

The benefits of costly signaling: Meriam turtle hunters

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Hunting, particularly when it involves large game that is extensively shared, has been suggested to serve as a form of costly signaling by hunters, serving to attract mates and allies or to deter competitors. Empirical evidence presented elsewhere on turtle hunting practiced by Meriam people of Torres Strait, Australia, supports several key predictions of the costly signaling account. Here we present evidence from the same study bearing on another key prediction, that signalers (hunters) gain social and reproductive benefits. Specifically, we find that successful hunters gain social recognition, have an earlier onset of reproduction, achieve higher age-specific reproductive success, and gain higher quality mates, who also achieve above-average reproductive success. Meriam hunters also average more mates (women who bear their offspring) and more co-resident sexual partners than other men, and these partners (but not mates) are significantly younger. Several lines of evidence thus support the idea that hunting is a form of costly signaling in this population. Alternative hypotheses involving reciprocity (from grateful recipients of meat) and direct offspring provisioning by hunters are not consistent with available evidence, but in the absence of experimental manipulation we cannot rule out a role for phenotypic correlation. *Key words*: foraging strategies, mate choice, reproductive success, signaling, Torres Strait. [*Behav Ecol* 14:116–126 (2003)]

Researchers in the field of human behavioral ecology have made considerable progress in explaining variation in human foraging strategies, life history, and related topics (Borgerhoff Mulder, 1991; Smith and Winterhalder, 1992; Voland, 1998; Winterhalder and Smith, 2000). Only recently, however, have researchers begun to draw on costly signaling theory (Boone, 1998; Hawkes and Bliege Bird, 2002; Neiman, 1998; Smith and Bliege Bird, 2000; Sosis, 2000). In studies of nonhuman species, signaling theory has proved to be a powerful framework for explaining how morphological or behavioral traits can convey reliable information about individually variable characteristics of social significance (Grafen, 1990; Johnstone, 1997; Zahavi, 1975).

In an earlier publication (Smith and Bliege Bird, 2000), we developed an argument as to how signaling theory might illuminate phenomena such as inefficient foraging strategies and the individually costly provisioning of collective goods and applied this argument to data collected among the Meriam people of Torres Strait, Australia. In a subsequent publication (Bliege Bird et al., 2001), we showed that Meriam practices of hunting of marine turtles conform to the following predictions derived from signaling theory:

1. Hunting is costly (to the hunter) in terms of time, material investment, risk of failure, and the opportunity to engage in more efficient foraging.
2. These costs are quality dependent, such that hunting success is an honest signal of hunters' phenotypic quality.
3. Hunters have effective methods of broadcasting costly signals, including unconditionally sharing large game at public feasts.

In this companion article, we present tests of hypotheses elaborated from a fourth key prediction concerning the benefits that accrue to signalers (i.e., Meriam turtle hunters)

and to those who receive such signals. In particular, we examine evidence bearing on the following hypotheses:

1. Frequent and successful hunters are widely recognized for these achievements.
2. These hunters obtain higher age-specific reproductive success than other men.
3. Hunters have a higher average number of mates.
4. Hunters have higher quality mates, as measured in several ways.

The evidence leads us to conclude that the signals sent by successful hunting in this population do indeed yield social and reproductive benefits to the hunters.

Field site and hunt types

Mer (aka Murray Island) is a small (1.6 km × 2.2 km) island on the northern end of the Great Barrier Reef, 140 km from Papua New Guinea in Australia's Torres Strait. The island's current population is 430 individuals of Meriam descent, scattered in approximately 85 households. The Torres Strait as a whole is administered by the State of Queensland and the Commonwealth of Australia. Although many Meriam men had long been engaged in industries in Australia (especially pearling, sugarcane, and railroads) until about 1975, when Australian welfare payments were first made available to all indigenous Australians, the Meriam on the islands were nearly full-time subsistence horticulturalists and marine foragers. Subsistence revolved around planting tropical yams, bananas, sugarcane, coconuts, and introduced New World crops such as manioc, sweet potatoes, and corn, and harvesting marine fish, shellfish, and sea turtles. Today, horticulture is nearly moribund, and carbohydrates and other goods are readily purchased at the community store. Yet fishing, hunting, and shellfish collecting remain a critical component of Meriam subsistence economy: mean daily per capita consumption rates average 630 kcal of meat and 40 g of protein. More than 80% of these calories are supplied by turtle during the nesting season. (For additional ethnographic description and previous ecological research among the Meriam, see Beckett, 1988; Bird and Bliege Bird, 1997, 2002; Bliege Bird and Bird,

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1997, 2002; Bliege Bird et al., 1995, 2001, in press; Haddon, 1906, Sharp, 1992; Smith and Bliege Bird, 2000.)

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 it is the only way to acquire turtles between May and September (*Kob Kerker*), when green sea turtles (*Chelonia mydas*) feed and mate on shallow reefs about 16 to 20 km from Mer. Hunting is a cooperative, entirely male pursuit with three distinct roles assigned to hunt participants based on their skill and experience. Only a few older men are considered turtle hunters (hunt leaders; *ariemer le*); younger men serve a period of apprenticeship as jumpers (*arpeir le*), and participants with less experience or skill may act as tiller-men (*korizer le*) steering the boat under the direction of the hunt leader (this last set of participants is not included in our analyses of turtle hunter below). The *ariemer le* organize and direct the hunts and are ultimately held responsible for their success or failure. The *arpeir le*, in contrast, are usually responsible for directly acquiring the turtles during the hunt by jumping from the bow of the boat onto a swimming turtle (Bliege Bird and Bird, 1997). During *Nam Kerker* (turtle nesting season), turtles may be intercepted at nesting beaches and collected. Collecting is a cooperative endeavor as well, but often involves participants of all ages and both sexes who usually travel to nesting beaches on foot or by dinghy in large family groups and relax on the beach waiting for turtles to arrive. When a turtle crawls onto the beach, it is flipped, trussed, and hauled into the boat. During *Kob Kerker*, turtles are only hunted and are consumed solely at feasts; during *Nam Kerker*, turtles are hunted for larger distributions (feasts and multi-household sharing) and collected for smaller distributions and household consumption. Turtle hunting, collecting, and meat sharing have previously been described extensively (Bliege Bird and Bird, 1997; Bliege Bird et al., 2001, in press; Smith and Bliege Bird, 2000).

Compared to collecting, turtle hunting has a number of features that are inconsistent with optimal foraging predictions, but which conform to a costly signaling framework. Hunters keep no meat for themselves unless hunting for household consumption, in which case they still keep less and share more than turtle collectors (Bliege Bird et al., 2001). 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 devote time to organizing and equipping the hunting team before the hunt, and they donate the entire catch to be consumed by large crowds at feasts. Previous analyses fail to find any evidence for reciprocation either in terms of turtle meat (Bliege Bird and Bird, 1997) or in terms of other marine resources (Bliege Bird et al., in press). The signals sent by hunting also are efficiently broadcast: hunts were associated with larger numbers of consumers overall (mean of 26.7, $n = 22$) than collections (mean of 18.7, $n = 80$) during the nesting season and during household consumption events, and hunted turtles often provision feasts attended by a large proportion of island residents (mean of 174.9 per feast, $n = 54$).

METHODS

To test whether the signals sent by successful hunting yield benefits to hunters, we gathered information on the degree to which frequent and successful hunters are widely recognized for these achievements. The data used to test this prediction were collected in 1998 through structured interviews of 19 adult males and 13 adult females, which included a number of questions regarding the interviewee's opinion about who

they considered to be the three or so best individual hunters, fishers, or spearfishers on the island. Respondents qualified their choices according to sex and age; most older male respondents preferred to list the best in "their day" along with the best current foragers. Questions about status or abilities focused on culturally relevant domains within which individuals compete for status, both in foraging and in other domains (such as dancing, political influence, and popularity with the opposite sex). As a control, we also posed questions such as "Who are the best three shellfish collectors?" and "Who are the best three turtle collectors?" Informants unfailingly told us they could not answer these questions because in these categories "everyone is good if they work hard."

To test the predictions that hunters achieve higher age-specific reproductive success (RS), a greater number of mates, and higher quality mates, we surveyed all households on the island in 1998, obtaining information on age, sex, and parentage of all permanent residents. Additional data on parentage were obtained through the collection of genealogies for islander patriline. Assignment of paternity was uncertain in a handful of cases, and where disagreement existed, we assigned the most frequently nominated father. Defining an individual's RS as number of living offspring has some possible weaknesses: only very old males may be sure to have completed reproducing, and age-dependent mortality of offspring may mean that individuals with younger offspring at time of census have inflated RS estimates. We dealt with the first weakness by using parental age as a covariate in all analyses of variation in RS and avoid making any claims about lifetime RS. In response to mortality of offspring, RS analyses often include only offspring older than a certain threshold, such as 5 years (e.g., Strassmann and Gillespie, 2002). We have determined that doing so with the Meriam data would make almost no measurable difference in the variation in RS which is investigated in this study (e.g., raising the percentage of all censused offspring fathered by turtle hunters from 59.8% to 60.6%), while lowering sample sizes considerably (e.g., 19.6% fewer total offspring available for analysis). Hence, we chose to include censused offspring of all ages in our RS analyses.

Because individual men and women may have multiple sexual partners, in relationships of varying duration, we used two alternative methods to link women with hunters and nonhunters, one involving co-parentage and the other co-residence. Thus, we defined an individual's mate as any person with whom at least one of that individual's surviving offspring were conceived; in assigning a woman to a category such as "hunters' mate," "nonhunters' mate," and so on, we used the criterion that the majority of her offspring were fathered by the relevant category of male. Out of 24 women with multiples mates (and 85 total women with known fathers of their offspring), there were 2 women who each had 1 child fathered by a hunter and another by a nonhunter. This 50% split between paternity of offspring also characterized one woman whose children's fathers are a jumper and a leader. In these cases, we classified the women as "hunter's mate," and "leader's mate," respectively. Because two offspring is below the mean RS for hunters' mates, this actually works against our prediction that these women will have higher RS than nonhunters' mates, and is thus a conservative decision. Second, we defined "partner" as the sexual partner with whom that individual was co-residing (as determined in our 1998 household survey), regardless of whether the couple was officially married or had produced any offspring together.

Mate quality was defined in terms of two measures: reputation for industriousness (via questions posed in the structured interviews), and reproductive success (established through parentage data collected during the household survey and in genealogical research). Reputation was assessed

Table 1
Demographic features of various categories of Meriam men

Category	<i>n</i>	Age (mean ± SD)	Age at first reproduction	Mean observed RS	Cumulative age-specific RS ^a
All men	114	34.8 ± 11.6	24.5 ± 6.3 (54)	1.7 ± 2.4	2.7 (98)
All hunters	53	35.2 ± 13.0	23.9 ± 6.6 (32)	2.3 ± 2.8	4.0 (50)
Nonhunters	61	36.2 ± 12.4	25.3 ± 5.9 (22)	1.3 ± 1.9	1.7 (48)
Hunt leaders (1994–1998)	18	36.3 ± 9.6	24.8 ± 6.3 (13)	2.8 ± 3.0	4.5 (18)
Hunt leaders (all)	29	41.6 ± 13.0	24.4 ± 5.8 (23)	3.5 ± 3.1	4.6 (29)
Jumpers (nonleaders)	24	27.6 ± 7.9	22.8 ± 8.5 (9)	0.8 ± 1.4	2.1 (22)

^a Reproductive success (RS) computed as the sum of the age-specific RS for each class, hence an estimate of lifetime RS if a man lived to at least age 50, experienced the observed age-specific rates over the ages 15–49, and no further reproduction occurred. Figures in parentheses are sample sizes, which may be smaller than those for other variables due to missing data on ages of some offspring.

for women by scoring responses to interviews in which we asked a sample of Meriam (see above) which women were considered “hardest working” of those currently living on the island. This is a culturally recognized category on Mer (as discussed further below). Reproductive success of both men and women as defined here refers to number of offspring alive in 1998 (regardless of age). We calculated age-specific reproductive success (ASRS) for any given set of individuals (e.g., turtle hunters) by dividing the number of offspring born to those individuals in each age class (e.g., ages 20–24) by the number of person-years lived in that age class by those individuals. Cumulative ASRS figures (e.g., Table 1, Figure 1) were calculated as the sum of the age-class figures for the indicated category of individuals.

RESULTS

What are the benefits to hunters?

For hunting success to serve as a form of costly signaling, hunters must signal qualities of interest to others, such as strength, skill, esoteric knowledge, or leadership ability. In turn, these qualities should lead others to prefer hunters as allies or mates, and/or lead other males to defer to hunters in contests for resource control and mate access. Thus, successful hunters—those who signal most frequently or consistently—should gain social benefits; in a behavioral ecology framework, at least, these social benefits should translate ultimately into reproductive gains. Evidence in support of the first two propositions (differential signaling and social recognition) is presented elsewhere (Bliege Bird et al., 2001). Here we examine evidence bearing on the expectation that signaling (success in hunting) leads to reproductive gains.

Reproductive benefits

Demographic data for the entire population on Mer allow us to examine if those men reputed and/or observed to be successful at turtle hunting have different reproductive profiles. These data do reveal consistent and statistically significant differences between hunters and other Meriam men in RS, as well as various demographic measures related to RS.

Observed RS is higher among turtle hunters than among other Meriam men, and higher still among hunt leaders (Table 1). However, since fertility is necessarily dependent on age, and most men in our sample are still in their reproductive prime, comparisons involving RS should employ age-specific rates. The cumulative age-specific RS (Figure 1,

Table 1) is higher for Meriam hunters in every (5-year) age class, an association that is even more pronounced among hunt leaders (though less so in the first two age classes). Given these age-specific rates, turtle hunters have a predicted lifetime RS about 2.4 times higher than that of nonhunters, and the estimated lifetime RS of the subset who are hunt leaders is about 2.8 times higher than nonhunters (Table 1).

Although our sample includes 50 hunters and 48 nonhunters for which age-specific reproductive rates can be calculated, when subdivided by age class the sample sizes in the older age classes become too small to guarantee robust tests of statistical significance. Nevertheless, our data reveal significantly ($p < .05$) higher RS for turtle hunters in age classes 20–24 and 25–29. (Using Mann-Whitney U tests, the results were: ages 15–19 years, $U = 1039.5$, tied $p = .07$, $n = 98$; 20–24 years, $U = 706.5$, tied $p = .01$, $n = 87$; 25–29 years, $U = 344.5$, tied $p < .001$, $n = 69$; 30–34 years, $U = 337$, tied $p = .11$, $n = 59$; other age classes far from significance.) The only other role categories for which we found significant differences in RS for more than one age class were for hunt leaders (ages 20–24, 25–29, and 30–34) and for spearfishers, but note that both of these overlap largely or completely with the turtle hunter category). To assess the statistical significance of these differences in RS more broadly, we conducted analyses of covariance between observed RS and being or not being a turtle hunter or a hunt leader (controlling for age). These ANCOVAs revealed a significant association with higher RS for turtle hunters in general ($F = 7.54$, $p < .01$) and a somewhat stronger one for hunt leaders ($F = 14.4$, $p < .001$), but no significant association for those Meriam who are classified (by field observation and by interview nomination) as outstanding fishermen, dancers, political leaders, or “popular with the ladies.” A maximum likelihood analysis also supported the hypothesis that turtle hunters produce more surviving offspring per unit time than other Meriam men (odds ratio = 1.959, $p < .001$).

Turtle hunters display a lower mean age at the birth of their first child than do nonhunters (Table 1), suggesting that enhanced RS is due in part to an earlier onset of reproduction. The overall pattern for men’s age at birth of first child is illustrated in Figure 2. If we consider men who have fathered at least one offspring, the observed difference is not statistically significant (unpaired t test, $p = .43$, $n = 52$). However, the proportion of men 30 and older who are childless is half as great for hunters (0.2) as for nonhunters (0.41), and is even lower for hunt leaders (0.17). This difference (between hunters and nonhunters) is statistically significant ($\chi^2 = 3.4$, one-tailed $p < .05$), but that for leaders versus other hunters is not. However, neither of these

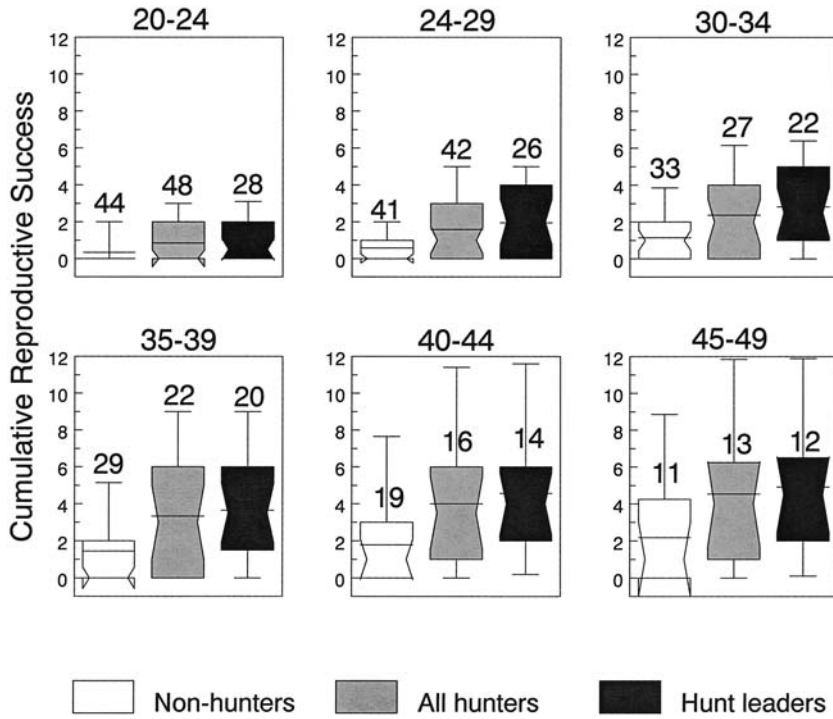


Figure 1
Cumulative age-specific reproductive success of Meriam men, by hunting role. Each panel presents data on non-hunters, turtle hunters, and hunt leaders for the indicated 5-year age class, with sample sizes for each category indicated above each box. The lower and upper box boundaries indicate 25th and 75th percentiles, the whiskers the 5th and 95th percentiles, the notch notes the median and its confidence interval, and the horizontal line bisecting each box is the mean.

measures account for censored observations (men who have not fathered a child prior to 1998, but may do so in the future). To address this, we conducted a hazards analysis of time to first reproduction using the Kaplan-Meier method, coding cases with no offspring as (right) censored. The results indicate that the “waiting time” to birth of the first offspring is significantly shorter for hunters ($n = 54$) than for nonhunters ($n = 59$; $p < .01$, Mantel-Cox log-rank test; $p < .01$, Breslow-Gehan-Wilcoxon test weighted for risk time length). The same analysis fails to find a significant difference in the hazard function for hunt leaders ($n = 29$) versus other hunters ($n = 25$; $p = .09$, log-rank test).

Why do hunters have higher RS?

As detailed above, the turtle hunter role does seem to be robustly correlated with enhanced RS among Meriam men, a pattern that is not true of such other roles as expert fisherman, good dancer, recognized political leader, or even

those reputed to be “popular with the ladies.” We have shown that the proximate reasons for this are that hunters begin reproducing at an earlier age and continue to father offspring at a higher rate at least through age 50. But these demographic facts do not reveal the causal pathways that connect turtle hunting with enhanced RS. We now examine a series of hypotheses aimed at uncovering these, including hypotheses unrelated to the costly signaling framework.

Do hunters have more mates?

One possibility is that costly signaling via turtle hunting is designed to attract mates. If so, quality signalers (successful hunters) may attract more mates or simply better (more reproductively successful) mates. The first hypothesis can be tested crudely by measuring the mean number of mates (defined as those women with whom an individual produces offspring) per male. Table 2 shows that turtle hunters and particularly hunt leaders have a higher mean number of

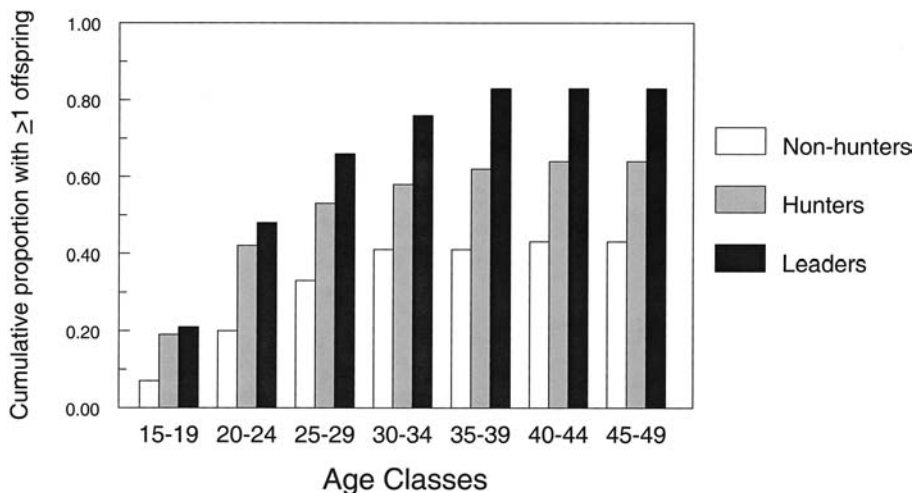


Figure 2
Cumulative proportion of Meriam men having at least one offspring, by hunting role and age class; see Table 1 for sample sizes.

Table 2
Differences in number of mates between Meriam hunters and other men

Category ^a	No. of mates (mean \pm SD) ^b	No. of mates in comparison group ^c	<i>t</i> test for difference of means	ANCOVA ^d
Turtle hunters	0.76 \pm 0.73 (<i>n</i> = 54)	0.46 \pm 0.62 (<i>n</i> = 90)	<i>t</i> = 2.7, <i>p</i> < 0.01 (142 df)	<i>F</i> = 10.1, <i>p</i> < .01
Hunt leaders	0.97 \pm 0.68 (<i>n</i> = 29)	0.52 \pm 0.71 (<i>n</i> = 25)	<i>t</i> = 2.3, <i>p</i> = 0.02 (52 df)	<i>F</i> = 1.9, <i>p</i> < .2

^a Includes all males who were nominated in surveys as outstanding in this category, or observed participating in it; "hunt leaders" is a subset of "turtle hunters" (see text).

^b "Mate" defined as any woman with whom a male has fathered surviving offspring.

^c All males \geq 15 years old who were classified as nonhunters or nonleader turtle hunters, respectively.

^d One-way, with age as covariate.

mates than the reference group (nonhunters and nonleader hunters, respectively) and that this is statistically significant for both categories. However, because the various sets of men differ in their age distributions, these simple comparisons might be misleading. Once we control for age, the association with number of mates remains statistically significant for hunters versus nonhunters, but not for hunt leaders versus other hunters (Table 2). We conclude that the higher RS associated with being a turtle hunter is probably due in part to the increased likelihood of having offspring with more than one woman.

Do hunters have relatively younger mates?

Because fertility rates are highly age dependent, particularly for females, and because male fertility declines more slowly than that of females, males can enhance their RS as they age by mating with younger females (i.e., with higher residual reproductive value). This pattern of younger mates for higher status men has been reported for a number of human societies, including ones where male status is linked to hunting prowess (Hawkes et al., 1997; Hill and Hurtado, 1996; Marlowe, 1999). The evidence for this pattern among the Meriam is mixed. In the case of men's mates (i.e., those women with whom they have produced offspring), a paired *t* test on a set of 15 turtle hunters and an equal number of nonhunters matched for age found no significant difference in age of mates (Table 3), and, indeed, hunter's mates were only slightly younger on average than nonhunters' mates. In contrast, when we examined men's co-resident partners, the same test for 19 age-matched pairs found a greater age difference, which was statistically significant (Table 3). Because co-resident partners were those women currently engaged in a mating relationship with Meriam men at the time of fieldwork, these results might indicate that hunters have been more successful than other men in securing younger mates as they age. However, the results overall suggest that age of mates plays a relatively minor role in accounting for the higher RS of Meriam hunters.

Do hunters have harder working mates?

A measure of mate quality that is culturally recognized by Meriam is whether one's spouse is "hard working." A hard-working woman fishes, nets sardines, collects shellfish, and makes gardens, as do all Meriam women, but to gain a reputation as being hard working, she must also produce so much food that she can share widely and frequently, and she must also be able to contribute time and effort to public feasts and other community gatherings. To assess which women had a reputation as being hard working, in our

interviews we asked each respondent to nominate the three hardest working women (*au dorge dorge koskir*) on the island. Analysis indicates that hunter's mates received significantly more nominations as hard working than are nonhunter's mates (*t* = 2.01, *p* < .05, unpaired *t* test, 165 df). Thus, this measure of mate quality is significantly associated with turtle hunting, although the causal pathways producing this association require further investigation. Such mates would be likely to produce more resources for household consumption, as well as to be respected more broadly in the Meriam community, both of which could enhance fertility and offspring survivorship.

Do hunters have more caretakers for their children?

Another possibility is that hunters have more offspring because there happen to be a greater number of alternative caretakers living in their households. If this were the case, we would expect a positive relationship between hunting frequency or the presence of hunters and the ratio of caretakers (females >14 years old) to dependents (boys or girls aged <15) in a household. However, there is no tendency for hunting to be associated with an increased ratio of alternative co-resident caretakers (Figure 3). Considering only households with at least one child resident, those with no hunters in the 1994–1995 sample period (*n* = 32) averaged 1.4 \pm 1.3 alternative caretakers per dependent, whereas households with at least one hunter (*n* = 17) averaged 1.2 \pm 0.9, a difference that is not statistically significant (and in any case in the opposite direction from this prediction). A linear regression of the frequency of turtle hunting on the care-

Table 3
Differences in the age of mates and co-resident partners of Meriam hunters and other men

Category ^a	No. of age matched pairs ^b	Mean age (\pm SD)		Paired <i>t</i> test
		Hunters	Nonhunters	
Men Mates	15	41.6 \pm 9.6 39.2 \pm 10.0	41.5 \pm 9.4 40.9 \pm 11.7	<i>t</i> = 0.9, <i>p</i> > .4 (14 df)
Men Partners	19	41.7 \pm 8.6 38.1 \pm 9.6	41.8 \pm 8.3 41.7 \pm 11.2	<i>t</i> = 2.3, <i>p</i> < .05 (18 df)

^a See text for definition of "mate" and "partner."

^b Men in each pair were matched by age and differ by no more than 2 years.

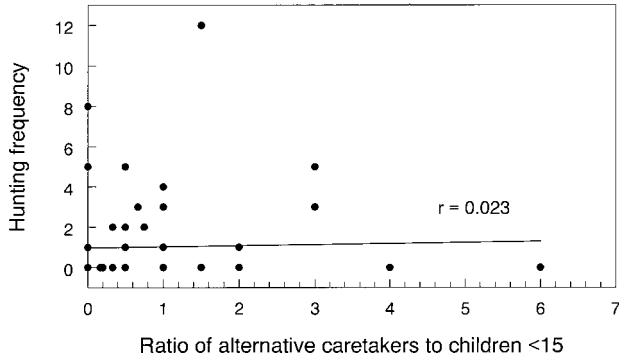


Figure 3
Regression plot of alternative caretaker to child ratio versus turtle-hunting frequency (number of times a member of that household participated in a successful hunt during 1994–1995) for households with at least one child present.

taker/dependent ratio yielded a nonsignificant coefficient of 0.02.

Alternative explanations

Although the results discussed thus far are almost all in agreement with predictions derived from the costly signaling framework, it is important to consider plausible alternative explanations of the relation between hunter status and reproductive success.

Direct provisioning

One obvious alternative hypothesis is that by acquiring meat and fish, successful hunters ensure that they and their mates and offspring have more to eat, thus enhancing fertility, survivorship, and good health. Although we lack systematic individual-level data on meat consumption, there are several reasons to doubt that this provides a direct explanation for

variation in RS among Meriam. First, although turtle hunting does yield high return rates, once these are adjusted to take account of the fact that most or all of the catch is shared with others (at formal feasts or more informally to adjacent households), the net returns are very low or, in the case of provisioning feasts, even negative (Bliege Bird et al., 2001). Second, analyses reported elsewhere fail to find evidence that such generosity is repaid through reciprocating gifts of food (Bliege Bird and Bird, 1997; Bliege Bird et al., in press).

Third, there are better ways to provision households than through turtle hunting. In particular, fishing can be a more reliable way of generating household income, including cash in the case of commercial fishing, in which some Meriam engage (Bliege Bird, 1999). If we divide the 13 men nominated in surveys as the “best fishermen” into those who are also turtle hunters ($n = 7$) and those who are not ($n = 6$), there is a dramatic difference in the observed and computed age-specific RS between the two subsets. The hunter-fishers average 4.3 surviving offspring and have a computed cumulative RS of 4.93 at age 50 (values similar to our larger sample of hunters), whereas the fishermen only group average 0.7 surviving offspring and are projected to attain a cumulative RS of only 1.01 at age 50 (Figure 4). Despite the small sample size, these RS differences are significant, both in a non-parametric rank test (Mann-Whitney, $U = 6.0$, tied $p < .03$) and in an ANCOVA controlling for age ($F = 5.4$, $p < .05$, 1 df). Although not a direct test of the provisioning hypothesis, these results are not what we would expect if the association between turtle hunting and high RS among Meriam men were due to the contribution hunters make to household food income.

Phenotypic correlation

Another possibility is that the RS data simply indicate phenotypic correlation, wherein factors other than underlying quality favor both higher RS and higher likelihood of hunting. One variant of this argument might be that those men who are physically robust and healthy are more likely to

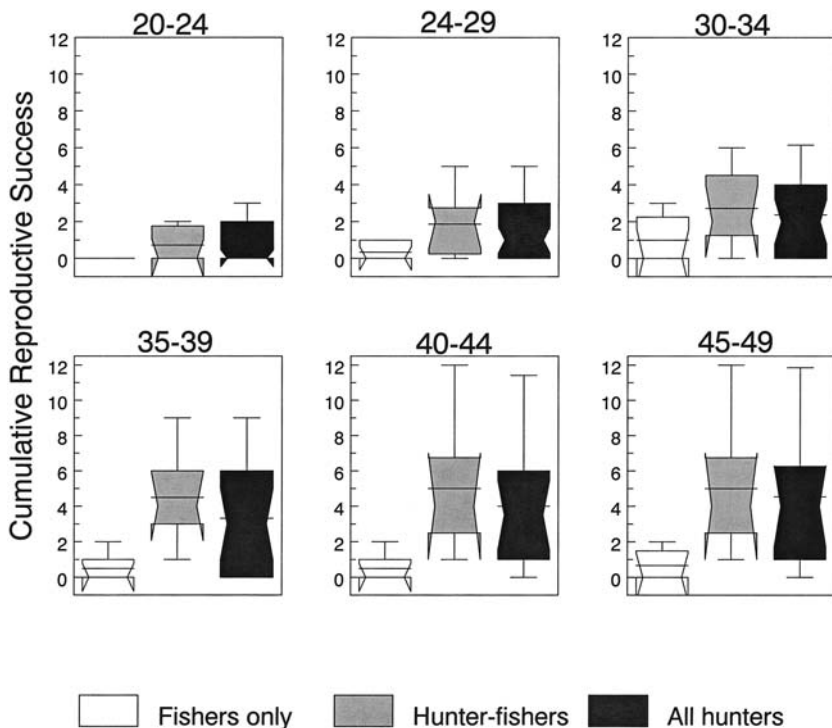


Figure 4
Cumulative age-specific RS of turtle-hunting versus nonhunting fishermen. Sample sizes for nonhunting fishermen range from 6 (youngest age class) to 3 (oldest), whereas those for hunter-fishermen range from 7 to 5; see Figure 1 for sample sizes of “all hunters” category. The lower and upper box boundaries indicate 25th and 75th percentiles, the whiskers the 5th and 95th percentiles, the notch notes the median and its confidence interval, and the horizontal line bisecting each box is the mean.

pursue turtle hunting successfully and also more likely to attract mates and produce healthy offspring. We do not have data to test this possibility directly; the conventional means of doing so is to conduct experiments, something that would be ethically problematic in the present case. However, we would argue that such phenotypic correlation is not such a clear alternative for costly signaling explanations as it is for other functional accounts. Indeed, one leading version of costly signaling is that the qualities being signaled are “good genes”—health, physical robustness, vigor, and so on. Turtle hunters may indeed be more phenotypically robust than average; if so, success in hunting would be an effective means of reliably signaling this to others. In sum, should such phenotypic correlation exist, it might strengthen rather than weaken the costly-signaling interpretation of Meriam hunting strategies. The key issue is whether the underlying quality (e.g., greater health and vigor) is observable by simple visual inspection or whether it is difficult to directly observe but can be reliably signaled by activities such as success in turtle hunting. Although our data are suggestive, we have not been able to establish that Meriam use hunting behavior per se to establish differences in male quality.

Another variant of the phenotypic correlation explanation posits some familial effect (e.g., men born into wealthy or high-status families tend to attain above-average RS and also have a better chance of becoming hunters). One way to indirectly test this is to compare hunters to their nonhunting brothers. Our genealogical and demographic information yields a set of 17 hunters with nonhunting brothers (or half-brothers in 3 cases) for such a comparison; where there were more than 2 men in a sibling set, we chose the pair closest in age. The RS comparisons are unequivocal. First, although mean age of the two groups of men is nearly identical (38.5 years for hunters, 38.9 for nonhunters), the observed RS of hunters (3.12 ± 2.85) is more than double that of their nonhunting brothers (1.18 ± 1.88), and this difference is highly significant (paired *t* test, $t = 2.9$, $p = .01$, 16 df). Second, the computed cumulative RS to age 50 is much greater for hunters (4.29) than that computed for their brothers (1.72), and it tracks the broader sample of hunters versus nonhunters very closely (Table 1). Finally, the number of mates is significantly greater for these 17 hunters than for their brothers (paired *t* test, $t = 2.8$, $p < .02$, 16 df). We conclude that the higher RS of Meriam hunters is not some effect of their familial environment, nor very likely any general aspect of their genetic inheritance, because it is completely absent in their nonhunting brothers. In addition, this data set allows us to refute the hypothesis that turtle hunting is determined by birth order, as elder brothers in the sib sets are equally divided between hunters ($n = 8$) and nonhunters ($n = 9$).

Recipient gratitude

A final alternative explanation considered here is that hunters are receiving benefits simply for providing meat to members of their community, rather than as a result of the costly signal they send in doing so. Although gifts of meat are certainly important to recipients, these do not appear to be the reason that hunters gain social benefits. This is because turtle collectors can also supply meat to public feasts or to neighboring households, and, in fact, turtle collection provides far more turtle for more consumers than does hunting (Bliege Bird and Bird, 1997). If status and resultant social benefits were simply a consequence of providing meat, frequent collectors who never hunt should achieve the same social status as hunters, but as noted above this is not the case. No men who only acquired turtles through collecting, and no men who supplied such turtles for public consumption at feasts,

Table 4
Demographic features of turtle collectors compared to turtle hunters

Category	<i>n</i>	Age (mean \pm SD)	Mean observed RS	Cumulative age-specific RS ^a
All men	114	34.8 \pm 11.6	1.7 \pm 2.4	2.7 (98)
All hunters	53	35.2 \pm 13.0	2.3 \pm 2.8	4.0 (50)
All collectors	54	34.7 \pm 12.0	2.0 \pm 2.5	3.1 (47)
All noncollectors	60	36.7 \pm 13.1	1.5 \pm 2.3	2.4 (51)
Hunter/collectors	37	33.4 \pm 12.1	1.9 \pm 2.4	3.4 (33)
Nonhunter/collectors	17	37.7 \pm 11.5	2.2 \pm 2.7	2.3 (14)

^a Reproductive success (RS) computed as the sum of the age-specific RS for each class, hence an estimate of lifetime RS if a man lived to at least age 50, experienced the observed age-specific rates over the ages 15–49, and no further reproduction occurred. Figures in parentheses are sample sizes, which may be smaller than those for other variables due to missing data on ages of some offspring.

were named as among the “best turtle hunters” or singled out for providing turtles.

A more direct test is to compare the RS of turtle collectors to noncollectors and to turtle hunters. We conducted this analysis in two steps, restricting the individuals compared in both steps to males 15 and older who had participated in turtle collecting in the 1994–1995 nesting season. (Of the 114 individuals of known age and sex who participated in turtle collection in the 1994–1995 nesting season, 72 [62.3%] were adult males, 20 [17.5%] were adult females, and the remainder were youths of both sexes.) First, we compared collectors and noncollectors, with age as a covariate, and found that the modest difference in cumulative RS (Table 4) was not quite statistically significant (one-way ANCOVA with age as covariate, $F = 2.9$, $p = .09$). However, of the 54 men in the collector sample for whom we have demographic information, 37 (68.5%) were also turtle hunters. Hence, in our second analysis we added turtle hunting as a covariate, which eliminated any association of turtle collecting with RS ($F = 0.2$, $p = .7$). In sum, reproductive and status benefits gained as a result of being a successful turtle hunter do not appear to be the result of gratitude for the meat these hunters provide.

Do receivers benefit?

Models of costly signaling generally assume that both signalers and receivers benefit from honest communication. It is not strictly necessary that receivers in fact benefit, as signaling could still be favored if it exploited existing sensory biases that had evolved in other contexts (Getty, 1998, Johnstone, 1998). However, such a situation would generally not be in evolutionary equilibrium, and it is reasonable to assume that receivers do benefit from signal discrimination unless there are specific reasons to believe otherwise.

There are a number of benefits Meriam might receive from information about hunting success, depending on their actual or potential relationship to signalers. One plausible form of receiver benefits might come from social alliances with successful hunters, particularly with hunt leaders who (we argue) have honestly signaled such qualities as leadership, organizational ability, and willingness and ability to invest in collective goods. Another form might involve competitors, who gain knowledge of hunters’ physical and social abilities that could prove useful in situations of social competition (including competition for mates). However, we have not been able to devise feasible tests of these forms of receiver benefits.

Table 5
Demographic features of various categories of Meriam women

Category	<i>n</i>	Age (mean ± SD)	Age at first reproduction	Observed RS	Cumulative age-specific RS ^a
All women	163	39.8 ± 17.0	23.4 ± 6.0 (76)	1.6 ± 2.2	2.3 (163)
Older women (b. < 1959)	82	54.2 ± 10.4	25.2 ± 6.5 (41)	2.1 ± 2.6	2.1 (82)
Younger women (b. ≥ 1959)	81	25.3 ± 7.3	21.2 ± 4.7 (35)	1.1 ± 1.5	2.7 ^b (81)
Hunters' mates ^c	29	41.8 ± 17.6	22.4 ± 4.7 (28)	3.9 ± 2.7	5.3 (29)
Other men's mates	56	44.2 ± 15.8	23.9 ± 6.7 (49)	2.5 ± 1.8	2.9 (56)
Leaders' mates	24	43.1 ± 17.0	22.9 ± 4.7 (23)	3.9 ± 2.8	5.1 (24)
Hunters' partners ^d	26	36.3 ± 10.5	21.7 ± 4.6 (20)	2.7 ± 2.5	3.7 (26)
Other men's partners	44	44.2 ± 10.5	24.5 ± 6.9 (23)	1.9 ± 2.3	2.1 (44)
Leaders' partners	19	38.4 ± 9.8	22.7 ± 4.6 (16)	3.1 ± 2.6	3.9 (19)

^a Reproductive success (RS) computed as the sum of the age-specific RS for each class, hence an estimate of lifetime RS if a man lived to at least age 50, experienced the observed age-specific rates over the ages 15–49, and no further reproduction occurred. Figures in parentheses are sample sizes, which may be smaller than those for other variables due to missing data on ages of some offspring.

^b Up to age 40 only; comparable computation for “older women” = 2.0.

^c For each category, “mate” is defined as having the majority of each woman's offspring fathered by a male in the indicated category.

^d For each category, “partner” is defined as 1998 co-residence in a sexual partnership (whether married or not) with a male of the indicated category.

A third form concerns benefits that women might get by mating with successful hunters. Meriam women currently have considerable freedom in making such choices, though in the past their parents and other close kin exercised considerable influence (at least concerning first marriages). Women might prefer better hunters as mates because they are better providers, a “direct benefits” or “good parent” explanation of female preference for signalers (Iwasa and Pomiankowski, 1999; Johnstone, 1995). Alternatively (or in addition), women might prefer better hunters as mates because they are of higher phenotypic quality, or because this higher quality has allowed them to gain status and some degree of social dominance among their male contemporaries (a point we return to in the Discussion).

Do Meriam women who choose to mate with hunters in fact obtain reproductive benefits? We have attempted to evaluate this question by comparing the RS of hunters' mates with that of other Meriam women, controlling for age. The analysis of age-specific RS for women who have produced offspring of known paternity reveals that turtle hunters' mates have higher cumulative RS in each 5-year age class from age 20 through 49. This results in an estimated lifetime RS that is 81% greater than that of other Meriam women who have at least one child (i.e., other men's mates), or an average of nearly 2.4 more surviving offspring (Table 5). A parallel analysis of the co-resident partners of hunters and nonhunters shows a similar pattern, with female estimated lifetime RS being 73% higher for hunters' partners as compared to women in co-resident relationships with other men (Table 5).

Although these analyses control for age effects on fertility by using age-specific rates, the resulting figures are estimates that assume that the age-specific rates observed for each age class will apply to younger women when they eventually enter that age class; furthermore, the sample sizes in the older age classes are quite small. Hence, as we did for males, we examined the female RS data using an analysis of the covariance between observed RS and membership in a given category (hunter's mate, etc.), controlling for the age of the women. This revealed a strong and statistically significant association with RS for mates of turtle hunters as compared to mates of other men ($F = 9.9$, $p < .01$, $n = 29$ and 55 respectively), and a weaker and nonsignificant association for leaders' mates as compared to other hunters ($F = 2.0$, $p < .2$, $n = 22$ and 8).

Comparing women's age at first reproduction, we find that the mean age is 2.1 years earlier for hunters' mates than that

of nonhunters' mates, with a similar pattern for co-resident partners (Table 5). By the end of their reproductive careers, more than 80% of hunters' partners have had at least one child, whereas less than 60% of nonhunters' partners have done so (Figure 5). A Kaplan-Meier hazards analysis of waiting time to birth of first child shows that it is significantly shorter for hunters' mates ($n = 30$) than for other Meriam women ($n = 132$; $p < .001$, Mantel-Cox log-rank test; $p < .001$, Breslow-Gehan-Wilcoxon test). Interpreting these associations as benefits obtained by mating with hunters is not necessarily warranted, however, because they could result from preexisting quality differences (see Discussion).

In terms of proximate causes, the higher RS of hunters' mates and co-resident partners as compared to other Meriam women could result from higher age-specific fertility, higher offspring survivorship, or some combination of the two. Yet the observed RS differences are so large and current, and recent child mortality rates so low (Arthur and Taylor, 1995) that we can confidently ascribe most of the effect to fertility differentials. Given the relatively high incidence of secondary sterility due to disease (particularly pelvic inflammatory disease) reported by medical personnel on Mer (Rickert K, personal communication), we hypothesized that some of the differential fertility is due to lower incidence of sexually transmitted diseases (STDs) among hunters' mates, perhaps because hunters are more effective at mate guarding and/or their mates are less likely to seek extrapair copulations, either of which would reduce exposure to STDs. The age pattern of surviving offspring does not support this hypothesis, however. First, hunter's mates and other men's mates have identical ages at most recent reproduction (29.3 ± 6.4 and ± 7.1 years, $n = 29$ and 56, respectively), and this pattern holds even if we look only at women more than 44 years old (hunters' mates = 34.3 ± 4.4 years, $n = 11$; other men's mates = 32.9 ± 6.2 years, $n = 25$). Second, the RS differentials between hunters' partners and other men's partners occur only in the 20–24 and 25–29 year age classes, and not in ages 30 and above as would be expected if secondary sterility due to STDs was the primary cause.

DISCUSSION

The analyses reported above test hypotheses derived from a key prediction of costly signaling theory—namely, that both signalers and receivers gain social and reproductive benefits

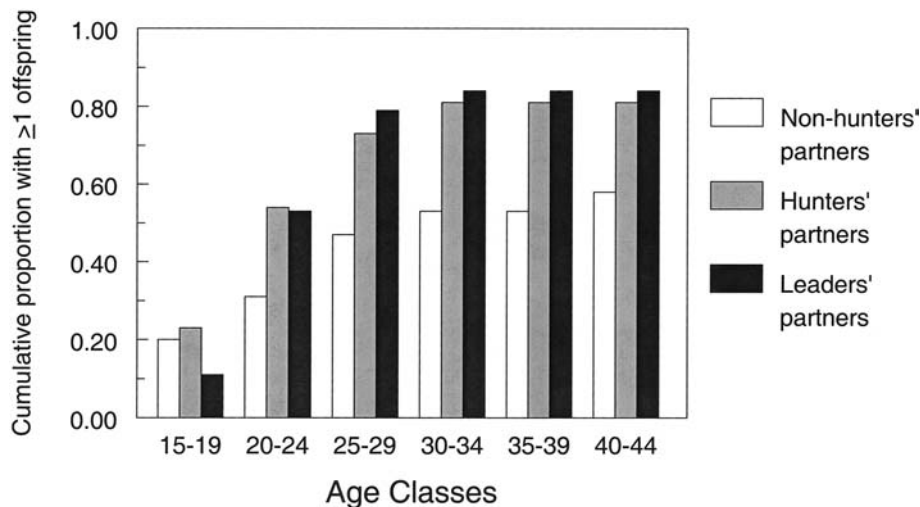


Figure 5
Cumulative proportion of Meriam women having at least one offspring, by co-resident partner's role and age class; see Table 5 for sample sizes.

from signaling interactions. Specifically, we analyzed hunting behavior among the Meriam people of Torres Strait, Australia, to see if it meets the design criteria of costly signaling. The main results are summarized in Table 6. These results indicate that successful hunters gain social recognition, have an earlier onset of reproduction, achieve higher age-specific reproductive success, and gain higher quality mates, who also achieve above-average reproductive success. Meriam hunters also average more mates (women who bear their offspring) and co-resident sexual partners than other men, and these partners (but not mates) are significantly younger than those of other men. We also examined alternative hypotheses involving reciprocity (recipient gratitude for meat supplied by hunters) and direct provisioning of offspring and mates by hunters to see if factors outside of the costly signaling framework could account for our observations and concluded that these hypotheses were not supported.

Because a hunt leader is an organizer and decision maker, his abilities peak as he gains skill and experience. Those observed to be hunt leaders (or named by Meriam as the best hunters) are significantly older than other hunt participants, such as jumpers (Table 1). Most feast-goers, when quizzed, know the identities of the hunt leader for turtles acquired at a given feast, although not the identities of the jumpers. Given the two distinct skill-based roles played by hunt participants (jumper and leader), we propose (but cannot currently test) that at least four distinct dimensions of underlying quality are signaled through turtle hunting: physical quality (such as strength, stamina, perception, and risk taking); cognitive skills (involving the ecological and ethological knowledge needed to successfully locate and capture non-nesting turtles); leadership skills (charisma and organizational abilities); and ability and motivation to bear the relatively high material cost (in time, energy, and money) of providing collective goods without direct compensation. We believe that the first dimension applies specifically to jumpers, whereas the other three apply primarily to hunt leaders.

Some of our analyses indicate that hunt leaders gain greater social and reproductive benefits than do jumpers, though these differentials are not always statistically significant. The statistical analysis is complicated by the fact that subdividing a sample of about 50 individuals into two groups (leaders and jumpers) reduces statistical power and that all leaders began as jumpers and in some cases may only have become leaders shortly before our data were collected. Nevertheless, hunt leaders do exhibit higher cumulative RS (Table 1) and a higher mean number of mates (Table 2), as well as a shorter

waiting time until their first offspring (Figure 2). The fact that leaders do not exhibit higher RS than other hunters until after age 24 (Figure 1) is consistent with the fact that men rarely assume this role before their late 20s (Table 1), and hence under the signaling framework we do not predict demographic effects of hunt leader status before this age.

Based on evidence discussed above, we suspect that the higher RS of hunters results from attracting both more and higher quality mates, which in turn is due to female choice for

Table 6
Summary of the main findings of this study

Category	Prediction	Supported?	Analysis
Turtle hunters	Success as hunt leader is socially recognized	Yes	Interviews, observational data
	Higher age-specific reproductive success (ASRS)	Yes	Cross-sectional computation of ASRS; ANCOVA with age covariate
	Earlier onset of reproduction (age at first birth)	Yes	Kaplan-Meier hazards analysis
	Lower proportion childless at age 30 and older	Yes	Chi-square contingency test
	Higher average number of mates	Yes	<i>t</i> test; ANCOVA with age covariate
	Mates are relatively younger	No	Paired <i>t</i> test (age-matched)
	Co-resident partners are relatively younger	Yes	Paired <i>t</i> test (age-matched)
	Mates are harder-working	Yes	<i>t</i> test
	More co-resident caretakers for offspring	No	Linear regression
	Hunters' mates	Higher age-specific reproductive success	Yes
Earlier onset of reproduction (age at first birth)		Yes	Kaplan-Meier hazards analysis

indirect benefits associated with high-status males, rather than the result of direct provisioning benefits. In general, Meriam men are not currently major providers of food supplies to their wives or children. As noted above, turtle hunting offers only moderate to very low rates of take-home food income, whereas lower-skill foraging activities such as sardine netting (primarily a female activity) or collecting nesting turtles (carried out by men, women, and children) offer much higher returns (Bliege Bird et al., 2001).

Do Meriam women have a mating preference for hunters per se? Interestingly, in our interviews Meriam women did not mention turtle hunting ability as a criterion they look for in a good marriage partner, but did nominate such criteria as fishing ability, as well as more general correlates of a paternal provisioning strategy, such as being hard working, the ability and willingness to do women's work as well as men's work, and contributing to food purchases for the household (Smith and Bliege Bird, 2000). Yet some respondents (primarily older men) expressed the opinion that in the recent past hunting was one means by which Meriam men gained higher quality mates. Although this divergence may reflect a recent decline in women's interest in men's hunting skill, it is also consistent with our view that men gain access to high-quality mates by status competition with other men, rather than by using hunting to signal directly to potential mates. Alternatively, it could be that Meriam women have subconscious mate preferences for turtle hunters that were not elicited by our interviews.

Although hunters do have significantly more mates (women with whom they have produced offspring), so do those classified in our interviews as "popular with the ladies." Yet the latter ($n = 21$) do not experience higher RS than other men (ANCOVA with age as covariate, $F = 0.01$, $p = .9$, $n = 113$). This suggests that the higher RS realized by hunters is not simply a matter of attracting more mates, but of attracting higher quality mates, and/or of providing reproductive benefits to their mates (see above). It could also indicate that hunters are better than average in guarding their mates from other males, or in inhibiting their mates' interest in other males. Unfortunately, we have not been able to devise an ethically acceptable means of testing these latter hypotheses.

In sum, we doubt that the direct-provisioning explanation for female mate preference applies in the Meriam case, and we believe that the primary reasons better hunters fare well in mate choice is that they gain higher status and social dominance, which in turn are cues used by women in mate choice. Testing these and alternative hypotheses would require additional data on individual variation in household food income, as well as direct measures of status or dominance, data which are currently unavailable.

In many systems, including the Meriam one, benefits to signalers can be more directly assessed than those that might accrue to receivers. Although we propose that receiver benefits might take the form of social alliances with successful hunters, or even deference granted to hunters in competitive situations, we have not been able to test these possibilities. Instead, we have focused on reproductive gains to hunters' mates (women whose children have been fathered by hunters) and partners (women currently co-resident with hunters) as our primary assay of receiver benefits. Our analyses show that hunters' mates and partners have much higher age-specific RS, as well as an earlier onset of reproduction (and hence longer reproductive careers, as age at last birth does not differ significantly).

In testing the hypothesis that hunters obtain mates of higher quality, our primary measure of mate quality is the rating of women as hard working in interviews with a broad sample of Meriam men and women. However, our data do

not allow us to control for the possibility that women's reproductive or labor output may be a conditional response to their mates' quality, a problem commonly encountered in behavioral ecology research on mate choice (Cunningham and Russell, 2000). Similarly, our analyses do not allow us to rule out the possibility that the higher RS of hunters' mates and partners are due to preexisting quality differences. To distinguish these possibilities nonexperimentally, we would need to analyze RS variation in women who had mated with both hunters and nonhunters at different times in their life; unfortunately, there are only two such "mixed-matings" among women in our entire sample. Although this problem prevents us from claiming to have shown that mating with hunters provides reproductive benefits or that hunters' mates are of higher (preexisting) quality, it is hard to explain the observed data without at least one of these being true, and both are consistent with a costly signaling explanation.

It is important to emphasize that we do not attempt to ascribe all the benefits of hunting to costly signaling. Thus, if Meriam turtle hunting provides a collective good in the form of meat distributed at public feasts (as we argue here and elsewhere), this benefit is not itself a signaling benefit. Costly signaling theory is relevant, however, in providing an explanation as to why signaling may take this form, because unconditionally providing turtle meat for a feast ensures a large audience for the hunter's signal (Bliege Bird et al., 2001; Smith and Bliege Bird, 2000). It may also be the case that receiver preferences for signals that provide not only information benefits but also material benefits (such as feast foods) may favor the evolution of signaling systems that provide such benefits (Gintis et al., 2001).

In summary, the analyses reported here, in conjunction with others reported elsewhere (Bliege Bird et al., 2001; Smith and Bliege Bird, 2000), provide rather broad support for the costly signaling analysis of hunting strategies among the Meriam. This suggests that this approach deserves further examination in other populations where hunting and sharing of game has characteristics that are difficult to explain using more conventional approaches such as conditional reciprocity or direct provisioning of offspring (Hawkes, 1993; Hawkes and Bliege Bird, 2002; Winterhalder, 1996). Costly signaling theory has the potential to account for many puzzling aspects of human foraging strategies: why men emphasize the pursuit of big game, why they often prefer high-variance hunt types, why they share many prey so widely and unconditionally, and why they sometimes make suboptimal energy maximization decisions compared to women. Signaling theory may be equally important in explaining human mating decisions, including why women seem to prefer to mate with successful hunters even in cases (such as the Meriam) where there do not appear to be provisioning or parental investment benefits.

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