle when in season. For additional ethnographic description and previous work among the Meriam, see Haddon (1906), Beckett (1988), Sharp (1993), Bliege Bird et al. (1995), Bird and Bliege Bird (1997, 2000), Bliege Bird and Bird (1997), and Smith and Bliege Bird (2000).

Observations of Meriam foraging choices, time allocation, and food-sharing strategies reported here were conducted over several periods totaling 27 months between January 1993 and July 1999. Much of this field research was specifically designed to test hypotheses related to the origin and maintenance of the human sexual division of labor, and to determine the nature of the tradeoffs affecting men's and women's foraging decisions.

Time allocation to intertidal activities (spearfishing, shellfish collecting) was measured through focal individual follows occurring during randomly selected days during the spring ebbing tide. Locations along the foreshore were observed from the midpoint of the ebbing tide, before the reef was fully exposed, for at least 2 h or until the last forager had left the reef. During the intertidal sampling period, we recorded the moment-by-moment behavior of at least one individual to arrive during the sample, and if the individual remained after the interval ended, we remained to completely record the episode. We observed the reef flat habitat for a total of 118.5 h over 41 spring ebb-tide days, recording 338.1 forager-hours of subsistence activity in 210 partial and full foraging follows of 94 men, women, and children entering the reef flat. We then analyzed the percentage of total foraging time each forager devoted to all potential intertidal activities during the follow.

We analyzed the reef as a bounded habitat within which there are "hunt types" sensu Smith (1991). All hunt types are simultaneously available options within the ecological habitat "reef flat at low tide": reef flat collecting, rocky shore harvesting, and spearfishing (Bird and Bliege Bird 1997, 2000). Reef flat collecting involves mobile search of shellfish, with in situ processing to increase the utility of the load (Bird and Bliege Bird 1997). Spearfishing involves search and travel across the reef looking for encounters with mobile prey (small fish and squid 250 g+) to the exclusion of all other prey; when prey are detected, the hunter stalks the prey and launches his spear from a distance. Both hunt types occur in the same patch during the same period of time, while the reef is exposed at low tide. The hunt types vary in how spatially exclusive they are within the habitat: spearfishing and shellfish collecting are the only two major hunt types in which the forager engaged in exclusive search for prey frequently encounters and ignores prey in the other hunt type. These are not the complete complement of hunt types simultaneously available, but they are the three in which adults spend more than 90% of their foraging time while on the reef at low tide. Other minor hunt types are handline fishing from the reef edge and in deeper lagoons, netting sardines, hunting octopus, and diving from the reef edge to take underwater prey by hand. Gross foraging return rates for each hunt type (not including energetic expenditure - assumed to be roughly equal for all reef hunt types) were calculated from the moment an individual stepped onto the exposed reef and began to engage in targeted search for particular prey types. The macronutrient content of fin-fish and shellfish was obtained through published sources and through individual analysis of samples collected on Mer (Hirth 1971; Sidwell 1981; Brand Miller et al. 1993).

For a detailed description of methods used to collect turtle hunting and sharing data see Bliege Bird and Bird (1997); the results presented here on turtle hunting and sharing are a reanalysis of those data. The acquisition of over 120 turtles was noted through daily sampling of the entire village during the nesting season (October-April) in 1994-1995, and ad lib sampling of the village during the 1994 and 1998 hunting seasons (May-September). Nearly every successful hunt or collection of turtle was recorded, with information obtained on acquirer(s), place acquired, method of acquisition, and subsequent distribution through informant interview.

There are two primary types of marine turtle acquisition on Mer: turtle hunting (*nam deraimer*) and turtle collection (*nam terpei*). Turtle hunting occurs throughout the year, but is the only way to acquire turtles between May and September (*Kob Kerker*), when green turtles (*Chelonia mydas*) feed and mate on shallow reefs about 16-20 km from Mer. Field observations indicate that turtles captured on hunts range from 100 to 150 kg live weight, with an average edible yield of 50.1 kg (Bliege Bird and Bird 1997). Hunters head out to the hunting grounds in open boats powered with outboard motors, often in cooperation with at least one other hunting boat. Among Meriam turtle hunters, there are three distinct roles: hunt leader (*ariemer-le*), jumper (*arpeir-le*), and driver, or tiller-man (*korizer-le*). Hunt leaders organize and direct the hunt; there is always only one leader per hunt, regardless of crew size. Hunt leaders bear the cost of organizing the hunt and ensuring boats and fuel to spare. They direct the crew to particular locations, decide whether prey encountered is worth pursuing, orchestrate the chase, and direct jumpers when to jump from the boat to secure the turtle. Hunt leaders are invested with public recognition and receive full credit for the kill regardless of whether or not they directly participate in capture.

The hunt proceeds as follows. While one man drives, the rest of the crew stands toward the bow scanning the reef for signs of turtle. The hunt leader directs the driver and coordinates with crews in other boats if present. When a turtle is spotted, the hunt leader makes a decision whether to pursue it based on its size (large turtles have more meat) and sex (female turtles have more fat). The boat(s) then give chase, keeping the turtle away from the reef edge. When the turtle tires, the hunt leader usually directs his jumper to launch himself from the bow of the boat with a rope attached to his upper arm. The jumper then attempts to secure the turtle by locking his arms around the flippers and, if

successful, the crew then pulls him and the turtle on board.

Turtle hunting occurs primarily in the context of public feasting events: hunters choose to hunt in response to a request from feast organizers to provide turtles for consumption at a previously announced feast. The biggest and most elaborate Meriam feasts occur in the context of coming-of-age celebrations and funeral ceremonies (see Smith and Bliege Bird 2000 for further details). In contrast to turtle hunting, turtles are also collected ($n=88$ events), primarily in the context of household provisioning, but also for feasts, by men of all ages, women, and children. This occurs only when they can be harvested on beaches during the nesting season (*Nam Kerker*: October-April), although during these months some turtles are also hunted on nearby reefs. In the nesting season, turtles are collected at night or during the early morning hours as they crawl onto sandy beaches above the mean high water mark to lay their eggs. Turtles are acquired by flipping them onto their backs, trussing their flippers with ropes, and hauling them by boat back to the acquirer's household where they are kept alive until butchered. When butchered for "private" consumption, turtle shares are distributed in large, uncooked portions (10-11 kg) of meat, fat, organs, and eggs among nearby households, with the size of portions kept by the butchering household determined primarily by the number of demanders (hereafter termed "household consumption" sensu Bliege Bird and Bird 1997). While hunting a turtle is a costly activity in which the benefit is acquired through the social value of the hunt, collecting a turtle is an activity which has little signaling potential and in which the benefit is primarily nutritional. However, there may be some signal value of displays of generosity among neighbors as turtle portions are shared according to the Meriam ethic of *debe tonar* ("the good way," which involves sharing without expectation of return).

All statistical analyses were performed using Statview (SAS). Large-sample means tests were performed after testing for normality and equality of variance using either one- or two-tailed t -tests depending upon the prediction tested, while tests on small samples and those violating the assumptions of parametric tests used two-tailed Mann-Whitney U -tests. All means are reported with associated SEs.

Results

Spearfishing as costly signal

There are significant sex differences in time allocation to hunt types in the intertidal: on average, men spend 63% of their reef foraging time spearing, while for women this value is only 9% ($t=6.00$, $df=66$, $P=0.001$), and women spend 76% and men 31% of their time shellfish collecting ($t=4.50$, $df=66$, $P=0.001$). The majority of men never collect shellfish at all, nor do they combine spearing with shellfish collecting in a single visit to the reef at low tide: 78.6% of 21 men in the time allocation sample spent *all* of their foraging time spearfishing.

Is spearfishing a signal? The decision men make to spear fish nearly exclusively (rather than collect shellfish) violates simple energy-maximizing prey choice models, because (1) on average, continuing to search for fish to spear (292 ± 135 kcal/h, $n=26$) offers lower overall energy returns than shellfishing ($1,492\pm 173$ kcal/h, $n=47$) while in the reef flat at low tide ($t=4.672$, $df=71$, $P=0.0001$) and (2) on-encounter returns for the most skilled spearfisher ($2,505\pm 778$ kcal/h) are equivalent to the on-encounter returns for the lowest-ranked shellfish prey still in the optimal diet breadth ($2,214\pm 414$ kcal/h) (see Table 1).

Table 1. Mean±SE return rates and mean time allocated to intertidal hunt types by Meriam men and women. On-encounter returns for each prey type are calculated from the moment a forager committed to pursuing a particular individual prey item. For shellfish, pursuits begin when a forager bends down to pick up the item; for spearing, pursuits begin when a forager spots the signs of prey and drops into a stalk stance to pursue it; for rocky shore harvesting, encounters are defined as the moment a productive patch is found. Encounter return rates for all prey types include time spent handling (pursuit and processing) the item while in the foraging habitat: no cooking times are included since cooking methods for each item can vary from minutes to hours depending upon the dish prepared. Mean time allocation per person shows the mean percentage of total "reef habitat at low tide" time devoted to each hunt type averaged for each of 19 women and 21 men observed more than once on the reef during the random time allocation scans

	Reef collecting	Reef spearing	Rocky shore
On-encounter returns (kcal/h) by prey type	<i>Tridacna gigas</i> : 13,064±4750	All fish: 2,505±778	<i>Nerita</i> : 1,106±465
	<i>Hippopus</i> : 6,859±464		<i>Asaphis</i> : 455±52
	<i>Tridacna maxima</i> : 4,418±708		
	<i>Trochus</i> : 3,904±467		
	<i>Lambis</i> : 3,412±205		
	<i>Cypraea</i> : 2,214±414		
Hunt type returns by macronutrient			
kcal/h	1,492±173	292±135	575±56
Protein (g/h)	284±31	6.6±2.9	88±9
Fat (g/h)	22±3	1.6±.7	9±.95
Mean time allocation			
19 Women	0.76±0.07	0.09±0.05	0.14±0.05
21 Men	0.31±0.07	0.63±.08	0.04±0.03

One explanation for this pattern might be that spearfishers are not maximizing calories, but other macronutrients. But this appears not to be the case: protein return rates from shellfish collecting at 284±31 g/h are higher than from spearfishing at 6.6±2.9 g/h ($t=6.78$, $df=68$, $P=0.0001$). Fat return rates are also higher for shellfish collecting at 22±3 g/h than for spearfishing at 1.6±0.7 g/h ($t=4.808$, $df=68$, $P=0.0001$).

Another possibility is that spearfishers prefer other benefits supplied by reef fish: they may be more valuable as trade goods than shellfish prey. But this seems unlikely: shellfish collecting produces larger harvests (1,962±247 g, $n=44$) than spearing (356±100 g, $n=26$) ($t=24.857$, $df=68$, $P=0.0001$). Shellfish prey are also more likely to be shared: following a harvest of shellfish, on average 22% of the take is shared to another household, while only 7.5% of a spearing harvest is shared.

Finally, could choosing to spear fish instead of collecting shellfish as women do provide greater consumption benefits in the long-term? The short-term costs are inescapable: while women maximize their patch returns and the size of their meat harvests by stopping to take shellfish when encountered on the reef, male spearfishers take a large cut in protein, fat, and energy income by ignoring shellfish and continuing to search for fish to spear. There could be long-term benefits of such specialization if by dividing labor and pooling harvests, male spearfishers and female shellfish collectors maintain long-term shellfishing productivity on the reef. This could happen if the cooperative pooling unit (the household) defended a reef territory, excluding other pooling units from foraging so that the future benefits of conservation could be realized. But they do not: while reef territories are owned, the group sharing use-rights to sections of reef is not equivalent to the pooling unit. Sections of reef are considered extensions of residential plots: use-rights to residential plots are shared by all members of a patriline. Only bounded clam gardens within reef territories are excludable and defendable by single households, and these gardens are approximately 2-4 m in diameter, not large enough to permit spearfishing. Any gains in long-term shellfish productivity would have to be shared by the entire patriline, and all men within the patriline would have to forgo shellfish collecting, which is unlikely since men do vary in the extent to which they collect shellfish. We cannot definitively exclude this possibility, only note that it seems unlikely.

Spearfishers interested in maximizing return rates should not ignore shellfish while foraging on the reef, but most of them do. The costs of choosing to spear fish do not appear to be balanced by benefits received through cooperative gender specialization in macronutrient harvesting, nor through reciprocal sharing. We propose that the benefits of spearfishing are gained through the honest signal value of acquiring the prey rather than through consumption, and that honesty is maintained through differential benefits: men of higher phenotypic quality benefit more than lower-quality individuals because they can signal more intensely each time they signal.

Prediction 1: men who signal more frequently obtain greater benefits

If spearfishing is a competitive display, signalers should reap social benefits associated with more frequent spearfishing, such as the benefits from gaining status through building a reputation as a skilled spearfisher. In interviews with 33 Meriam men and women, none would nominate a slate of "the best shellfish collectors," claiming that "being better than others" (i.e., getting larger harvests) depends solely on working long hours, not on qualities intrinsic to the forager, and most nominated the most frequently observed woman on the reef as "hardest-working shellfish collector." Across individuals, shellfish-collecting harvest sizes are strongly contingent upon foraging time, whereas spearfishing harvest sizes are not (Fig. 1). All interviewees were willing to nominate a slate of "the best spearfishers." Because there was little variance in signal frequency among the majority of men observed on the reef, we divided the signalers into the most frequent (1 man with 10 observed bouts) and the least frequent (14 men with 19 bouts total). The most frequent signaler obtained 23 out of 61 (37.7%) total nominations by the 32 respondents (who nominated as many as three individuals). More than 75% of respondents named the most frequent signaler as the best spearfisherman. None of the less frequent signalers in our sample obtained any nominations at all. The remainder of the nominations went to deceased individuals or those currently not active as spearfishers.

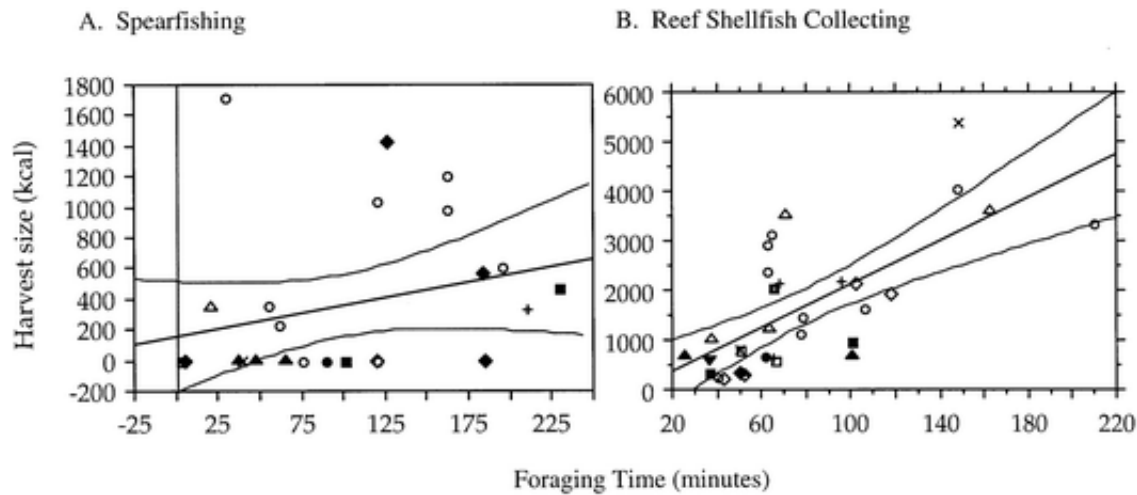


Fig. 1. Relationship between harvest size and bout length for spearfishing (A) and shellfish collecting (B). Foragers can predictably expect larger harvests with longer foraging time in shellfish collecting but not spearfishing. *Each point* represents one randomly selected, fully observed bout, with the *open circle* representing the most active individual. Episodes are distributed throughout the tidal season of 1994. **A** Linear regression with 95% confidence intervals for mean harvest size in kcal (y) on reef patch foraging time in minutes (x). Harvest size= $155+2x$; $r^2=0.074$, $P=0.1990$. **B** The same regression for mean reef shellfishing (female foragers only) harvest size in kcal (y) on reef flat collecting time in minutes (x). Harvest size= $-6682+21.86x$; $r^2=0.479$, $P=0.001$

Prediction 2: signal intensity is linked to phenotypic quality

For the qualities signaled by spearfishing to be honestly advertised, high-quality spearfishers should signal more intensely, because they gain greater marginal benefits or endure lower marginal costs per unit signal. In addition to signal frequency (see above), good measures of signaling intensity are harvest size and success rate. The mean harvest size per bout (in kcal) of the most frequent spearfisher (680 ± 197 , $n=9$) was larger than that obtained by other spearfishers (209 ± 101 , $n=15$; $U=32$, $P=0.05$). His hunt type return rates were also higher at 616 ± 356 kg/h versus 137 ± 75 kg/h ($U=32$, $P=0.49$), although his bouts were of equal mean length as those of the less frequent signalers (106 ± 17.2 vs 102 ± 15.6 min). The most frequent signaler's return rates were still lower than he could achieve shellfish collecting ($U=72$, $P=0.002$). The "frequent signaler" also had a much lower bout failure rate than other men (failure rate per bout= 22.2% vs 66.7% ; $\chi^2=4.444$, $P=0.03$).

Prediction 3: the signal is designed to be perceived by the intended audience

Since spearfishing is a solitary hunting activity that produces no large, widely consumed common good, the signal elements contained in spearfishing are subtle and difficult to observe. Yet reputations are still built in the absence of any overt boasting or tale-telling on the part of the forager himself, who when successful, displays the typical behavior of a male solitary hunter: he returns home carrying his catch quietly, albeit very visibly. The signal elements incorporated in spearfishing are conveyed to observers in three distinct ways. (1) Reef activities are highly visible to a large section of the village surrounding one's residence, which contributes to the ease of observer perception of bout frequency. (2) Spearfishermen make perception of harvest size easier by carrying their harvests openly in hand, rather than carrying them in a bucket, as line fishers and shellfish collectors do. (3) Although bout frequency is the signal element most easily observed, harvest size is usually made known to a large

number of individuals through verbal communication. Hunts with large harvests are recounted many times over, and stories about such success become part of local legend.

Turtle hunting as costly signal

Turtle hunting could serve as a competitive display if foragers can distinguish themselves from others based on their skill. The signal(s) thus produced by turtle hunting would depend upon the kinds of costs incurred. If turtle hunting is associated with lower foraging returns than other options, signals of skill sent through hunting could honestly indicate the ability of the forager to expend time and energy in a wasteful pursuit. If hunting has a high return but is associated with wide, unconditional, and costly distributions of food, signals of skill could honestly indicate one's quality (prosocial tendencies, or ability to gain resource reserves through skill in other activities) by expending time and energy in providing goods for public consumption.

Hunting turtles is indeed a competitive pursuit, with a very different complement of participants than collecting. As the Meriam put it, *anyone* can collect turtle in the nesting season, but only certain men have the ability to succeed at turtle hunting. Older and younger men, children, and women of all ages participate in turtle *collecting* during the nesting season: 21% of turtle collections involve adult females. In contrast, for turtle *hunting*, the only participants are males between the ages of 16 and 47 (mean age=31.6, $n=38$). Though a substantial proportion of Meriam men participate in turtle hunting at some point in their lives, relatively few do so with regularity. In our sample of 37 turtle hunts extending over two periods (1994-1995, and 1998), there were a total of 102 man-days expended, or 2.76 hunters per hunt (all hunts last 1 day or less). For the 87 man-days where hunters are individually identified, there were a total of 40 unique individuals, or 2.18 hunts per hunter. But the 3 most active men participated a total of 16 times, or 18.4% of the hunter-days of known individuals. Thus, 44.4% of the 90 Meriam males aged 16-47 hunted at least once in the study period, but the 3 most active participants (3.3% of males) were over five times more likely to engage in a turtle hunt than the average Meriam male in this age range.

Turtle hunting entails a variety of costs that could ultimately be linked to signaler quality in a way that ensures signals sent by hunting will remain honest (Smith and Bliege Bird 2000). Hunting may involve (1) high opportunity costs in the form of passing over opportunities to acquire other resources with a higher rate of return, (2) low consumption return rates (Bliege Bird and Bird 1997) as hunters distribute meat to non-hunters following the hunt, or (3) high energetic, monetary, or time investment costs of preparing for and conducting the hunt that reduce energetic return rates below that of other more easily acquired resources. There may be other costs or risks of a social nature that provide a link between turtle hunting and hunter quality, particularly the loss of social status should a hunter fail to deliver turtles to a feast (see below).

Hunting season hunts

During the hunting season, between April and October, the goal of all hunts is to capture turtle for a previously arranged feast. During major feasts, all those who come must be fed by the feast-giving family and their allies, and the family can never predict precisely how many people will come to the feast itself. Theoretically, the entire population of the island (over 400 men, women, and children) plus many off-island visitors could attend, though attendance by 200 or fewer from both on and off the island is typical (mean=174.9, range=49-343, $n=54$). Failure to provide turtle is a substantial cost to the hunter's status since all feast-goers will note the absence of turtle meat at the feast. Since hunts are only undertaken a day or two prior to a feast, there are only as many hunts as there are feasts during this season: in 1994 there were ten hunts for public feasts. During the hunting season, the turtle patch is more distant, encounters with turtle are less common, and turtles are more difficult to detect and

follow under water that is often murky and broken by swells and whitecaps created by the nearly constant 20-knot southeast tradewinds during this season. After a successful hunt, hunters could expect to obtain a per capita net return of 4,653 kcal/h if they divided the turtle among themselves; however, all hunts during this season provision feasts, and hunters keep no share of the turtle they provide. Hunters deliver the turtle whole to the feasting location. Hunters thus obtain negative per capita consumption returns of -1,086 kcal/h, including the costs of traveling to the patch (see Bliege Bird and Bird 1997 for details of the method of calculating net returns from turtle hunting).

Nesting season hunts

During the remainder of the year, hunts are undertaken for two reasons: to provision previously arranged feasts ($n=13$), and to provision households ($n=9$). In this season, hunting is much easier and hunters take on fewer costs: turtles are found on nearby reefs waiting to crawl onto the beaches to lay eggs at night, the tradewinds have largely ceased, and in between monsoon storms, the water is clear, calm, and visibility is excellent, allowing hunters to dog turtles more closely, to lose fewer, and to more finely discern size and sex. Considering only successful hunts, hunters in the nesting season could potentially obtain per capita returns of 8,061 kcal/h hunting for household consumption if they did not share the meat with others. But hunters share more widely than collectors during the same season, leaving their personal return rate from hunting for a feast at -1,633, and those from hunting for household consumption at 814 (Table 2). Hunts during the nesting season should not happen at all if hunters were interested solely in maximizing energetic return rates: during the nesting season, collected turtle offers higher after-sharing energetic returns than hunted turtle. In addition, other available resources are also more energetically productive: sardine netting provides $11,008 \pm 1,705$ ($n=28$) kcal/h before sharing - sardine harvests are shared only 5% of the time, leaving on average 10,864 kcal/h. If hunting turtle were solely about ensuring feast-goers can eat plenty of meat and fat, men should net 50 kg of sardines with no chance of failure rather than spending the entire day chasing turtle to risk coming back to the feast empty-handed.

Table 2. Turtle hunting per capita mean \pm SE net returns (kcal/h), number of hunts/collections (n), and total number of participating acquirers by consumption type (house or feast), season (hunting or nesting), and acquisition method (hunting or collecting). Net return rates are calculated as gross edible energy captured minus energy expended in travel divided by time spent in travel, search, and handling. Since travel costs are primarily the cost of fuel expended in outboard motors, the cost of fuel used (l) is converted to calories of meat that could have been purchased in the local shop with the money used to buy fuel for the hunting trip. Further details in Bliege Bird and Bird (1997)

		Before sharing		After Sharing	
		Hunting season	Nesting season	Hunting season	Nesting season
House	Collecting (108 acquirers)		21,875±2279 (<i>n</i> =44)		5,068±922
	Hunting (27 acquirers)		8,061±970 (<i>n</i> =9)		814±526
Feast	Collecting (56 acquirers)		16913±1842 (<i>n</i> =44)		1329±1127
	Hunting (40 acquirers)	4,653±1,213 (<i>n</i> =10)	10,607±3566 (<i>n</i> =13)	-468±660	-1,633±325
Total number of hunts		10	22		
Total number of collections		0	88		
Number of turtles		13	116		

Turtle hunting in both seasons thus satisfies two of our criteria for consideration as an honest and costly signal. Unlike turtle collecting, observers can distinguish skilled from unskilled individuals and participation is restricted to a subset of the community; second, hunting has the potential to generate high return rates among simultaneously available foraging alternatives (second only to sardine netting), but does not result in much consumption benefit to the hunters since they share widely and take no portion for themselves. As with spearfishing, we hypothesize that the benefits of hunting are gained through the honest-signal value of acquiring the prey, rather than through consumption, and that honesty is maintained through differential costs and benefits: men of higher phenotypic quality benefit more or pay less than lower-quality individuals per unit signal.

Prediction 1: turtle hunting is differentially costly or beneficial

The relative costs and benefits of hunting turtle vary with the season: hunts are less costly in the nesting season because the prey are found closer to home, but they are more ambiguous as a signal, since turtles may also be collected at this time. Since there is the potential for dishonest signaling (acquiring a turtle through collecting and passing it off as a hunted turtle), we predict that the benefits of hunting during the nesting season are lower as well. We would thus expect that more skilled hunters would be over-represented among hunting season hunts, which have the highest cost and the lowest signal ambiguity, while the least skilled hunters would be over-represented among nesting season hunts, when hunts are less costly as well as harder to discriminate from collecting. Among turtle hunt participants, age is usually a good proxy for skill, since hunt participants move up in the hierarchy of roles as they gain in skill over time, and since the skills necessary to be a good hunt leader are not dependent upon size and strength. We thus expect jumpers to make the move to become hunt leaders only during the nesting season. Hunt leaders during the hunting season (*n*=8) are in fact an average of 7.9 years older than hunt leaders (*n*=22) during the nesting season, a difference that is statistically significant ($U=41.5$, $P=0.05$). In contrast, there is no difference in age of jumper according to season ($df=37$, $t=-0.253$, $P=0.80$). Of the 17 known current hunt leaders, the 4 youngest (aged 18-22) were observed as hunt leaders only during the nesting season, and served only as jumpers during the hunting season.

Prediction 2: signal intensity is linked to phenotypic quality

Turtle hunting provides evidence of skills that could honestly signal several relevant qualities: environmental and ethological knowledge, risk-taking, strength and agility, leadership and organizational abilities, and prosocial tendencies (e.g., expending time and energy in providing goods for public consumption at feasts). Such information is presumably of interest to potential female mates, their families, potential political alliance partners, or competitors for social status.

As detailed above, the most active hunters are a subset of the adult male population. The best turtle hunt leaders are well known to community members: in a series of 32 interviews we conducted with men and women in which informants were asked to nominate any three individuals of their choice for "best turtle hunters," 3 men (all ones we had observed as the most frequent hunt leaders) garnered 38 (39.6%) of the 96 nominations (a total of 30 men were nominated for "best hunter" out of a pool of 90 or more males aged 16 and older). While several deceased individuals or older men no longer active as hunt leaders were named among the "best hunters," no men currently active solely as jumpers were so named. Jumpers are rarely individually credited by others for acquiring a turtle, and drivers are rarely publicly credited with participation in the hunt. Feast-goers can readily name hunt leaders as providers of the turtle, even several years after the feast, but when pressed for the names of other hunt participants, lump all others together as "the boys." Jumpers may begin in this role as young as 15-17 years old; anecdotal evidence indicates that those who excel in this role and gain increasing knowledge and peer respect eventually become hunt leaders, while others remain jumpers or cease participating in turtle hunting.

Prediction 3: the signal is designed to be perceived by the intended audience

Signals do little good if they are not perceived and the information contained is not deciphered. We propose that when signals are designed to acquire general social status or political dominance, broadcast efficiency will be increased by directing them at larger audiences, rather than small subsets of interested parties (as might be predicted if the signal elements of hunting were directed solely at potential mating partners). Thus, we predict that hunted turtles should be shared more widely than collected turtles; in other words, that individuals should choose to hunt for larger audiences, and to collect when audiences (the number of households attracted to the turtle and consuming portions) are predicted to be smaller. Because turtles cannot be collected during the hunting season, we control for the effects of season. We thus predict that audience size should have a significant effect on acquisition method within the nesting season only: when larger audiences are available, men should prefer to hunt rather than collect. During the 1994-1995 nesting season, hunts for which the number of consumers were known ($n=22$) averaged 26.7 ± 23.7 households, while collections ($n=80$) averaged 18.7 ± 19.0 households consuming, a significant difference ($t=-1.649$, $df=100$, $P=0.05$).

Individuals who acquire turtles for feasts have a large built-in audience; however, turtles acquired for household provisioning will be shared among a smaller number of households. If hunting serves as an honest signal and hunters wish to broadcast the signal widely, turtles acquired for household provisioning should also be shared more widely when hunted than when collected (controlling for season). During the 1994-1995 nesting season, there were 9 hunts and 44 collections to supply turtles for household consumption (Table 2). As predicted, hunted consumption turtles were shared to more households (7.5 ± 3.0) than collected consumption turtles (4.6 ± 2.5), and the statistical difference is strongly significant ($U=64$, $P=0.015$). Because the number of households receiving portions of a hunted turtle is larger than the number receiving portions of a collected turtle, portions shared to each household should be smaller, but they do not seem to be so, because hunters kept less for themselves and their own households than did collectors (mean portion kept (kcal) for hunters= $7,780 \pm 2,194$ kcal, $n=38$; for collectors= $14,387 \pm 2,631$ kcal, $n=123$) although the difference is not significant (t -test on

log-transformed kcal kept, $t=0.682$, $df=159$, $P=0.50$).

Discussion

Although our sample of spearfishers is too small to define a continuum in level of skill, spearfishing does seem to exhibit strong potential for competitive signaling. The most frequent signaler obtains much higher gains per unit patch residence time than other spearfishers. Harvest size (the most easily observed indicator of return rates) is likely to be linked to phenotypic quality in the form of hand-eye coordination, stealth, and patience, and provides an immediate signal of forager quality. Success rate is a signal element contributing to the long-term reputation of the spearfisher. High success rates in conjunction with large harvest size ensure that large harvests are more likely due to skill (forager-dependent variability) than to luck (forager-independent variability). As a result, the most active spearfisher gains the benefits of an enhanced spearing reputation that more infrequent signalers do not seem to enjoy. Spearing thus has the potential to serve as an honest signal of a spearfisherman's phenotypic quality.

Although we have demonstrated the potential for signaling, and the bias in men's foraging toward resources which have high competitive signaling potential, precisely how both signaler and observer ultimately benefit from the signal is not clear. We do know that good spearing men are widely recognized, and that this adds to their social status within the community. Potential competitors might also gain from knowing who is a better man with a spear, although the knowledge certainly would have been more useful in the past when spears were the major means of ambushing competitors. Spearing signals may not be designed to appeal to potential mates interested only in marrying provisioners. A man who demonstrates his intention to provision a household by collecting shellfish may be more attractive to such women than a man who demonstrates his intention to engage in a competitive, status-enhancing pursuit.

Turtle hunters seem to have very different goals than turtle collectors. Compared to collecting, hunting is more costly (in time, energy, and risk), provides meat less efficiently, and is associated with wider distributions of meat and larger audiences to witness the hunters' prowess. Hunters keep no meat for themselves unless (quite rarely) hunting for household consumption, in which case they still keep less and share more than turtle collectors. Hunters take on a variety of costs for which they are not materially compensated: they expend more time and energy in hunting than they do collecting, they spend more money for fuel, they spend time organizing and preparing the hunting team and its equipment prior to the hunt, and they deliver the meat to be consumed by large audiences at feasts. The ability to bear such costs appears to be linked to hunter quality. Because a hunter is an organizer and decision-maker, his abilities peak as he gains skill and experience: Those named as the best hunters are older than other hunt participants, such as jumpers. As we predicted, when hunting was less costly and more difficult to discriminate from collecting (i.e., during the nesting season), hunters were younger, in fact composed almost entirely of ambitious jumpers preparing to be hunt leaders themselves. Furthermore, the signals sent by hunting are efficiently broadcast: hunts were associated with larger numbers of consumers overall than collections during the nesting season and during household consumption events. Most feast-goers (audience members), when quizzed, know the identity of hunters, but not the identity of jumpers.

Since the low take-home returns of hunters providing turtle for household consumption and the negative take-home returns of hunters providing turtle for a feast are due to widespread sharing, the argument could be made that the signal cost is eventually recovered in the form of meat or other goods or services returned as payback for the hunter's gift. In other words, perhaps RA by the recipients of a hunter's largesse erases the cost of his signal (Sosis and Hill 1997). The stable maintenance of RA requires that the provisioning of a turtle be contingent upon the eventual receipt of counterbalancing

benefits which compensate the hunter for the marginal cost of giving up turtle that could have been used in other fitness-enhancing ways. Previous tests of predictions based on RA in the form of risk reduction reciprocity for sharing of collected and hunted turtles combined received little support (Bliege Bird and Bird 1997). Further tests of alternative forms of reciprocity are being conducted to evaluate this line of explanation (R. Bliege Bird, G. Kushnik, E.A. Smith, D. Bird, C. Hadley, unpublished data), as will be detailed in future publications.

While we have measured the cost of hunting using direct material currencies such as time, energy, and money, there are additional social costs that, though difficult to measure, may be of equal or even greater importance. Turtles provided for feasts are needed by community elders (feast hosts) to enhance their own status by ensuring there is plenty of meat for guests. If successful hunting is a reliable signal of the hunter's underlying quality (as defined above), lower-quality individuals would be expected to fail on turtle hunts more often and thus pay a higher marginal cost per turtle delivered to a feast (i.e., per unit signal). Failing to deliver a turtle to a feast also entails significant social costs, since the feast-holders are expected to serve turtle to their guests, and everyone will know when a hunter has failed. High-quality individuals should have a lower probability of failure and thus a high ratio of social benefits (from successful hunts) to costs (from failures). Low-quality individuals may face a large enough risk of failing to produce a net social deficit from their signaling attempts, and hence may avoid signaling at all, making it difficult to test this hypothesis. We do have anecdotal evidence that some men have attempted turtle hunting in the past, and given up when they found they were "no good at it." In addition, the facts (detailed above) that only certain men engage in turtle hunting, that only an older and more experienced subset of these become hunt leaders, and that hunt leader status is widely recognized in the community, all indicate that success in this endeavor is not equally available.

To qualify as costly signaling, hunting must not only be honest, but must also reveal signaler quality. Given the three distinct roles played by hunt participants, we propose (but cannot currently test) that at least four distinct dimensions of underlying quality could be signaled through turtle hunting: (1) physical quality (such as strength, stamina, agility, and risk-taking); (2) cognitive skills (involving the ecological and ethological knowledge needed to successfully locate and capture turtles); (3) leadership skills (charisma and organizational abilities), and (4) generosity (ability and willingness to bear the high immediate cost in time, money, and energy of providing collective goods without direct compensation). We expect the first dimension to apply primarily to the younger men who serve as "jumpers," whereas the other three dimensions refer primarily to hunt leaders.

The results of additional analysis in progress show that the display of such qualities is correlated with higher social status and higher age-specific reproductive success of hunters and their mates than other Meriam (E.A. Smith, R. Bliege Bird, D. Bird, unpublished data). As explained to us by Meriam hunters and their mates, the signals sent by hunters are likely to be part of both political strategies, in which hunters demonstrate to other men their honest intention to work for the public good, and reproductive strategies, in which hunters demonstrate their "willingness to work hard" in order to gain access to the "best girl" (Kaddy, personal communication; Passi, personal communication). Hunters know that spreading one's influence widely via the provisioning of collective goods at feasts increase social status over the long-term among the community as a whole, while less public-minded status-enhancing activities (like stealing land or selfishly hoarding resources) provides narrow, short-term status in only a small pool of competitors.

Implications for the sexual division of labor

One intriguing result of our analysis are the gender differences in participation in those activities with high signaling potential. With spearfishing particularly, the differences were not consistent with the common notion that a sexual division of labor in humans functions to maximize the productivity of a cooperating male-female pair (see Bliege Bird 1999). We propose that the signaling benefits attached to certain foraging strategies may often change the valuation of certain prey items for some individuals. While foraging on the reef, males make choices that fail to maximize their macronutrient return rates. These choices appear to be due to the tradeoffs men face over foraging for highly productive resources which have little signaling value (shellfish) against foraging for less productive resources with high signaling value (speared fish). Likewise, choosing to hunt turtle for feasts provides much lower consumption benefits than collecting turtle for the household, but greater signaling benefits. Adult women only participate in cooperative turtle collection, comprising 21% of all participants, and do not hunt.

These data suggest that foraging sex differences may not simply be a result of women preferring plants and men meat, or women preferring small harvests while men prefer large ones, or even women preferring prey which can be more easily harvested while children are present (shellfish are just as difficult as fish to collect with small children). Where there is a choice in foraging method, men seem to prefer to acquire meat through more risky methods that more easily differentiate the skill of individual foragers, while women seem to prefer less risky methods carrying little potential for discrimination of forager quality. We propose that sex-biased foraging preferences may arise due to the differing benefits each sex receives from investing in competition for status through signaling certain genotypic or phenotypic qualities.

Foraging as communication

As Hawkes (1990, 1991, 1992, 1993) first hypothesized, some kinds of hunting may persist in human populations because some foragers gain benefits from widely disseminating knowledge about their prowess relative to other individuals through the hunting of large and risky prey items. While Hawkes (1993) stressed the benefits that hunters obtain from providing collective goods (as with turtle hunting and unconditional sharing), our results show that benefits may also come in the absence of any material good provided to observers (as with spearfishing) as a result of honestly revealing hidden information to interested parties. Differential costs and benefits for signalers of higher and lower quality serve to keep the information honest and valuable to observers.

Our results suggest that CST has the potential to account for many puzzling aspects of human foraging strategies, and to substantially modify received views about optimal foraging, food sharing, and other phenomena central to studies of human behavioral ecology in small-scale societies (Winterhalder and Smith 2000). CST may illuminate otherwise puzzling behaviors such as preference for prey and patch types which provide fewer energetic benefits than other possible choices and are more costly on other levels, if the costs (or benefits) incurred are linked to signaler quality, so that poorer-quality signalers cannot consistently maintain or reach the same level of signaling as higher-quality signalers. Signaling hypotheses have only just begun to be tested as a cause for variability in human foraging strategies. Sosis (2000) has suggested that the benefits of signaling may explain why Ifaluk men engage in energetically inefficient fishing methods associated with costly ritual preparations. Such benefits may also explain why Ache men prefer to hunt widely shared game even though palm starch collection would offer higher on-encounter energetic returns (Hill et al. 1987; Hawkes 1991).

We are not proposing that the signaling benefits provide the *only* motivation for hunters and meat recipients, but simply that they provide an additional factor of evolutionary and motivational significance shaping hunting and sharing decisions. Thus the social and political signaling benefits of at least certain forms of hunting may compensate for any economic "wastefulness," in the same way that Veblen (1899) explained both "conspicuous consumption" of material goods and "conspicuous leisure" as instances of "conspicuous expenditure" designed to gain or maintain social benefits only indirectly related to economic advantage. However, CST has the potential to explain not only "wasteful" foraging activities, but any behavior in which higher-quality individuals obtain higher marginal benefits because they can better absorb the cost of the behavior, and where such behavior is efficiently broadcast to the proper observers (potential mates, allies, or competitors).

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