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Hunting, Social Status and Biological Fitness

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Hunting, Social Status and Biological Fitness

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ABSTRACT: Hunting performance may be one of the most important routes to high prestige or social status among men in hunter-gatherer societies. Higher social status based on hunting performance has been linked to higher biological fitness outcomes almost everywhere this relationship has been investigated. This paper explores the proximate pathways underlying the positive correlation between hunting success and fitness, and discusses these in light of recent debates concerning the role of men in hunter-gatherer societies. Meat obtained from hunting directly provisions families and is also distributed to other group members, who may directly or indirectly pay back good hunters with meat, other food, services or favors. The display of hunting abilities may also increase men's fitness through extra-marital reproductive gains. We discuss prior results and provide a novel additional example using data collected among Tsimane horticultural-foragers of Bolivia. Despite the impression that most of the benefits that accrue to good hunters are in the form of extra-marital mating opportunities, we argue instead that most benefits may be gained within rather than outside marital unions.

INTRODUCTION

Hunting ability is a common route to high status among foragers cross-culturally (Wiessner, 1996). Good hunters have been shown to display higher reproductive success almost everywhere the relationship has been investigated (Smith, 2004). Women also show higher average total fertility in forager societies where men contribute more food to the diet (Marlowe, 2001) and women in several societies produce less food when their husbands produce more (Hurtado et al., 1992). On average, men contribute about 65% of the calories, and 85% of the protein, in forager diets (Kaplan et al., 2000; Marlowe, 2001; Cordain et al., 2000). It is largely accepted that successful hunters (1) contribute valuable protein and fats to the diet, (2) gain prestige and social status, and (3) tend to have higher reproductive success than poor hunters.

These observations alone, however, are not sufficient to distinguish between two alternative views of the maintenance of nuclear family formation among extant small-scale foragers. These two views concern whether hunting behavior is better viewed as a form of family provisioning or as "show-off" behavior designed primarily to gain personal (reproductive) benefits (Hawkes, 1991; Hawkes, 1990; Bird, 1999). These two views have generated substantial controversy in the social sciences, with important implications for our understanding of the origins and maintenance of nuclear families and the sexual division of labor.

The traditional perspective of the evolution of the nuclear family is based on a division of labor where men hunt wild

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animals and women gather plant foods (Lovejoy, 1981; Murdock and Provost, 1973). The pair bond between men and women is viewed as a cooperative venture geared towards the joint provisioning and care of highly dependent offspring, where women trade paternity certainty for long-term provisioning by men (Washburn and Lancaster, 1968; Isaac, 1978; Lancaster, 1978; Lovejoy, 1981; Lancaster and Lancaster, 1983). According to this view, "family organization may be attributed to the hunting way of life" (Washburn and Lancaster, 1968: 295).

While the ubiquity of men's hunting among foraging peoples is not contested, the benefits men receive, and presumably the motivations for engaging in hunting activities have been the subject of a lively debate. The "show-off" hypothesis of Hawkes (Hawkes, 1991; Hawkes, 1990; Hawkes, 1993) initially proposed that men hunt because of the social attention and mating benefits that come from providing game resources that are widely shared. This hypothesis was reformulated using costly signaling theory (Zahavi and Zahavi, 1997; Bliege Bird et al., 2001) to suggest that men's subsistence behavior is designed to provide an honest signal of underlying genotypic or phenotypic quality by targeting large game that are difficult to acquire. This signaling is particularly effective because the transfer of shares of large prey is believed to be outside the control of the hunter and all consumers pay careful attention to men's hunting results in order to obtain shares for themselves (see Bird, 1999; Hawkes and Bliege Bird, 2002). Here hunting is seen as a form of mating effort or status competition, rather than familial provisioning, so pair bonds and marriage have been reinterpreted as publicly recognized property rights designed to reduce mating competition among men, rather than as cooperative unions designed to reap gains from the joint production of offspring (Blurton Jones et al., 1999; Hawkes, 2004).

The ethnographic observation that hunting is a common route to prestige is consistent with either of these views. That good hunters have high reproductive success is an evocative observation, but alone cannot be used to distinguish between these alternative depictions of why men hunt. Critical to this debate is the extent to which the status that is achieved from being known as a good hunter or from widely sharing meat mainly benefits men or if wives and children also benefit substantially from men's investment in hunting and sharing. As described in a recent review by Smith (2004), the positive relationship between hunting success and reproductive success can be explained in five ways. If good hunters preferentially provision their wives and children, if they engage in reciprocal exchanges of meat for sex, services or alliances, and if they receive goods and services from others in order to encourage their continued hunting, then hunting success and fitness will be correlated. Additionally, hunting prowess may serve as a costly signal of underlying phenotypic quality to others who will thereby wish to confer sexual or social benefits on the hunter and/or his family members. Good hunters may also possess certain traits, such as intelligence and physical vigor, that are independently associated with both hunting ability and biological fitness. There is an additional complication not considered in Smith's review in interpreting the correlation between hunting performance and fitness because once men start having families, there may be increased motivation to produce more food and to do so more efficiently by hunting more intensively.

This paper is organized as follows. First, we briefly review existing studies that have investigated the relationship between hunting ability and reproductive success. Second, we elaborate upon Smith's dissection of the hunting and fitness relationship by describing the multiple pathways by which hunting production is likely to impact fitness, separating by levels of motivation, material advantages and fitness benefits. In particular, we focus on the importance of food sharing and displays of generosity as common means of reputation building among foragers. To date, relatively few of the key intermediary paths have been investigated thereby complicating the drawing of strong inferences concerning men's activity profile and the sexual division of labor. Third, we add to existing data by exploring the relationship between hunting ability, sharing behavior and reproductive success among the Tsimane of Bolivia, a group of forager-horticulturalists who frequently engage in hunting activities. Finally, we discuss implications of the results for understanding men's work motivations and the sexual division of labor.

ETHNOGRAPHIC OBSERVATIONS

Most traditional ethnographies of hunter-gatherers note that an important pathway to high status among men is through demonstration of hunting prowess. For example, among the Western Apache, "although some were more adept than others, all Apache men participated actively in hunting. The good hunter was highly respected." (Buskirk, 1986:160). Among Mbuti Pygmies, "male status depends primarily on skill in the hunt" (Turnbull, 1965:247). In a review of ethnographic information on hunting and social status, Wiessner (1996) shows evidence that good hunters achieve high status in at least 60% of 25 societies. The true percentage is probably higher considering at least two of the ten societies, where Wiessner claims good hunters do not gain high status, show the reverse (Hill and Hurtado, 1996; Marlowe, 2003). Smith (2004) also reviews additional studies that highlight the positive relationship between hunting and social status in forager populations. Among horticultural populations that also engage in foraging, hunting ability is also viewed as one of the most important sources of status. For example, among the Cubeo of Brazil, "hunting, in summary, is a distinctive pursuit and marks one for prominence" (Goldman, 1979). The Kuna of Panama maintain records of individual tapir kills and accord status to those men having made the most kills (Venctocilla et al., 1995).

Hunting is not the only route to high status among forager men. Other skills-intensive or privileged positions such as shaman, warrior, storytellers, medicine man, as well as chief, are also highly valued and honored with prestige. In some ecological contexts these other prestigious positions might associate more strongly with reproductive success than does hunting ability. Nonetheless, while other positions may provide alternative routes to achieve high status and reproductive benefits, it is possible that good hunters are more likely to garner these honored positions later in life when their hunting performance declines (e.g. !Kung trance healers, Wiessner, 2002). When leadership roles or prestige are based only on age or elder status, whereby key older individuals have more influence over others' decisions, the positive relationship between hunting performance and reproductive success suggests that these elders were likely good hunters in their prime. This is likely to be true if leaders are men

whose influence stems in part from having larger families and social allies.

Despite the ethnographic impression that hunting leads to status and that status leads to higher reproductive success, published quantitative studies exploring these relationships have been done in only six societies: Ache of Paraguay (Hill and Hurtado, 1996; Kaplan and Hill, 1985), Lamalera of Indonesia (Alvard and Gillespie, 2004), Hadza of Tanzania (Marlowe, 1999; Hawkes et al., 2001), !Kung of Botswana and Namibia (Wiessner, 2002), Meriam of the Torres Strait (Smith et al., 2003) and Piro of Peru (Anderson and Kaplan, 2002). In these studies, reproductive fitness is typically operationalized in several simple ways. These include the total number of live births, total number of offspring surviving to age 5 or 15, age of wife relative to the age of the hunter, age at marriage or first childbirth, and number of (extra-marital) mates. Age is usually controlled for in these analyses because it independently associates with hunting ability and most fertility outcomes. To make longitudinal inferences using cross-sectional data, it is assumed that differences in hunting performance observed during the period of ethnographic study are constant over individual lifetimes (Minnegal and Dwyer, 1986).

Overall, existing quantitative studies show that better hunters usually have a greater number of total births and of surviving children (summarized in Table 1). Two studies do not distinguish between good and poor hunters based on the rate at which meat is obtained per unit time spent hunting (i.e. caloric return rate), but between those who actively hunt and those who do not. Among Lamalera whalers, the fertility differences between active and infrequent hunters are minor, but harpooners, who have important specialized skills, do show a two-fold fertility advantage and also marry and reproduce earlier than other hunters and non-hunters. Among Meriam, the distinction made was between those who do and do not hunt large marine turtles. Turtle hunters show almost twice the number of surviving children, have their

TABLE 1
SUMMARY OF QUANTITATIVE RESULTS RELATING HUNTING PERFORMANCE TO MEASURES OF BIOLOGICAL FITNESS (MODIFIED FROM SMITH 2004: TABLE 1)

POPULATION	HIGHER FERTILITY?	MORE SURVIVING OFFSPRING?	YOUNGER AGE AT FIRST CHILDBIRTH	MORE TOTAL MATES	YOUNGER MATES?
Hadza	Yes	?	?	No	Yes
!Kung	Yes	Yes	?	No	?
Lamalera	Yes	Yes	Yes	?	No
Meriam	Yes	Yes	Yes	Yes	Yes
Ache (forest)	Yes	Yes	?	Yes	?
Piro	Yes	Yes	No	?	?
Kubo	?	No	?	No[e]	?
Ache (settled)	Yes	No	No	?	?
Tsimane (1)[a]	Yes[f]	Yes[f]	Yes[f]	Yes[c]	No
Tsimane (2)[b]	Yes	Yes	No	No[d]	No

[a]Tsimane (1) sample is based in two remote villages using actual hunting production data.
[b]Tsimane (2) sample is based in one acculturated village using others' ratings of focal men's hunting ability.
[c]Mates here refers to number of wives.
[d]Mates here refers to number of extra-marital liasons in the acculturated village (where there are no polygynous marriages).
[e]Mates here refers to number of wives and no man had two wives simultaneously.
[f]Hunting performance was here defined as total kilograms of meat produced over the sample period.

children early and have more mates. As can be seen from Table 1, good hunters do not consistently marry early, have more mates nor do they consistently have younger wives, although not all of these measures have been systematically investigated in several of the populations included.

There are several test cases among acculturated foragers that show inconsistent results and are worth mentioning even though these studies may be based on small numbers of participants. Kent (1996) argues that among the Kutse of the Kalahari, better hunters spend less time hunting than do poor hunters in order to promote equity in the group, and shows that better hunters do not have a higher number of births or surviving offspring. However, her sample of hunters is very small (6 people) and her analysis did not control for hunter's age. In another study conducted with the Kubo of Papua New Guinea, Dwyer and Minnegal (1993) report that "show-off" hunters do not have a greater number of offspring than non-show-off hunters, where show-offs are defined as the four hunters who consistently obtained high quantities of meat per unit time spent hunting. Our own reanalysis using updated, unpublished Kubo data on 12 hunters kindly provided by Dwyer and Minnegal confirm that hunting performance (whether measured as return rate, total kilograms of meat produced, percentage of days that meat was produced) does not significantly correlate with the total number of surviving children, nor with fertility rate, even after controlling for age of hunter. One possibility suggested by Dwyer and Minnegal (1993) is that hunters specialize on different game animals in order to diversify the collective group foraging portfolio, and reproductive benefits therefore are not associated with hunting performance as measured by the mean caloric return rate[1].

PATHWAYS UNDERLYING THE RELATIONSHIP BETWEEN HUNTING PERFORMANCE AND FITNESS

There are multiple ways in which being a good hunter can increase the hunter's reproductive success. These are illustrated in Figure 1 and described here. We separate proximate level motivations from ultimate level benefits that determine fitness. The economics underlying time budgets allocated to hunting must take into account the sum of the proposed pathways. As discussed below, and summarized in Smith (2004), various evolutionary mechanisms may link proximate level motivations with benefits that are potentially fitness-enhancing. These include in-kind and trade-based reciprocal altruism, indirect reciprocity and costly signaling.

First, provisioning of spouse and offspring is achieved through the production of meat that provides protein, lipids and important micro-nutrients that are difficult to obtain from gathered fruits and vegetables (Cordain et al., 2001). Macronutrient diversity and rich calories have straightforward impacts on offspring growth, immune function, health and survivorship (Larsen, 2003; Carpenter, 1994), as well as supporting female fecundity. Given the gathering activities of women and the benefits to eating a nutritionally diverse diet, men's hunting is unlikely to be a poor subsistence strategy (cf. Hawkes 1993; Bird 1999). The "variance" problem associated with risky hunting strategies can be solved by daily sharing, which makes hunting a reliable source of abundant calories. Even in foraging societies where the majority of the

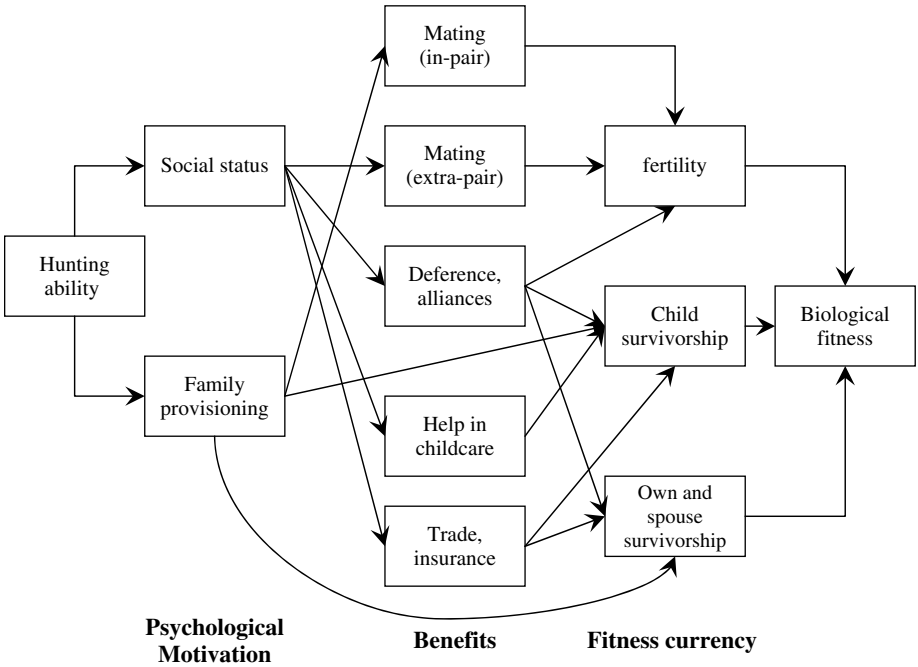

FIG. 1.—Causal paths mediating relationship between hunting success, social status and biological fitness. The pursuit of social status from hunting can provides many benefits in addition to in-pair and extra-pair mating access, including deference, coalitionary support, aid in childcare and social insurance. Overall impacts of hunting ability on fitness are mediated by increases in fertility and survivorship of self, spouse and children. Unmeasured genotypic quality ("phenotypic correlation") could also independently associate with hunting performance and fitness outcomes.

diet is not meat, such as among the !Kung, meat is highly valued and still considered "the only real food" (Tanaka, 1976:108). Cross-culturally, meat is shared more widely than are other foods among foragers. While it has been documented that large game is shared extensively and under certain conditions family members are no more likely to eat from kills than are other band members (Kaplan and Hill 1985), meat sharing is usually biased towards family members and other members of their hunting parties (Gurven, 2004c).

While provisioning is typically viewed as male parental investment, provisioning behavior may also represent mating effort designed to maintain sexual access to a current mate (Anderson et al., 1999b; Marlowe, 1999). An extreme form of this view argues that all male parental care is really mating effort (van Schaik and Paul, 1996). According to this hypothesis, step-children should receive similar investments as biological offspring, while divorce or spousal death should lead to a termination of offspring provisioning. These hypotheses have not been widely tested. However, Marlowe (1999) shows that among Hadza foragers of Tanzania biological children received more food, meat and direct care such as playing, holding and communication, than did step-children. In a related analysis, Tsimane fathers did not provide care only when

mothers were present and could therefore observe their behavior, as would be predicted if paternal care were mating effort, but rather provided complementary forms of care, especially when mothers were absent from the household (Winking et al., in press). Several tests have also been conducted among non-foragers. Amongst Xhosa and Albuquerque men, men's parental care behavior is consistent with a mix of motives compatible with mating effort and parental investment (Anderson et al., 1999a; Anderson et al., 1999b).

Figure 1 also outlines the paths by which prestige and social status due to hunting ability are expected to produce benefits that are typically attributed only to direct provisioning. The mating effort or status signaling model posits that extra-pair mating benefits accrue due to women choosing to mate with skilled hunters for their "good genes". Hunting is difficult and requires substantial skill, strength, endurance and knowledge (Gurven et al., 2006; Walker et al., 2002; Ohtsuka, 1989). Hunting performance is therefore difficult to fake and can be a costly signal of underlying genetic quality (Smith and Bliege Bird, 2000). According to this view, women will choose good hunters because of presumed genetic quality, rather than for their work effort, actual production or for their willingness to provide resources. Due to the wide distribution of game outside the family, it is expected that good hunters should therefore receive fitness benefits outside marital unions in the form of extra mates.

Our proposal here is that status enhancement need not only improve the hunter's extra-pair mating success, but can have short-term and long-term impacts that ultimately affect in-pair reproduction via improvements in child survivorship, reduced interbirth intervals and marriage with younger, or more fecund partners. High social status from hunting may also yield non-reproductive benefits, either through direct or indirect reciprocity (Smith, 2004; Alexander, 1987) or via the costly signaling of cooperative intent (Gurven et al., 2000; Frank, 1988; Smith and Bliege Bird, 2005). These three models focus on benefits that come with the strategic sharing of meat, where meat is a valuable and limited currency. In direct reciprocity, meat may be exchanged for meat, other foods, favors and services by other group members, where benefits are usually conferred some time after the initial transfer of meat. Meat should only be given by hunters to specific others who share with them. There is some evidence that reciprocity of this type does occur among foragers (Hames, 2000; Ziker and Schnegg, 2005; Gurven, 2004b), although exchange does not seem to be governed by a rigid tit-for-tat rule (Gurven, 2006). For example, high levels of sharing could act as a form of health insurance and social security provided by social partners (Sugiyama and Chacon, 2000; Gurven et al., 2000). Meat may also be exchanged with important allies who are expected to back up donors with coalitional support in the event of a conflict, as among the Achuar (Patton, 2005). Meat and other food may also be exchanged for alloparenting services by recipients, as has been described among the !Kung (Wiessner 2002). Lastly, fathers who are good hunters may also be more likely to transmit their skills to offspring, either genetically or through learning and apprenticeship.

Costly signaling of intent may be designed to give honest information to specific others concerning one's trustworthiness and willingness to engage in collective action, both of which are useful qualities of social partners and allies (Gurven et al., 2000; Smith and Bliege

Bird, 2005; Frank, 1988). This type of signaling supports dyadic reciprocity by helping to insure that one chooses partners who are unlikely to defect in exchange relationships, especially during circumstances when opportunities for defection are available. Sharing of this type may be viewed as investment in one's reputation for the purpose of reaping positive gains from social interactions with dependable individuals (Alexander, 1987). Of course it may be desirable to have a good reputation in the eyes of many individuals. With indirect reciprocity, others that do not receive but perhaps observe meat distributions and impressed by the hunter's reputation for generosity may instead confer benefits on the hunter as an incentive to hunt and share. These models may explain some key observations among foraging populations. For example, children of good Ache hunters have higher survivorship than those of poor hunters, and children of good hunters receive more attention and food from others in camp (Hill and Hurtado, 1996). Wives of good hunters whose catch is generously shared may receive help and attention from other women and assistance in childcare. During times of sickness, disease and injury, where production is difficult or impossible for periods of time, aid was more likely to be given to Ache if they had previously shared a large proportion of their food, and more so if they were high producers (Gurven et al., 2000). This type of aid may result from prior commitments made by specific social partners within the context of dyadic reciprocity and costly signaling. However, those who aid sick or injured individuals may also be signaling good intentions, either to the injured party or to a larger audience.

Having outlined the varied means by which hunting could yield fitness-relevant benefits, we now explore the ways that men's subsistence behavior is linked to both social status and reproductive success using preliminary data collected among the Tsimane of Bolivia.

TSIMANE HUNTING, SOCIAL STATUS AND FITNESS OUTCOMES

Background and Methods

The Tsimane are a forager-horticulturalist population living in lowland Bolivia. Most food the Tsimane consume derives from horticulture, fishing, hunting, and gathering activities. They cultivate plantains, rice, corn, and sweet manioc in small swiddens, and regularly fish and hunt for meat. Hunting is more common in the remote villages located some distance from major rivers. Tsimane regularly hunt using shotguns, less commonly with bow and arrow and often with the tracking assistance of dogs. Hunting is viewed as one of the most important activities for men, and is accorded high status, even in acculturated villages. Women frequently comment that prospective husbands must know how to hunt. Meat from collared peccaries, paca and brocket deer are especially valued. Boys will apprentice with older men while in their teens, and begin hunting by themselves by the late teens or early twenties. The use of efficient contraception is rare and fertility among the Tsimane is rather high, with a total fertility rate (TFR) of about nine births over a woman's lifetime. More information on Tsimane hunting practices and the development of hunting skills over the life course is described in Gurven et al. (2006). General ethnographic background is given in Chicchón (1992), Reyes-García (2001), Godoy et al. (2004), and Gurven (2004a).

Two samples of Tsimane men are available to explore the relationship

between hunting performance and reproductive outcomes. One sample of 59 men from two remote communities (Aperecito and Cuverene) includes data from 420 foraging trips from 2002–2003 elicited by interviews, where recorded information concerning total time spent and number and weights of animal kills allow us to calculate hunting return rates and total meat production (Gurven et al., 2006). A second sample from an acculturated community (Tacuaral de Mato) in 2005 uses evaluations of 57 men's hunting ability[2], generosity in meat sharing, whether specific men are "hard workers", and several measures of prestige by other men in the village. These prestige measures include "influence", "respect" and "coalitional support". Definitions for these measures are given at the bottom of Table 2. A sample of 29 Tsimane males representing all ages, families and social standing was used as evaluators of their fellow villagers for this study. To measure hunting skill, generosity in meat sharing and whether the man is a hard worker, each of the 57 men's photographs was shown to eight of the raters who answered "yes or no" questions about the presence or absence of the trait for the man in the photo. A subject's score

TABLE 2

MULTIPLE REGRESSION ANALYSIS OF STATUS OUTCOMES (INFLUENCE, RESPECT AND EXTENT OF COALITIONAL SUPPORT) AND FITNESS OUTCOMES (TOTAL NUMBER OF LIVE BIRTHS AND CHILDREN SURVIVING TO AGE 15) AS A FUNCTION OF EVALUATION SCORES FOR 57 MEN'S HUNTING ABILITIES AND EXTENT OF MEAT SHARING

		UNSTANDARDIZED COEFFICIENTS		STD. COEFF.		
OUTCOME VARIABLE	PREDICTOR VARIABLE(S)	BETA	STD. ERROR	BETA	T	P-VALUE
(1) INFLUENCE	(Constant)	26.175	5.266		4.971	0.000
	Age	–0.091	0.097	–0.121	–0.943	0.350
	Hunting Ability	1.092	0.720	0.204	1.516	0.136
	Meat Sharing	1.901	0.842	0.297	2.258	0.028
(2) RESPECT	(Constant)	20.309	3.695		5.496	0.000
	Age	0.033	0.068	0.056	0.486	0.629
	Hunting Ability	1.478	0.505	0.354	2.925	0.005
	Meat Sharing	1.710	0.591	0.343	2.896	0.005
(3) COALITION	(Constant)	28.932	4.853		5.962	0.000
	Age	–0.095	0.089	–0.138	–1.064	0.292
	Hunting Ability	0.788	0.664	0.162	1.187	0.240
	Meat Sharing	1.641	0.776	0.283	2.115	0.039
(4) TOTAL LIVE BIRTHS	(Constant)	–7.944	1.725		–4.606	0.000
	Age	0.190	0.019	0.758	10.219	0.000
	Hunting Ability	0.982	0.274	0.550	3.585	0.001
	Meat Sharing	1.145	0.427	0.538	2.684	0.010
	Hunting*Meat Sharing	–0.153	0.070	–0.595	–2.199	0.032
(5) TOTAL SURVIVING OFFSPRING	(Constant)	–6.687	1.875		–3.567	0.001
	Age	0.142	0.020	0.655	7.019	0.000
	Hunting Ability	0.930	0.298	0.603	3.124	0.003
	Meat Sharing	1.193	0.464	0.648	2.573	0.013
	Hunting*Meat Sharing	–0.164	0.076	–0.734	–2.157	0.036

Predictor variable definitions: *Hunting ability*: "He really knows how to hunt, compared with other people his age"; *Meat sharing*: "He gifts meat a lot to other people (in other families)"; *Influence*: "When there is a dispute in the community, what this person says has more influence"; *Respect*: "He is well respected by others"; *Number of Allies*: "When he has a conflict with another person, he will have more people who will defend or help him in the conflict"; *Work ethic*: "He works all the time, he really works hard".

therefore ranges from 0 to 8 and indicates the number of raters who answered "yes" to the question.

For other characteristics, such as level of influence in the community, whether the individual is well respected, and whether the individual is likely to have more supporters or allies in the event of a conflict, a different rating procedure was employed. To assess these traits, each evaluator was shown an array of photographs of eight Tsimane men and asked to rank them from highest to lowest for each variable, with a score of 8 assigned to highest and 0 for lowest. The photographs were counterbalanced using a block design such that no two subjects appeared together for the same question more than once. Thus, each of the 57 men was ranked 8 times by 8 different evaluators, yielding a range in scores from 8 (lowest) to 64 (highest).

All demographic data come from extensive reproductive history interviews done by MG during 2002–2004 (see Gurven et al., 2007 for description of methods). Demographic data in Tacuaral were updated during the 2005 field season. Data on extramarital liaisons were recorded by CVR in consultation with several local informants. The demographic data allow calculation of total number of live births, total number of offspring surviving to age 15, age at marriage, age at first birth and wife's age.

RESULTS

In the first sample that uses quantitative data on hunting returns, there is no relationship between hunting caloric return rate and fertility, number of surviving children, nor age at first marriage and first birth, after controlling for age. However, total kilograms of meat acquired over the sample period does marginally predict total number of live births (partial r = 0.220, beta = 0.00693, p = 0.12) and number of surviving children (partial r = 0.238, beta = 0.00621, p = 0.09). Each standard deviation unit increase in hunting production is associated with an additional 0.6 births and 0.5 surviving children. Hunters in the top decile of production have 1.4 more births and 1.2 more surviving children than those in the bottom decile. In examining the relationship between hunting performance and age at marriage, we perform a survival analysis in order to include the right-censored cases of unmarried men. When dividing men based on hunting production above or below the median, we find a marginally significant difference between ages of marriage for good and poor hunters (mean difference = 0.5 years, log-likelihood test, chi-square = 3.19, df = 1, p = 0.074). When defining good and poor hunters according to the top and bottom deciles, good hunters are more likely to marry earlier than poor hunters (mean difference = 5.4 years, log-likelihood test, chi-square = 5.18, df = 1, p = 0.023).

We also find that more productive hunters are more likely to have more wives (partial r = 0.359 controlling for men's age, p = 0.009). Again, caloric return rate is not significant but total quantities produced or hours worked are highly significant. Relative to those with no wives (n = 15), those with one (n = 34) and two wives (n = 4) captured 2.9 and 3.6 times more kilograms of meat, respectively. They also hunted for 1.5 and 1.6 times more hours, respectively. As stated previously, higher dependency may be a motivation for, rather than a direct result of, men spending more time hunting and bringing in more meat. Finally, in this sample, more active hunters were no more likely to have younger wives than were less active hunters.

In the second Tsimane sample, hunting returns contribute on average only 22% of men's total daily food production. Men also hunt for an average of 7 hours per week. In the first, less acculturated sample, men hunt for about 11 hours per week and hunting returns contribute about 50% of men's total calories produced each day. Thus, it is reasonable to conjecture that the acculturated sample would show less of a relationship between hunting ability and measures of reproductive success. However, the opposite is true, which suggests that wild game may be more of a limited resource in the acculturated community. In the second Tsimane sample, there was a highly significant relationship between others' ratings of men's hunting ability and several measures of reproductive success. Controlling for men's age, men rated as good hunters show a higher number of total births (partial $r = 0.469$, $p < 0.001$) and of surviving births (partial $r = 0.379$, $p = 0.004$). Each standard deviation unit increase in assessments of hunting ability is associated with an increase of 1.1 total births and 0.9 total number of surviving children. The difference between hunters in the top and bottom deciles is 2.8 total births and 2.3 total surviving children[3].

Good hunters are no more likely to marry earlier, have their first child earlier, marry younger wives nor are they more likely to have had more mates outside of marriage. In this acculturated sample, polygynous marriage is rare. There is little information about potential births that may have resulted from extra-marital liaisons, and so the significant correlations described above between hunting ability and fertility are based mostly on within-pair marital unions. However we do find that men with greater in-pair fertility (both total fertility and total surviving offspring) also had a larger number of extra-pair mates (partial $r = 0.288$, $p = 0.031$, partial $r = 0.317$, $p = 0.017$, respectively). Better hunters are also more likely to have wives rated as more attractive by other men (standardized parameter estimate = 0.390, $p = 0.009$).

We find that even in this fairly acculturated community that good hunters are rated by other men as worthy of respect (partial $r = 0.457$, $p<0.001$), are considered influential members of the community (partial $r = 0.293$, $p = 0.029$), and likely to have more coalitional support during a conflict (partial $r = 0.248$, $p = 0.065$). Standardized parameter estimates from the multiple regressions show that one standard deviation unit increase in hunting ability is associated with a 0.463, 0.298 and 0.252 standard deviation unit increase in respect, influence and allies, respectively. Each of the status measures of respect, influence and likelihood of coalitional support is a highly significant predictor of in-pair fertility and number of extra-pair mates, and hunting ability is an important avenue towards achieving high status. However it is not the only one.

As illustrated in Figure 1, sharing meat may yield benefits that are conferred by other individuals as described by the reciprocity and costly signaling models. Men who are recognized by others for sharing meat are more likely to be respected (partial $r = 0.454$, standardized parameter estimate = 0.451, $p < 0.001$), have more influence (partial $r = 0.360$, s.p.e. = 0.359, $p = 0.006$) and have more allies (partial $r = 0.334$, s.p.e. = 0.332, $p = 0.012$). These effects are as strong or even stronger for meat sharing than for rankings of hunting ability. Generous sharers also show higher achieved fertility and are more likely to have wives rated as more

attractive by other men (partial r = 0.342, p = 0.016). After controlling for men's age, the difference in total and live offspring among men in the top and bottom deciles for meat sharing is 1.9 and 1.7 children, respectively. Rankings of meat sharing do not significantly predict the number of extra-pair mates (partial r = 0.245, p = 0.069), an observation that marginally contradicts the notion that the chief benefits from meat sharing are non-marital mating benefits.

It is reasonable to expect that good hunters can better afford to give more meat away than poor hunters. Higher producers have often been observed to share more frequently and to cast a wider net with their sharing practices (Gurven et al., 2001). Indeed, we find that good hunters are more likely to be named as distributors of meat to non-family members (r = 0.303, p = 0.022, Figure 2). Nonetheless, hunting ability and meat sharing are both roughly equally significant predictors of respect, when examined simultaneously in a multiple regression analysis (Table 2: Models 1–3). Meat sharing is a better predictor of influence and coalitional support through allies. There is no significant interaction effect between meat sharing and hunting ability in predicting any of the three status measures. However, while the constituent effects of meat sharing and hunting ability are significant positive predictors of fertility, the interaction effect of hunting ability and meat sharing on fertility is actually *negative* (Table 2: Models 4 and 5). According to the statistical model which explains 74% of the adjusted variance in male fertility, poor hunters who are recognized meat sharers fare almost as well as good hunters who share little! Thus, when examining meat sharing and hunting ability simultaneously, the model reveals that the largest discrepancy in fertility differences is among poor hunters, and similarly among those least recognized for sharing meat. The incremental effects on fertility of increased recognition for meat sharing diminish more rapidly for better hunters, and similarly the incremental effects on fertility of increased recognition for hunting diminish more rapidly for active meat sharers.

Men recognized as hard workers also show higher levels of respect (partial r = 0.296, p = 0.027). There is no relationship between being known as a hard worker and either influence or coalitional support. Hard workers do have a greater number of live births (partial r = 0.386, p = 0.003) and surviving children (partial r = 0.334, p = 0.012), as might be expected if the prime recipients of hard working men are family members. However, men recognized as hard workers are also very likely to be recognized as good hunters (r = 0.672, p < 0.001, Figure 2) and generous sharers of meat (r = 0.306, p = 0.021). In multiple regression analysis that controls for hunting ability and age, being known as a hard worker does not significantly predict any of the status measures, fertility or any of the other fitness measures.

DISCUSSION AND CONCLUSION

The view that hunting is largely motivated by mating benefits is incomplete. Previous treatments tend to conflate psychological motivations underlying men's time budgets and the fitness effects that are a result of men's subsistence choices. If men desire high status and if hunting is the primary route to obtain status because of the valuable currency of meat, then we need to focus attention on how higher status contributes to higher fitness among foraging and other populations. Cross-culturally social status, as it is locally

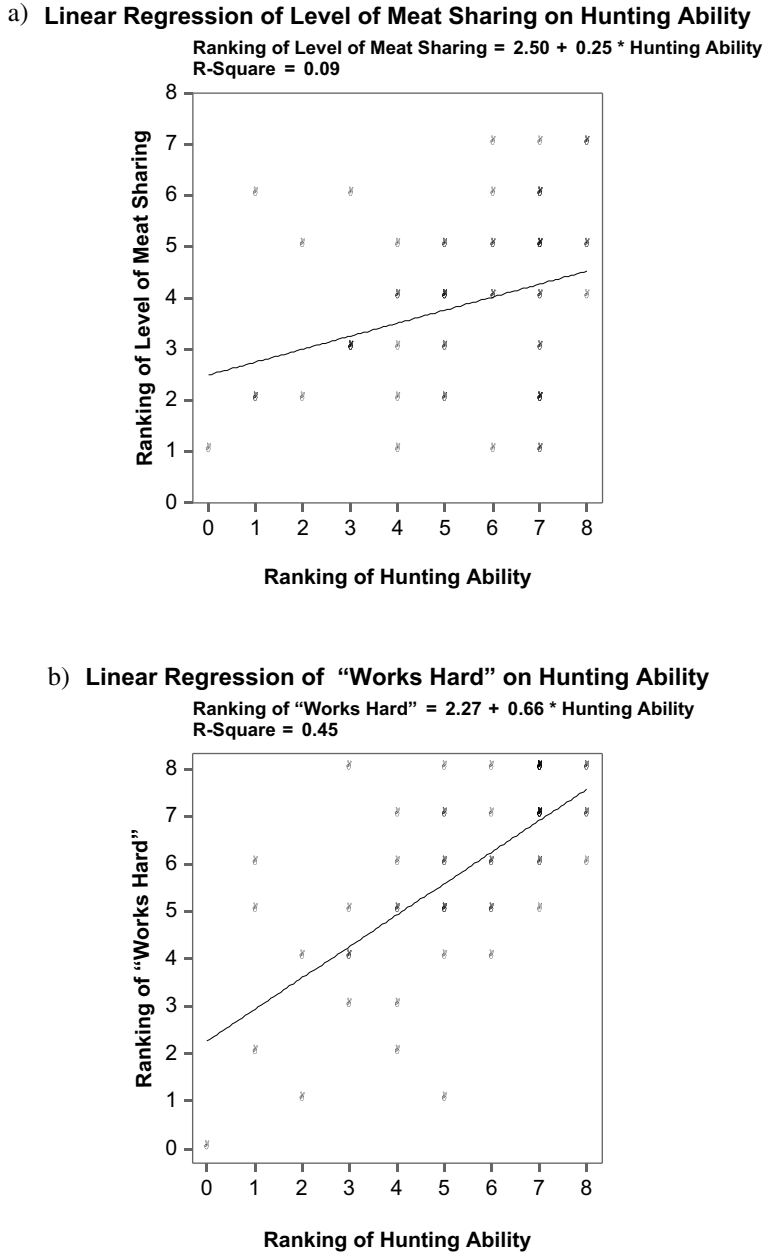

FIG. 2.—Relationship between rankings of 57 Tsimane men's hunting performance and their a) propensity to share meat and b) to be a hard worker.

895 defined, is positively associated with reproductive success in traditional, non-contracepting societies (Irons, 1979; Barkow, 1977; Flinn, 1986; Chagnon, 1988; Borgerhoff Mulder, 1987). Despite a number of correlations between hunting

ability (or other commodities that determine social status) and reproductive fitness measures, the relative contribution of the different pathways in Figure 1 has not been quantitatively estimated in any society. However, as we saw among the Tsimane, hunting performance is but one (albeit important) component of male status. Our results are consistent with the observations of the government official Edward Horace Man concerning the Andaman Islanders made in the late 19th century: "Social status [is] dependent not merely on the accident of relationship, but on skill in hunting, fishing, etc., and on a reputation for generosity and hospitality" (Man, 1932:42).

More importantly, we find that much of the reproductive benefits associated with hunting and social status are realized *within* and not outside marital unions. Good hunters are also more likely to share meat and be regarded as hard workers—qualities that are especially important to mates and existing and potential social partners. Although good hunters tend to also share meat generously we find that meat sharing is associated with an increase in in-pair fertility, but bears no strong relationship with extra-pair mating in the Tsimane sample. Cross-culturally, good hunters may marry early, marry younger or more attractive and fecund wives because their higher production ability and generosity gives them leverage in the mating market. Once they are married, good hunters and their families may benefit from the many pathways suggested by Figure 1.

Apart from the household benefits of hunting outlined in Figure 1, male food sharing in a public forum may have important signal value regarding the qualities of the producer male, thereby further increasing male status. The costly signaling of high phenotypic quality could then result in more favorable treatment by any or all members of the social group (Hawkes, 1990). For example, successful hunters might gain sexual access to more and higher quality females or obtain more and better male allies, and competitors might be more reluctant to confront them in a variety of arenas. Although some of these payoffs impact male fitness only through mating success, many of the imagined payoffs could also benefit offspring (e.g. father having more allies and fewer competitors). Indeed we believe that some examples of food sharing by women foragers might also best be understood as costly signaling, yet the payoffs to that sharing are not thought to be mating opportunities. Women as well as men compete for status (Hrdy, 1999; Campbell, 2002; Rucas et al., 2006; Hess and Hagen, 2006). In modern societies wealthy females also engage in public philanthropic activity. There is no reason to suspect that all male status displays are motivated by mating gains. In fact, as suggested by the review of existing studies, the aspect of "hunting performance" that sometimes may be correlated most strongly with fitness outcomes is not necessarily caloric return rate, targeting of large or difficult-to-acquire prey, or other honest indicators of skill and prowess, but rather the total amount of meat that is produced (and shared with others). Actual quantities produced and shared are a combined outcome of skill, work effort and sharing behavior, rather than just underlying genetic quality. Achieved hunting production, especially when meat is widely distributed, may be more amenable to evaluation by other group members than underlying skills. Hunting production may therefore be an important combined signal of skill and commitment to others.

The costly signaling of cooperative intent through generous donations of meat, other food and services may be an important

means of establishing a favorable reputation and thereby of being recognized as a valuable potential social partner or ally. The gains of cooperation from repeated interactions with valued partners is believed to make the costs of signaling worthwhile over the long term (Frank, 1988; Gintis et al., 2001). Presumably these repeated interactions will involve some level of dyadic and indirect reciprocity. These possibilities are only now beginning to be investigated. For example, do men receive other goods and services from those who obtain portions of their production? Do other individuals who eat from men's kills give them other kinds of food (e.g. honey, roots, fruits), make tools for them, bring them firewood, babysit their children, feed their children more often and care for their families more often when they are absent or ill? Do others defer to wishes of good hunters and their family members in regards to certain decisions, such as residential migration, foraging locations, etc. Among the Ache high-return hunters' children experience higher survival (Hill and Hurtado, 1996) despite the fact that they receive no larger portions of father's game than do other children in the foraging band. Ache children also experience higher mortality after paternal death or divorce of their parents. The mechanism of these survival effects is not known but one possibility is that the offspring of good hunters receive preferential treatment and intermittent feeding by others. Ache orphans tell detailed stories of the hunger they experienced after their father's death (ibid), and a recent study shows that Ache families who share more on reservation settlements are more likely to receive food from others when they are ill or injured (Gurven et al., 2000).

Hunting may be an ubiquitous enterprise for men cross-culturally precisely because of the multiple pathways by which it can impact fitness via both private and public household gains. The early historical focus on the impact of good hunters on child survivorship and the recent emphasis on the benefits from extra-marital mating are both only partial explanations for why men may hunt. The fitness that accrues to hunters is likely due to the summed direct and indirect pathways shown in Figure 1 and discussed above. We believe that current evidence suggests that the provisioning pathways alone probably favor hunting in many societies, but the commitment to hunting is reinforced further by the signaling payoffs that aid in extra-marital mating success and coalition building. Why else would women desire marriage, and with good hunters, if the products of male hunting were public goods that led only to increased mating opportunities for men? If the gains of hunting were purely personal, we should expect women to discourage their husbands from hunting. Instead we have observed just the opposite. Ache, Hiwi, Tsimane and Machiguenga women often vigorously encourage their husbands to hunt[4], and men who don't hunt often have poor mate choice (because women don't want to be married to men who only gather vegetable foods).

Our argument concerning men's hunting and in-pair benefits supports the commonly observed division of labor among the sexes in forager societies. As developed elsewhere (Gurven and Hill, n.d.), four critical aspects of hunter-gatherer socioecology have led us to expect a sexual division of labor among foragers: 1) high dependency of individual offspring and compound dependency of multiple offspring; 2) an adequate diet that requires macro-nutrients typically found only in mutually exclusive food

types; 3) delayed productivity for efficient foraging due to time-dependent on-the-job learning in subsistence activities; 4) sex-differentiated comparative advantage (and disadvantage) due primarily to breastfeeding and childcare constraints. We believe that these conditions are common to all foraging groups and that this is the reason that men alone hunt in 166 of 179 hunter-gatherer societies examined, both men and women in 13 societies and in not one society do women alone hunt (whereas women are the main gatherers in 2/3rd of these societies) (Ember, 1978). When utility is provided by multiple foods, and acquisition of these foods require separate subsistence strategies, including substantial learning investment and increasing returns with increased time investment, specialization is a likely, if not inevitable, outcome. Specialization maximizes household utility among cooperating individuals that divide their labor to obtain complimentary objectives. This is essentially Becker's argument concerning familial division of labor applied to the hunter-gatherer context (see Becker, 1991; Bergstrom, 1997). Further explanation of the variation in male and female subsistence behavior across and within cultures, and especially status striving and its associated costs and benefits will require further theory development and novel empirical investigations.

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NOTES

1. If certain game animals are more difficult to acquire, then men who are successful hunters of those animals might gain social and reproductive benefits, according to costly signaling theory.

2. Inidividuals in small-scale, hunting-based societies are usually good at assessing the hunting ability of men. Different ranking procedures have been shown to correlate with quantitative data on production rates among the Ache (Hill K, and Hurtado AM (1996) Ache Life History: the ecology and demography of a foraging people. New York: Aldine de Gruyter.) and the Hadza (Marlowe FW (2003) A critical period for provisioning by Hadza men: Implications for pair bonding. Evolution and Human Behavior *24:*217–229.)

3. It remains possible that the ratings of hunting ability in the more acculturated sample inflate the actual relationship between hunting and reproductive success. Ratings of a man's hunting skill are likely influenced by his social status, which correlates with both hunting ability and measures of fertility. In a partial correlation controlling for age, respect, influence, and coalitional support, ratings of hunting ability in the more acculturated sample still significantly predict total fertility (partial $r = 0.372$, $p = 0.006$).

4. One is reminded of John Marshall's 1957 film "The Hunters", where the !Kung man, Toma, is actively encouraged to hunt by his wife because her "breasts are lacking milk".

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