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# Why Do Men Hunt?

## A Reevaluation of “Man the Hunter” and the Sexual Division of Labor

by Michael Gurven and Kim Hill

The role of men in hunter-gatherer societies has been subject to vigorous debate over the past 15 years. The proposal that men hunt wild game as a form of status signaling or “showing off” to provide reproductive benefits to the hunter challenges the traditional view that men hunt to provision their families. Two broad assumptions underlie the signaling view: (1) hunting is a poor means of obtaining food, and (2) hunted game is a public good shared widely with others and without expectation of future reciprocation. If hunters lack the ability to direct food shares and obtain subsequent benefits contingent on redistribution, then the ubiquitous observations of male hunting and universal pair-bonding cannot be explained from a perspective that emphasizes kin provisioning and a division of labor. Here we show that there is little empirical support for the view that men hunt for signaling benefits alone. The ethnographic record depicts a more complex relationship between food sharing patterns, subsistence strategies, mating, and the sexual division of labor. We present a framework incorporating trade-offs between mating and subsistence strategies in an economic bargaining context that contributes to understanding men’s and women’s roles in hunter-gatherer societies.

The traditional perspective of the hunter-gatherer nuclear family depends on a division of labor where men hunt wild animals and women gather plant foods (Lovejoy 1981). The pair-bond is considered a cooperative venture geared toward joint production of highly dependent offspring, where women bear and care for offspring in exchange for long-term provisioning (Isaac 1978; Lancaster 1978). According to this view, “family organization may be attributed to the hunting way of life” (Washburn and Lancaster 1968, 295), where “males hunt and females gather, the results are shared and given to the young, and the habitual sharing between a male, a female, and their offspring becomes the basis for the human family” (Washburn and Lancaster 1968, 301). This hunting-based model for the evolution of the nuclear family and a cooperative sexual division of labor has dominated much anthropological thinking over the past 40 years.<sup>1</sup>

Recent proposals have painted a different portrait of the hunter-gatherer family. The ubiquity of men’s hunting among

foragers is uncontested, but the benefits men receive and their motivations for hunting are the subject of lively debate. The “show-off” hypothesis (Hawkes 1990, 1991, 1993) initially proposed that men hunt to gain social attention and mating benefits by widely sharing game. This hypothesis was reformulated using costly signaling theory (see Bird 1999; Bliege Bird, Smith, and Bird 2001; Hawkes and Bliege Bird 2002) and is hereafter referred to as the “signaling model.” This model proposes that hunting functions mainly to provide an honest signal of the underlying genotypic or phenotypic quality of hunters, which later yields a mating advantage or social deference. Big game hunting is considered an effective means to signal because of the large audience, as consumers will pay attention to hunting yields in order to obtain their shares. Hunting is thus viewed as status or mating competition, not familial provisioning, and marriage is reinterpreted as a convention of publicly recognized property rights that reduces competition among men (Hawkes 2004).

Proponents of the signaling model suggest that were men primarily concerned with familial provisioning, their subsistence patterns would mirror those of women. Therefore, the sexual division of labor should be most pronounced when activities effective for signaling differ from those for producing

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1. Occasional protests highlight the importance of women’s subsistence tasks (e.g., Dahlberg 1981), diminishing the traditional emphasis on hunting, but do not deny the centrality of cooperative unions among men and women.

the most food. As Bird (1999, 72) states in a recent review, “the sexual division of labor seems to make more sense as an outcome of conflicts rather than similarities in reproductive goals.”<sup>2</sup> This view is incongruent with the observation that subsistence-behavior dimorphism is rare among most mammals where males engage almost entirely in mating effort. Divisions of labor are common among “cooperative breeder” species and social insects where individuals collaborate to achieve genetic contribution.

The extent to which men’s food contributions serve to provision families or display status is important for interpreting archaeological signs of hunting in the fossil record, understanding the evolution and maintenance of long-term pair-bonds, and understanding how fundamental human life-history traits (delayed childhood, long postmenopausal life spans, and large brains) evolved (Hawkes et al. 1998; Kaplan et al. 2000).<sup>3</sup>

The first section of this article assesses four key assumptions of the signaling model: (1) men forage for large-package-size items even when alternative foraging strategies yield a higher long-term average food value, (2) high-variance daily acquisition activities cannot effectively provision offspring, (3) food transfers by hunters are not paid back later in currencies directly affecting familial welfare, and (4) women prefer gathering over hunting only because of its higher reliability and productivity.

The second section explores men’s and women’s foraging and reproductive decisions by incorporating bargaining theory in economics, recognizing the potential for cooperation due to shared fitness interests of men and women and for conflict under changing conditions and disparities in bargaining power. While Washburn’s and Lovejoy’s original depiction of the nuclear family was simplistic, we choose not

2. Primatologists have considered similar proposals emphasizing male coercion and mate guarding rather than provisioning in the evolution of pair-bonds and monogamous mating systems (Mesnick 1997; van Schaik and Dunbar 1990). Parental conflict over offspring investment is part of a general framework of family dynamics in evolutionary biology (Parker, Royle, and Hartley 2002). Conflict-oriented views are based on the fundamental differences in the reproductive biology of male and female mammals, where fitness gains accrue to males primarily through increased access to mates and to females by increased access to resources (Trivers 1972). Because most mammals are polygynous, human pair-bonds are usually compared with those among bird species that exhibit high levels of biparental care and monogamy. However, recent DNA fingerprinting has shown that many species of so-called monogamous birds show significant extrapair copulation, where up to 47% of broods may be fathered by other males. In a similar reassessment of avian social systems, it has been argued that monogamy in birds may be common not because each sex has the greatest success with monogamy but because of limited opportunities for polygyny (see Black 1996).

3. These issues have reached a new audience of archaeologists who use costly signaling theory to reinterpret the significance of Archaic period hunting practices in the western United States (e.g., Broughton and Bayham 2003; McGuire and Hildebrandt 2005). These studies benefit from not having to rely on contemporary forager ethnography, and they cover broad stretches of time, but they also raise particular concerns (Coddling and Jones 2007).

to abandon the notion of a complementary, advantageous sexual division of labor. Our graphic model emphasizes that underprovisioning, mixed mating and parental investment, and desertions are all possible outcomes in human marriage.

## Assessing Empirical Evidence for the Signaling Model

### *Mean Productivity of Hunting*

Do men opt for activities providing lower mean nutrient return rates but higher variance than those of women in the same society? Studies among three foraging populations—the Ache of Paraguay, the Hadza of Tanzania, and the Hiwi of Venezuela—sparked this view and provided data for its evaluation.<sup>4</sup> In her original article on male show-offs (Hawkes 1991), Hawkes cited a report that Ache men could gain energy at higher rates by extracting palm products all day rather than hunting (Hill et al. 1987). That analysis was incorrect due to laboratory error in assessing edible portions of palm fiber and failure to measure the time required to find suitable palms (experiments now show that only one in 35 encountered palms has exploitable starch). Twenty-seven years of data show that Ache men obtain a mean ~830 cal/h by hunting, and men typically obtain a total of ~1,340 cal/h from all resources (meat, fruit, larva, honey) during normal foraging activities (Hill and Kintigh, forthcoming). New experimental data also show that male or female groups extracting only palm products (starch and hearts) could obtain 850–1,200 cal/h (mean 1,050 cal/h). Given the sensitivities of these means to population age structure, sampled season, and sample error in acquisition rates and caloric values, we conclude that the current male mixed hunting/collecting pattern produces comparable calories per unit time as would foraging exclusively for palm fiber.

Hawkes and colleagues have also argued that Hadza big game hunters could gain more calories by gathering or hunting small game, but published data contradict that claim (Hawkes et al. 1991, 2001). Hadza men acquired ~1,500 cal/h hunting large game and only 375–1,170 cal/h hunting small game or trapping (Hawkes et al. 1991, 2001). Hadza women obtained ~900 cal/h foraging for roots or berries (Hawkes, O’Connell, and Blurton Jones 1989). These estimates of gathering efficiency may be inflated because recent laboratory analyses of edible tubers show caloric densities lower than those used by the Hawkes team (Schoeninger et al. 2001, table 2). Thus, Hadza large game hunting produces nearly twice the energetic-gain rate as gathering and up to four times the rate potentially achieved by targeting small game. Nevertheless, men hunting large game diversify their production port-

4. Contemporary hunter-gatherers are neither modern relics nor mirrors into the past but instead represent an imperfect but constructive lens for learning about past adaptations and behavior under a diverse set of ecological conditions.

folio by opportunistically hunting small game and by collecting nonmeat foods such as honey (Marlowe 2004b).

Among Hiwi foragers of the Venezuelan savannas, hunting is also more productive than gathering (Hurtado and Hill 1990). In the late wet season, pregnant and nursing women obtained 1,300 cal/h, and those with no small children obtained 1,600 cal/h (Hurtado and Hill 1990, tables 6, 8). Men acquired 2,700 cal/h by hunting, and in other seasons, men obtained three to five times as many calories per hour by hunting as females did from gathering.

Such comparisons are only partially relevant because return rates are expressed in terms of caloric energy. Lipids and proteins derive primarily from meat, while plant products consist largely of carbohydrates and micronutrients. Nutritionally, 1 g of carbohydrate and protein each contains 4 cal, while 1 g of fat contains 9 cal. Protein-lipid resources and additional animal-source micronutrients are more nutritionally valuable than carbohydrate in most human societies (see "Why the Sexual Division of Labor?" below).<sup>5</sup> Men hunt because meat often has higher marginal nutritional value than carbohydrate foods given the differences in macronutrients and overall supply of the two food types.

#### *Risk-Prone Hunters?*

Hunting is characterized by significant daily variation in returns, where even the best hunters may return to camp empty-handed. Societies dependent on large game, such as whalers, experience tremendous daily variation in meat production (Alvard and Nolin 2002). Big game hunters like the Hadza make large game kills only 4% of the time (Hawkes et al. 1991), whereas the !Kung, Ache, and Hiwi, targeting smaller game, make kills 27%, 50%, and 44% of the time, respectively.

Under most circumstances, hunting returns are less predictable than those from gathering, but many economic activities yielding variable returns can provide a viable livelihood. Individuals simply adapt to such situations so that production variance does not result in high daily consumption variance. Food sharing, food storage, and greater diet breadth are biocultural means of reducing acquisition variance in animal and human foraging societies (Winterhalder 1990). Sharing is a common solution to acquisition variance among foragers, and therefore, the number of receiving families and the proportions given away are both greater for resources characterized by higher acquisition variance (Hames 1990; Kaplan and Hill 1985). Without sharing, large game hunting may never have been viable for our hominin ancestors.

While hunting is often a risky method of daily food acquisition, dependence on plants may also involve problems of temporal variability. Plants are usually seasonal, and for-

5. As in many foraging groups, Ache and Tsimane commonly complain of hunger even though carbohydrate-rich foods such as sweet manioc and plantains are abundant. The hunger refers specifically to the desire to eat meat.

agers may experience long periods when few edible plants are available.<sup>6</sup> Extreme seasonal plant shortages characterize many Arctic foraging societies at high latitudes (e.g., Balikci 1970).<sup>7</sup> During these shortages, foragers may depend on hunted game despite daily variation in their acquisition.

Men in some foraging populations target small to medium-sized game, and even Hadza hunters often hunt small game opportunistically (F. W. Marlowe, personal communication). Small game has been a component of human diets for at least 200,000 years (Stiner 2002), and its acquisition was unlikely motivated by signaling. Small game hunting is more predictable than large game hunting, and in documented hunter-gatherer societies, small game shares are preferentially consumed within the family (Gurven 2004).

Bliege Bird, Smith, and Bird (2001) and Bliege Bird (2007) show that men in one foraging society regularly opt for high-variance, low-return foraging when faced with the same alternatives as women and that the sex differences cannot be explained by macronutrients. Meriam women of the Torres Strait collect shellfish or hook-and-line small fish. Men employ techniques to fish for larger prey at a lower gain rate. The general division of labor where women collect shellfish while men pursue larger marine resources is typical of marine foragers, but the suggestion that men obtain less food over the long run is novel. These findings suggest that research is needed to determine how often men pursue foraging strategies that are suboptimal for familial provisioning.

#### *Sharing and Reciprocity*

Hunting is argued to be a poor family provisioning strategy because it is believed that meat transfers to others are not paid back in some form at a later date (Bird 1999; Blurton Jones et al. 2000; Hawkes 1993; Hawkes and Bliege Bird 2002). Signaling proponents view shared meat as lost resources because men supposedly cannot control the distribution of their hunted game and nothing is returned in exchange. Men's food production is therefore discounted such that only the kept portion contributes to family provisioning.

A recent comprehensive review shows little support for the notion that hunters do not (or cannot) influence resource distributions or that meat is unconditionally shared (Gurven 2004). Empirical evidence does not support the assertion that

6. Among the Hiwi, the primary carbohydrate staple, roots, is only available 4–5 months during the year. Because metal digging tools are significantly more efficient than traditional wooden ones, it is likely that the productive carbohydrate season was shorter before the introduction of metal tools (Hurtado and Hill 1990).

7. Fifteen years ago, there was much debate about whether tropical foragers could survive without trading with farmers or cultivating swidens, because seasonal shortages in carbohydrate-rich foods are so common (Headland and Bailey 1991).

hunted prey are undefendable public goods.<sup>8</sup> Studies reveal sharing bias by categories of individual recipients and in the size of transferred shares. Kin, neighbors, and cooperative partners often receive more meat than other group members in quantitative studies, suggesting some control over distribution by acquirers, even when hunters do not butcher or divide their prey. Indeed, a hunter's nuclear family obtains more from his kill than do other families in all sharing studies except those among Ache during forest treks.

Preferential food sharing with those who reciprocate is referred to as "contingency" (Gurven 2006; Hill and Kaplan 1993). Receipt of food that is contingent on having given food is commonly observed in the ethnographic literature on foragers and has been found in most societies where tested statistically (Gurven 2004).<sup>9</sup> The amount of meat given by one Hiwi family to another was the strongest predictor of how much meat was returned by that same family over a 4-month sample period (Gurven et al. 2000*b*). The statistical association between amounts shared and received suggests on average 35%–45% of game and fish shared by men was returned by the recipient family because it was shared (i.e., with factors such as kinship and proximity controlled). A much higher percentage of transferred food was actually returned to donor's families, considering the additional, independent, positive effects of kinship and residential proximity on amount shared (Gurven et al. 2000*b*).

The amount of meat received was also significantly associated with the amount given to each family among the Pilaga (Gurven 2004), Yanomamo (Hames 2000), Dolgan, and Nganasan (Ziker and Schnegg 2005). Among the Ache, meat sharing is highly contingent at reservation settlements (Gurven, Hill, and Kaplan 2002), and nonmeat foods are shared contingently in both the forest and reservation when other confounding factors are controlled. Contingency trumps kinship on Ache reservations, with shares going preferentially to kin who give them large amounts of food rather than those who share little (Gurven, Hill, and Kaplan 2001). Only Ache forest meat sharing shows no relationship between amounts given and received among nuclear family pairs (Gurven, Hill, and Kaplan 2002); however, on forest treks, meat may still be shared in a contingent fashion (Hill 2002). Informants state that a man must hunt and attempt to kill something in order for others to give him a share in the band's daily production. Teenage boys are warned that if they do not hunt, they will not be fed. Men failing to hunt or help in

cooperative hunts are generally not invited to participate on future treks.<sup>10</sup>

Hadza meat sharing has been described as noncontingent because individuals approach undefendable kills and take portions for themselves. However, Hawkes, O'Connell, and Blurton Jones's (2001, table 3) recent data reveal that a hunter's family receives a larger portion of his kill (29.9 kg/kill) on average than do other families (13.5 kg/kill) for the largest animals. Other biases in meat distribution (to close kin, nearest neighbors, sharing partners, etc.) have not been examined among the Hadza, but Marlowe (1999) shows that men with biological children rather than stepchildren produce more food, suggesting that Hadza men acquire food partially to feed their families. Hawkes et al. (2001) report no relationship between the total amount of meat a hunter provides to all others and the amounts received in return from all others, but this does not test contingency. The right of a man or his family to take a portion of the kill may depend on his attempts to acquire food (and sharing the results) or provide some useful good or service, as we suggest among the Ache. If so, obtaining a share of meat among the Hadza may be contingent on cooperative behavior that benefits hunters who share; indeed, part of demand sharing (Peterson 1993) may reflect debt obligations based on expected repayment. Whatever the explanation for demand sharing among the Hadza, our reanalysis does show significant contingency for meat transfers among pairs of Hadza hunters (Gurven 2004).<sup>11</sup>

Women's sharing patterns, a rarely examined feature of hunter-gatherer life, also contradict the signaling hypothesis. It is argued that women target items for which they can control resource package size and rarely acquire more than their families can eat (Bird 1999, 68). This is not true of the Ache, Hiwi, and probably the Hadza as well. Women often intentionally collect larger amounts of food than their family can consume, then widely share outside their nuclear family. Plant foods come in small increments, and women could stop working upon obtaining enough for their families. Ache women extract palm fiber starch one handful at a time, producing between 3,000 and 6,000 calories in each extraction session. Anecdotal reports suggest similar rates for Hadza root and berry collection and that Hadza women share with unrelated individuals (Blurton Jones, Hawkes, and O'Connell 1997). Ache and Hiwi women must therefore acquire large packages of collected foods intentionally because they gain from food transfer. Theory suggests that those gains cannot be increased by number of mates; gains from sharing should be in some form that affects women's or offspring's well-being. Ache and

8. It is also inconsistent with the observation that the same resources are shared differently across societies or in different contexts (e.g., Ache: Gurven, Hill, and Kaplan 2002; Huaroni: Franzen and Eaves 2007), which suggests that game can be defended, if necessary.

9. Even nonhuman primates have been observed to engage in contingent reciprocal food exchange (de Waal 1997).

10. Anthropologists, providing no meat but sharing in kills, feel pressure from the contingency sharing system and offer gifts and services to groups such as the Ache and Tsimane in exchange for accompanying them on treks.

11. An independent assessment of pairwise contingency that controlled for the presence of different hunters during distributions shows a similarly strong positive relationship (W. Allen-Arave, personal communication).

Hiwi women give away about 55% of all collected food (Gurven 2006; Kaplan and Hill 1985). Ache women at reservation settlements share an even higher fraction of their collected resources (76%). As package size increases, Hiwi and Ache women keep a smaller percentage for their nuclear family.<sup>12</sup>

It has long been known that men share a greater percentage of their production than women; however, this may be because they often bring in large food packages. Analyses among the Hiwi (Gurven et al. 2000b), Ache on reservation settlements (Gurven et al. 2001), and Ache on forest treks (Gurven, Hill, and Kaplan 2002) show no sex differences in amounts shared outside the family for resources obtained by men and women after controlling for resource size. If women's sharing patterns are identical to those of men, and the production of large packages and subsequent sharing by women is paid back in a form useful for parental investment, it seems parsimonious to assume the same for men's sharing.

Many ethnographies report complaints concerning failures to meet sharing obligations or expectations, particularly in the context of pairwise exchange (see Gurven 2004). Men who hunt only as a form of mating effort should not be concerned with receiving conditional shares from previous recipients, nor should they complain or become upset when shares are not returned.<sup>13</sup> If signaling provides fitness benefits, and signalers compete for an audience, men should prefer *not* to have their shares repaid, but no evidence supports this conjecture.

Estimates of contingency show that producers receive back on average at least a third of what they give away to other families. These estimates are imperfect windows into complicated cooperative exchange relations (Gurven 2006). There are reasons to expect that cooperation may not result in complete exchange balance in foraging societies. Among hunter-gatherers, nuclear families are part of larger extended kin networks that often subsidize each other's reproduction over long time periods. Over any short time period, some individuals always produce more than they and their families consume. Even if we consider isolated nuclear families as independent units, each should have a minimal threshold for acceptable exchange with others that constitutes an "insurance policy" guaranteeing resources from reciprocators on shortfall days or periods of debilitation from sickness and injury. In understanding the exchange of A's present production for B's future production, there will be a set of potential exchanges (many unequal) where both A and B can benefit above what might be expected if no exchange occurs. This region is re-

12. Hiwi women kept about 40% of nonhunted resource packages over 15 kg, while Ache women kept 20% of fruit, 25% of larva, 25% of palm heart, and 30% of palm starch packages over 2,000 calories.

13. Anecdotal reports suggest this is not the case for most foragers, just as abundant studies in economics and psychology show that people in urban and rural settings around the world get upset and seek to "punish" perceived defectors in dyadic interactions (e.g., Henrich et al. 2006).

ferred to as a "bargaining zone," the oval region in an Edgeworth box diagram (Gurven 2004; fig. 1). The final exchange agreement should be influenced by the relative bargaining power of each party, reflecting expected costs from giving and benefits from receiving food. Costs and benefits vary with the amount of existing resources, influence, production ability, status, or dependent offspring (e.g., Boyd 1990).

Evolutionary models of sharing do not adequately explain cultural sharing norms or other conventions that support extensive cooperation among non-kin. Quantitative analyses repeatedly show that "need" is one of the strongest predictors of food flows among hunter-gatherers (Gurven 2004), where families with more children or greater dependency often receive larger shares. High family need can be permanent due to low production ability, or it can be temporary when families pass through a stage of high dependency (fig. 1). Signaling proponents argue that flows of food to the needy indicate "tolerated theft," but evidence of high producers intentionally producing and distributing shares to the needy (Gurven 2004) undermine that suggestion. Net resource flows to needy families may make more evolutionary sense considering the cooperative nature of human social organization and the novel proposal that altruistic punishment in the context of intergroup competition may favor "hyper-cooperation" (Bowles 2006; Boyd et al. 2003).

#### *Why Don't Women Hunt?*

The signaling model suggests that women avoid hunting because it provides low unpredictable payoffs. We have shown that hunting yields comparable or higher caloric returns and more favorable nutrient content than collecting in several societies. The Agta of the Philippines are often cited as evidence that women can hunt as proficiently as men, despite encumbrances of childcare. In fact, many forager women, including Ache and Hiwi, participate in hunting activities. However, women rarely make kills of medium-sized or large game; instead, they engage in activities that help men hunt successfully. In contrast, Agta women hunt with bows and arrows and kill the same prey as do men. The Agta data are important because they indicate conditions under which women may actively hunt. However, fewer than 100 Agta women claimed to have ever hunted from a population of about 9,000 on Luzon Island (P. B. Griffin and T. Headland, personal communication). Most women who reported having hunted were no longer hunting during the ethnographic observation period, and most late-twentieth-century Agta had never heard of women hunters (P. B. Griffin and T. Headland, personal communication). Hunting production data exist for a sample of only six women hunters (Goodman et al. 1985), and available data suggest several patterns relevant to women's hunting: (1) carbohydrate resources provided low returns and were rarely encountered; (2) meat was traded for carbohydrates at a favorable rate; (3) fertility and ratios of dependent

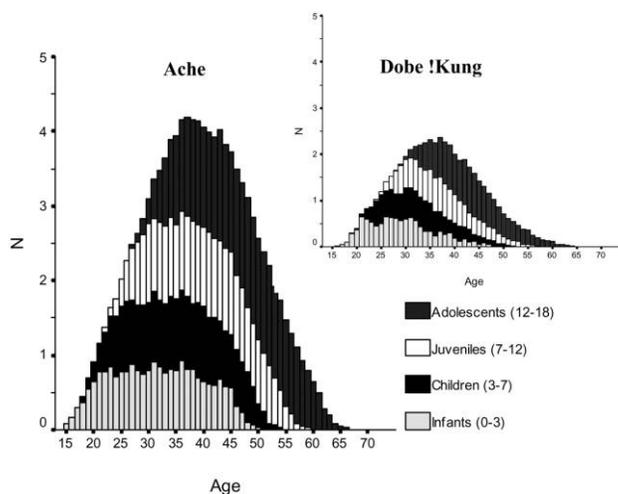


Figure 1. Number of dependents by age for Ache and Dobe !Kung (*inset*) females based on age-specific fertility and mortality measures for these populations. Ache women have high fertility over their lifetimes (total fertility rate = 8), and !Kung women have low fertility (total fertility rate = 4). Adapted from Gurven and Walker (2006).

children to adults were low, with high availability of alloparents; (4) women who hunted were often sterile or postreproductive; (5) all women's kills resulted from hunting with dogs; and (6) women's hunting always took place less than 5 km from camp, allowing rapid return to dependent offspring (Estioko-Griffin 1985, 1986; Goodman et al. 1985). The first three points may explain why African Pygmy women participate in communal net and bow hunting activities. Dogs immobilize Agta prey, perhaps explaining why they regularly dispatch prey without men whereas Hiwi and Ache women rarely do. No study of Agta women hunters has examined whether active hunting is related to women's reproductive status at the time of hunting, but anecdotes suggest that women hunted infrequently or not at all when pregnant or lactating (Estioko-Griffin 1986, 42).<sup>14</sup>

Brown (1970) proposed that women do not hunt because it is incompatible with childcare demands rather than because of strength demands or physical constraints such as endurance

14. Women's involvement in some hunting activities is probably typical of most foraging groups, but there are still strong sex differences. Ache women search for game (and call men when they find it), dig out some burrowing animals, spot monkeys during hunts, and help track wounded prey. Hiwi women paddle canoes while their husbands stand and hunt with a bow for aquatic game. Time allocation data on Ache women suggest that they spend about 10% of their foraging time helping in hunts (Hill 2002). During 30 years of fieldwork with the Ache, K.H. has seen women actively attempting to kill prey a couple dozen times (only once with bow and arrow) and has heard stories of two women who hunted regularly before fieldwork. However, in a recent Ache sample of all game killed by 25 families from 1994 to 1999, men killed 4,437 animals, and women killed 3. Women help in hunts but do not often make kills.

or spatial abilities (see also Hurtado et al. 1992). Keeping offspring alive is a top priority for forager women, and it precludes hunting in most environments. Nursing women adjust gathering rates according to the age of the youngest child with them at the food patch, and as infant age increases, collection rates increase substantially (Hurtado et al. 1992).

Mothers obligatorily care for infants because on-demand lactation occurs frequently throughout the day. Women would often lose prey were they to interrupt hunting pursuits to meet immediate childcare demands. Infants cry and fuss for many reasons, and failure to react to distress calls lowers infant viability. The situation is quite different for sessile-collected resources and some small vertebrates, where pursuit can be interrupted at any time without loss.

Hunting is also dangerous for infants because of long distances traveled under arduous conditions and dangers inherent in rapid burst pursuits. Males experience higher accident rates than females among Ache foragers (Hill and Hurtado 1996) and higher death rates from animal attacks and snakebite among Tsimane (Gurven, Kaplan, and Zelada Supa 2007). Because maternal loss is more detrimental than paternal loss (Sear and Mace 2007), women may be more averse to risk of injury than men.

Finally, successful hunting requires at least 15–20 years of experience to obtain maximum return rates. Boys who miss sensitive-period skill development rarely become proficient hunters (Gurven, Kaplan, and Gutierrez 2006; Kaplan et al. 2000; Walker et al. 2002). The steepest gains in men's hunting returns occur during the years when women experience high fertility and are constrained from hunting. This may explain

why postreproductive women, free from childcare constraints, do not hunt in most societies.

## Cooperative Pair-Bonds Revisited: A Bargaining Perspective

### *Why the Sexual Division of Labor?*

Five critical aspects of hunter-gatherer socioecology lead us to expect a sexual division of labor: (1) long-term dependency of high-cost offspring, (2) optimal dietary mix of macronutrients from mutually exclusive foods, (3) efficient foraging based on skill-dependent learning, (4) frequent spatiotemporal segregation of important resource types, and (5) sex-differentiated comparative advantage in tasks. These combined conditions are rare in nonhuman vertebrates but common to human foragers and perhaps suggest why men alone hunt in 166 of 179 hunter-gatherer societies examined. Men and women hunt in 13 societies, and in none do women alone hunt, whereas women are the main gatherers in two-thirds of these societies (Ember 1978).

To understand the sexual division of labor, we must consider the costs of joint offspring production. The average female forager can expect to have five children over her lifetime (Hewlett 1991a) that grow and develop slowly and consume more food than they produce until their mid- to late teens (Kaplan 1994; Kramer 2005). A reproductive-aged woman often has multiple offspring of various degrees of dependency (fig. 1). Even at peak adult production, adult pairs often cannot feed themselves and their children without assistance (Gurven and Walker 2006). Even foragers at the age of peak food production may experience net food deficits due to the composite net caloric demand of offspring.

Offspring need is insufficient to cause specialization in subsistence activities by sex or age; macronutrient composition of foods also matters. There is no consensus on the optimal combination of lipids, proteins, and carbohydrates in the human diet, but each is necessary for healthy growth, development, body maintenance, and reproduction (see Milton and Demment 1988 and references therein). Protein-lipid resources and animal-source micronutrients are often difficult to obtain, produce greater biological benefit per unit weight or energy, and are more valuable than carbohydrate in most societies. Increased protein and lipid consumption facilitates improved growth and health in most societies (Carpenter 1994; Larsen 2003) and are critical to brain growth, immune function development, and female reproductive function (Murphy and Allen 2003).<sup>15</sup> The human gut is adapted to a mixed macronutrient diet (Aiello and Wheeler 1995), and biochemical evidence suggests that several essential nutrients

(e.g., taurine, 20- and 22-carbon fatty acids) are only obtained from animal tissues and more so in large game (Cordain, Watkins, and Mann 2001). Finally, plant diets are low in protein, vitamins B6 and B12, zinc, iron, and long-chain omega-3 fatty acids, and plants are often high in toxic antinutrients (Cordain, Watkins, and Mann 2001).

Foragers should therefore acquire complementary plant carbohydrates, animal protein-lipids, and micronutrients for optimal health and growth. Specific macronutrients are packaged in different foods, thus many separate food items must be included in the human omnivore diet (see Harris and Ross 1987 volume). Game, fish, roots, fruits, honey, nuts, insect larvae, berries, and other forager foods are often difficult to acquire and require specialized knowledge, contributing to the long dependency of hunter-gatherer youth (Kaplan et al. 2000). Productivity in gathering, collecting, and fishing activities may often be more size-dependent than skills-dependent, and adult-level return rates may be easily attained (Bird and Bliege Bird 2002, 2005; Tucker and Young 2005). Conversely, efficient hunting requires years of practice among Ache, Hiwi, Tsimane and other hunting groups. Encountering and killing animals upon pursuit are the two most difficult components of hunting that require the longest time delays to reach peak levels (Gurven, Kaplan, and Gutierrez 2006; Ohtsuka 1989; Walker et al. 2002).

Healthy diets are provided by different foods whose acquisition requires separate skills and additional time investment in learning and practice for increasing returns. Under these circumstances, specialization is a likely, if not inevitable, outcome *even if group members are equally capable of performing all tasks*. This is essentially economist Gary Becker's argument concerning the familial division of labor applied to hunter-gatherers (Becker 1973, 1974).

Specialization does not imply that men should hunt and women gather. Without comparative advantage by sex, each need only coordinate on a particular complementary set of activities. Without increasing returns to specialization, both sexes might become generalists and freely alternate between complementary activities. However, in the section titled "Why Don't Women Hunt?" (above), we presented reasons why men hunt and women gather. Childcare constraints give men a comparative advantage in hunting activities, amplified by men's greater average strength and body size. Signaling benefits from killing large prey may also motivate male hunting, but in our view, these are not necessary to explain why men hunt in foraging societies. Instead, signaling payoffs to hunting may increase the likelihood that men will hunt more and under conditions that might otherwise favor greater male involvement in gathering.

### *Marriage, Parental Investment, and Children as Public Goods*

The signaling model does not account for human marriage. A cooperative pair-bond model explains marriage but does

15. Experimental manipulation with isocaloric diets shows improvements in health and growth rates among rats fed with higher protein-lipid diets (reviewed in Hill 1988). Frugivorous primates regularly forage at lower caloric return rates in order to obtain protein-lipid foods (see Milton 1999 for review).

not presume that males and females contribute equally. Children are shared public goods because they represent fitness outcomes for both parents regardless of the levels of investment each of them provides. To model optimal parental investment, we consider partner utility (fitness) functions that contain shared household (public) and personal (private) components. The task is to determine optimal time allocations for each marital partner and the resulting level of equity in the distribution of effort and gains. Extreme possibilities include “symmetrical” marriages, where similar effort and gains are realized by each partner; “dictatorial” marriages, where one partner determines allocations by both (Manser and Brown 1980); and pair-bond dissolution. The existence of noncontributing “deadbeat dads” does not deny the benefits from an economy of scale associated with cooperation in marriage unions; even with low investment by one partner, a sexual division of labor may still be optimal. Unstable unions and unequal bargaining power due to different options available to each partner can lead to dissolved unions and/or a failure for one or both partners to invest in household production and childcare.

The optimal amount of time spent investing in offspring can be illustrated graphically using indifference curves. Each partner decides how much of their daily time budget to spend in each alternative activity. For simplicity, we group all work activities and label them “household production,” and all activities that yield private gain are labeled “leisure.” Work activities include direct resource acquisition, food preparation, camp maintenance, childcare, and activities such as building social alliances that may benefit the family. Leisure includes other social visits, relaxation, grooming, pursuing extrapair relationships, play, sleep, or any other activity that does not provide utility to other household members.

Each partner attempts to maximize fitness gains from a marriage union subject to time constraints by choosing an optimal set of activities (see fig. 2 for details). Concave isofitness curves describe the combinations of public and private goods that provide the same fitness. These are called indifference curves because decision makers receive equal benefits from any combination of activities on the same curve. The shape of indifference curves depends on several key functional relationships, such as the shape of the fitness gains for (1) investments of care and food for offspring, (2) investments in mate acquisition, and (3) investments in status activities that may provide both private and public benefits.

The indifference curve approach is useful for visualizing trade-offs and has been used to model women’s optimal time allocation to childcare versus food production (Hurtado et al. 2006). When men’s activities have minimal impact on child welfare and when mating opportunities are high, indifference curves are shallow, and expected male parental investment is low (Blurton Jones et al. 2000; Hurtado and Hill 1992). When men’s contribution to the diet is high (e.g., Ache, Hiwi), indifference curves are steep, and greater paternal investment is expected. Empirical evidence suggests instead that male

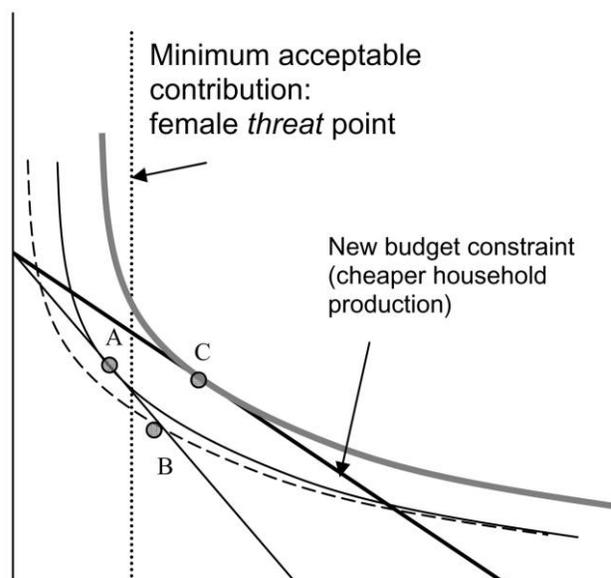


Figure 2. Isofitness framework underlying a man’s optimal mix of household contributions and private gains. Isofitness curves define combinations of household production and leisure that result in equal fitness gains. The different budget constraints (*straight diagonal lines*) are defined by the total number of hours available that could be spent in either household production (X-axis) or leisure (Y-axis). The budget-constraint lines intersect the two axes at the point where all time would be dedicated only to that activity. Usually a budget is a straight line, although the budget line might be bowed outwards if public and private activities can be performed simultaneously, as when hunting both feeds children and signals mate quality. A is the optimal allocation of a man’s time to household goods and private gain given the budget constraint of the thin line, but this point lies below the woman’s minimum acceptable level of household contribution. Therefore, a man will choose the suboptimal allocation at B. The thick black budget line illustrates the case where household goods are more cheaply acquired than with the thin black line. Under this scenario, the optimal mix includes more household investment (C).

impact on offspring is highly variable cross-culturally (Sear and Mace 2007). However, measuring the effects of paternal care is methodologically complex because the presence of others who contribute aid during father absence obscures the true fitness impact of paternal contribution (Winking 2006).

Examining time allocation of men or women in isolation might lead to the erroneous result that both partners should become generalists. If pair-bonding entails substantial costs, individuals may hold minimal expectations of the household contributions that they demand of potential spouses, or “threat points.” These describe the contribution threshold below which an individual may abandon the marriage rather than compensate for lowered partner investment (fig. 2; Manser and Brown 1980). Studies among several tribal societies suggest that while men value physical attractiveness more, both partners are concerned that a prospective spouse be hard-working, generous, and a high producer (Hill and Hur-

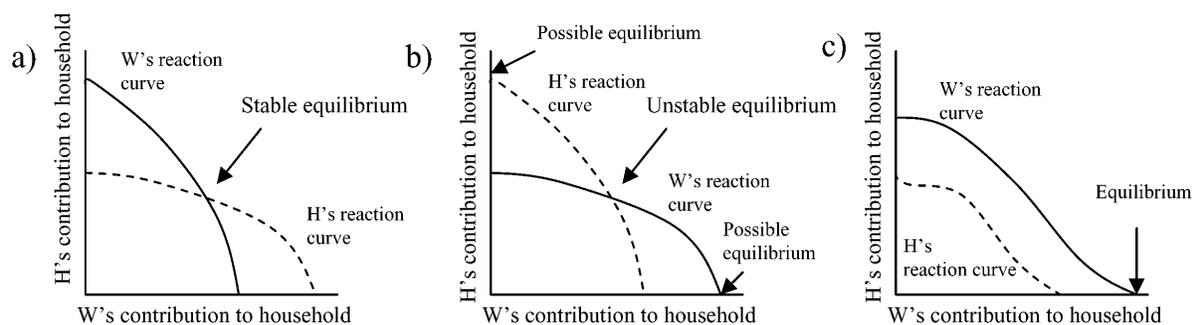


Figure 3. Reaction curves for husbands (*dashed curve, H*) with respect to wives (*solid curve, W*), and vice versa. An initial level of *W*'s contribution on the *X*-axis invokes a reaction by *H* that defines *H*'s contribution level on the *Y*-axis, which then invokes an investment response by *W* based on her reaction curve. This maps back to the *X*-axis, where *W*'s new contribution level invokes a new response by *H*, and so on until an equilibrium is reached. Regardless of initial conditions, *a* results in a stable equilibrium mix of *W* and *H* contributing (albeit unequally) to the household. *c* results in *W* contributing everything to the household, and *H* contributes nothing. If *W* initially contributes more than the equilibrium amount in *b*, she will eventually contribute everything to the household, and *H* will contribute nothing. If *W* initially contributes less than the equilibrium, the reverse outcome will hold. Adapted from Chase (1980).

tado 1996; Marlowe 2005). Mutual preferences for these traits make sense if partners seek gains from marriage that are both productive and reproductive. If women gained little from marrying men and were instead only gene shopping, we would expect more polygyny than observed among foragers and only brittle pair-bonds.

In the conceptual model, an initial allocation decision is made by one partner, a reactionary allocation is made by the other partner, and so on until one of the following outcomes is reached: (1) both partners arrive at a stable equilibrium of household contributions (not necessarily equal); (2) the equilibrium is unstable, and eventually one partner's contribution falls below the dissolution threshold; or (3) one partner always defects, and pair-bonds never form (Chase 1980). These outcomes are illustrated by the utility response curves in figure 3. The second scenario represents the downward spiral of a marriage heading for divorce, where lower investment by one partner results in higher investment by the other. For example, a man living with his wife's kin may reduce familial investment if he has additional mating opportunities, while his wife and her kin compensate by investing more until finally the male is deemed expendable. The third scenario should also result in divorce, unless the contributing partner has no other options; if the wife from the above example has no kin or other bargaining chips, she may always have to invest heavily in the household, regardless of her husband's investment. Normally, optimal time allocation for the male partner (*A* in fig. 2) will not match the optimal solution from the female point of view. Instead, there is a region between the optimal

male and female solutions (i.e., "bargaining zone"; see "Sharing and Reciprocity," above) that defines a set of time allocations for each sex that is open to "negotiation."<sup>16</sup>

Individual attractiveness, status, wealth, specialized skills or abilities, and other bargaining chips vary across men and within men over their lifetimes. For example, attractive men by virtue of their "good genes" might invest less in children while other men compensate with more long-term investment (Waynforth 2001); indeed, high-status Aka men spend less time with their children than lower-status men (Hewlett 1992). Ecological features—the cost of obtaining mates given the number of competitors, payoffs to male coalitions, difficulty and productivity of foraging, and social currency of different foods—will affect opportunity costs of men's time spent in subsistence tasks that provision family members.

It might seem that marital commitments are highest when children are young and spouses have high reproductive value. Due to long child dependency and serial reproduction, high

16. This process of declaring expectations and responding to a partner's level of commitment may implicitly underlie the logic of matrilineal residence and bride-service patterns commonly found in forager and forager-horticultural societies (Collier and Rosaldo 1981). Men must demonstrate the willingness to work hard and contribute food to the household under the supervisory gaze of their new spouse and in-laws. The important point here, as argued in "Sharing and Reciprocity," is that the bargaining outcome need not insure equal levels of contribution by men and women in marriage but rather need only insure that men and women gain more from these unions than they would from alternative options.

caloric demands of children in foraging environments may last into parents' midforties and fifties (see fig. 1), after which newly married "independent" offspring may require help. Insuring survival through the high-mortality period of infancy and childhood (~50% for hunter-gatherer populations) is only one way that fathers contribute to the welfare of their children. Fathers may improve child welfare in many ways: through improved growth and nutrition, with foraging skills and hunting proficiency, by facilitating alliances and providing support during conflict, and through protection from violence. Pair-bond defection during middle age might be more costly than earlier in life, especially if male mate value decreases with his expected productive life span.<sup>17</sup> Thus, divorce rates decrease rather than increase with age, and in at least two societies, men are more likely to engage in extramarital sex early in their reproductive careers than they are later, despite their wives' declining reproductive value (Winking et al. 2007). Some high-status men may reap gains from defection when spouse mate value declines, or they may support two wives, but these are likely to be exceptions rather than the rule for most men. These insights help explain why socially imposed monogamy is the dominant marriage pattern for hunter-gatherers (Marlowe 2004a).

An implication from this conceptual exercise is that even if mating effort were a priority for men, the sexual division of labor need not be more pronounced in societies where mating effort gives higher payoffs. The sexual division of labor may not be affected much at all, although paternal contribution to offspring may be lower when payoffs from mating effort are high. The Hiwi have a more pronounced sexual division of labor than the Ache (Hurtado et al. 1992), but Ache men have much greater mating opportunities and higher divorce rates. Factors other than mating probably explain why these societies each show sex differences in resource acquisition. Men may engage in activities yielding high nutritional utility after accounting for economic choices made by women, and this may be more so if these activities provide social or mating benefits. Women may also maximize nutrient gain rate subject to the constraints of lactation and childcare and adjust their behavior if men provide certain foods. In such a scenario, men still face decisions about whether to use resources for mating or parenting investment. In either case, men should acquire foods of highest utility to women and children, resulting in a division of labor regardless of whether mating or parenting provided them the highest payoffs.

17. Economists solve the free-rider problem by incorporating interdependency into personal utility functions. At a proximate level, such interdependency may reflect love, companionship, or "growing old together." While we do not deny the importance of these emotions in regulating commitment levels within relationships, we are more interested in the evolutionary logic that should lead to the development of these emotions in the first place.

## Discussion

On average, men contribute about 65% of the calories and 85% of the protein to the forager diet (Kaplan et al. 2000; Marlowe 2001). The observation that men hunt and women gather supported the simplistic view of marriage as a cooperative enterprise. Greater sophistication suggests that males may often be motivated by mating and status rather than offspring investment. Evidence illustrates that humans are exceptionally cooperative among primates (Henrich and Henrich 2007) and that long-term pair-bonding and extended kin-group cooperation are common. Despite extensive theoretical debate over the past 15 years, the question of why men hunt can only be settled with empirical observations. Are the fitness benefits from meat provisioning sufficient to explain hunting regardless of whether signaling also provides fitness benefits? If so, then hunting is "explained" by its provisioning effect on close kin. If signaling or mating benefits alone make hunting the fitness-maximizing activity of males, then additional benefits might be irrelevant to why men ultimately hunt. However, we may find that payoffs from both provisioning and signaling together explain why men hunt rather than gather under most circumstances in all foraging societies.

Numerous observations contradict the signaling view of hunting. Men isolated from a potential audience still hunt for a living. When foragers disperse, fission into family-based foraging parties, are lost, or are out on a raiding party, men still hunt to feed themselves or their families. Women prod their husbands to hunt, not to gather. If male payoffs to hunting were mainly in the form of increased mating opportunities, would forager wives be so anxious for their husbands to hunt? We have never heard a forager woman pleading with her husband to spend the day collecting. Instead, Ache, Hiwi, Tsimane, and Machiguenga women often vigorously encourage their husbands to hunt.<sup>18</sup> Men who do not hunt often have poorer mate choices. Finally, many human populations voice strong desires to eat meat when it is absent from the diet for a few days, and many tribal populations have specific vocabulary terms for "meat hunger" (Simoons 1994).

In addition to nutritional benefits, hunting is a common route to high status among foragers (Wiessner 1996). Good hunters display higher reproductive success everywhere the relationship has been investigated (Smith 2004), but this does not mean that the status quest is equivalent to mating effort. Instead, good hunters are chosen as spouses, even in arranged marriages, because their higher production ability and generosity gives them leverage in the mating market, and fitness effects of status likely accrue to wives, children, and close kin. Forager women show higher average total fertility the more

18. 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."

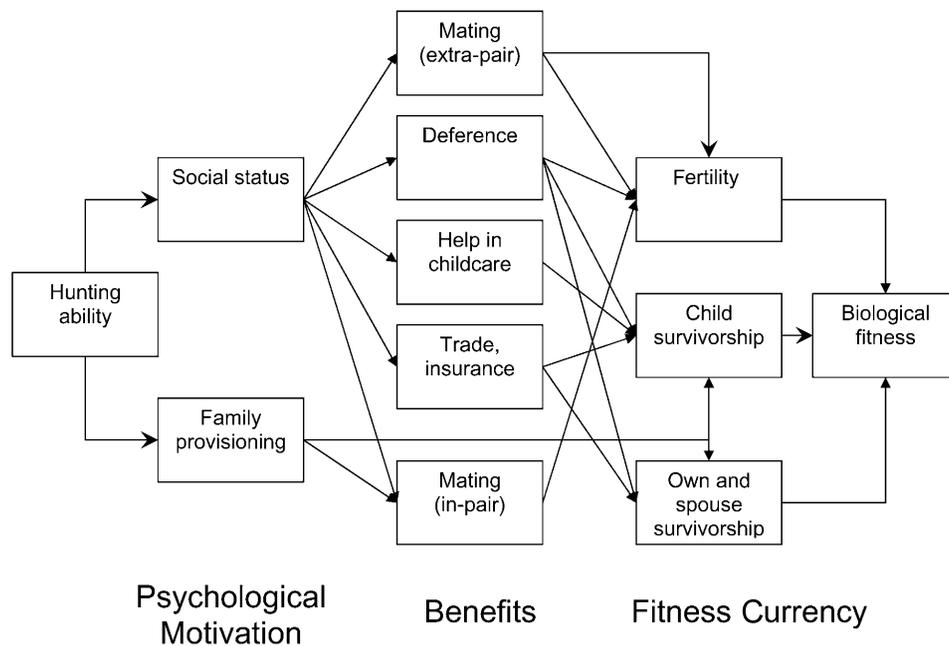


Figure 4. Causal pathways mediating the relationship between hunting success, social status, and biological fitness. The pursuit of social status from hunting can provide many benefits in addition to in-pair and extra-pair mating access, including deference, coalitionary support, aid in childcare, and social insurance. Overall impacts of hunting ability on fitness are mediated by increases in fertility, survivorship, and well-being of self, spouse, children, and probably other kin as well. Adapted from Gurven and von Rueden (2006).

that men contribute to the diet (Marlowe 2001), and women produce less when their husbands produce more (Hurtado et al. 1992). There are multiple pathways by which hunting ability can increase reproductive success and thus motivate male economic behavior (fig. 4). Figure 4 illustrates the alternative routes by which social status striving can produce benefits typically attributed only to direct provisioning (Gurven and von Rueden 2006).

The signaling model posits that extrapair mating benefits due to partner choice for good genes (rather than for production ability or willingness to provide resources) explain the correlation.<sup>19</sup> However, the view that hunting is motivated by mating payoffs conflates psychological motivations underlying men’s time budgets and the fitness effects resulting from men’s subsistence choices. It is unlikely that all male status display should be motivated by mating payoffs. While good hunters often have higher mating success, a study among Tsimane hunters shows that hunting ability, meat sharing, and social status associate with increased in-pair fertility but

bear no relationship to extrapair mating success (Gurven and von Rueden 2006). Proficient Tsimane hunters are likely to share meat and are regarded as hard workers—important qualities to mates and social partners.

Costly signaling of high phenotypic quality could then result in favorable treatment by many members of the social group (Hawkes 1990). As described for the Tsimane, successful hunters might gain sexual access to more high-quality females or obtain more valuable allies, and competitors may be more reluctant to confront them in a variety of arenas. Such payoffs affect male fitness through mating success, and some payoffs might also benefit offspring (e.g., father having more allies and fewer competitors).<sup>20</sup>

The gains from repeated long-term cooperation with valued partners seem to make the costs of signaling cooperative in-

19. A modified version of the signaling model posits that food provisioning within the pair-bond is also a form of mating effort designed to reap reproductive gains from the current relationship. In this view, any form of provisioning can be interpreted as a form of mating effort.

20. Women’s food sharing might also best be understood as costly signaling, yet the payoffs to that sharing are clearly not in mating opportunities. Women as well as men compete for status (Campbell 2002), presumably because this benefits their offspring. In modern societies, wealthy women engage in public philanthropy, and postreproductive women buy expensive jewelry and other luxury items clearly designed to signal status but with no payoff that would qualify such purchases as mating effort.

tent worthwhile (Frank 1988). Presumably, these repeated interactions involve dyadic and indirect reciprocity. The benefits of a reputation for generosity are just beginning to be investigated in foraging societies. Do individuals who eat from men's kills give them other food types, make tools for them, bring them firewood, babysit or feed their children more often, or care for their families when they are ill? Ache children of good hunters experience higher survival (Hill and Hurtado 1996) despite receiving no larger portions of father's game than other children. Men who share larger percentages of their food obtain more help when sick or injured (Gurven et al. 2000a). Ache children experience higher mortality after paternal death or the divorce of their parents. The mechanism of these survival effects is not known, but we suspect that it is due to preferential treatment and intermittent feeding of the offspring of good hunters.<sup>21</sup>

## Conclusion

The fitness that accrues to hunters is due to the summed direct and indirect pathways shown in figure 4. The provisioning pathways may favor hunting in most societies, but commitment to hunting is reinforced by the signaling payoffs that aid in mating success and coalition building. Hunting may be ubiquitous among men cross-culturally precisely because of the multiple pathways by which it affects fitness via both private and household gains. Both early historical focus on family provisioning and recent emphasis on mating payoffs provide only partial explanations for why men hunt. We have described a model of the sexual division of labor in which men hunt and women gather because of maternal constraints, long learning periods for many foraging activities, and male comparative advantage combined with the goal of providing a diverse multinutrient diet. Furthermore, men's hunting production is not lost through sharing but is biased toward family members and channeled to others strategically via contingent reciprocity, social insurance, "cooperative breeding," and costly display. Other models that emphasize political goals, enhanced group size, and well-being in the context of intergroup competition deserve careful consideration.

Long-term pair-bonds cannot be explained by the signaling model alone because it implies that women should be indifferent to marrying good hunters and men should abandon their wives as their fecundity declines. Men in foraging societies voice concern for spousal and offspring welfare; they engage in daily activities that indicate such concern, especially when spouses are pregnant. Among the Ache, Hiwi and Tsimane, men often take custody of children after maternal death or divorce and provide extensive support. Several scenario-based experiments conducted with Ache and Hadza men with

21. Ache orphans tell detailed stories of the hunger they experienced after their father's death despite the widespread sharing that characterizes Ache forest life.

dependents show that they prefer to reside in groups with good hunters who will help provision their families rather than in groups of poor hunters where status signaling opportunities are high (Wood 2006; Wood and Hill 2000). New physiological data on male-female and male-offspring bonding mechanisms and hormones that promote such bonding (e.g., oxytocin, vasopressin, dopamine, decreased testosterone) may demonstrate that human males were designed by natural selection to increase cooperative sentiment with female partners and to help raise highly dependent offspring (Gray et al. 2004). These mechanisms may set humans apart from other apes and may provide a window into the social structure of our hominin ancestors.

Undoubtedly, spousal conflicts arise because of male mating goals, and these conflicts may modify men's behavioral patterns. Rather than continue to argue over monocausal explanations of men's hunting, new studies should examine how costs and benefits of male mating and parenting investment vary with ecological circumstance, partner status, condition and need of offspring, and availability of substitutable aid. In addition, they should examine how hunting rather than gathering might best meet male goals given the constraints of human social living.

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## Comments

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The question addressed by Gurven and Hill is whether big game hunting is mating or parental effort or a combination of the two. They bring clarity to an extremely one-sided characterization of male work in foraging societies. They show that Hawkes's claim that hunting is mating effort rests on unsure foundations, and they conclude that male economic endeavors, including large game hunting, is largely parenting effort. They present a model of reproductive and parenting decisions from the vantage of bargaining theory that captures much of the realism necessary for modeling marital trade-offs.

A surprising dimension of the signaling hypothesis comes from its claims of generality. O'Connell, one of Hawkes coauthors in the development of the "show-off" theory, makes the following general claim (Bird and O'Connell 2006, 159):

In fact, paternal provisioning is actually not practiced among the best-documented low-latitude foraging populations, including those occupying habitats most similar to the ones in which early humans evolved.

This claim was preceded by Hawkes et al.'s (2001, 705) dismissal of the relevance of Arctic foragers, where men periodically are the sole providers for their families. This nebulous argument about the Environment of Evolutionary Adaptedness (EEA) leads one to ask what is it about the nature of high-latitude environments that makes such foragers irrelevant. African environments were highly unstable and variable during much of late hominid evolution. Even today we find African foragers in desert, savannah, and tropical forest environments. Such claims lead some to suggest that claims about the EEA as it relates to the physical environment are "a patently narrow conceptualization of the hominid past" (Potts 1998, 94). This restriction ignores a large number of foraging societies that may provide comparative tests of the show-off hypothesis. In many foraging societies, local bands disperse into family units for several months a year. Once dispersed, all male economic activity was devoted to providing for his family. Exemplars include the Western Shoshone (Steward 1936, 230–232), the Netsilik (Balikci 1963, 1968), Copper Eskimo (Damas 1972, 26–28), and the G/wi (Silberbauer 1972, 298; 1978, 116). The G/wi are notable because they are African low-latitude foragers.

A potential collective action problem is considered when Gurven and Hill reveal that highly productive hunters produce more than they receive (for the Hiwi, the amount returned is about a third of what is given). In an early version of this paper, they argue that these hunters simply pay a higher premium and that there is room for bargaining. This is a very useful conceptualization, but I would add, however, that paying a higher premium would also make sense if insurance coverage was greater. Productive hunters may have more children; therefore, they need more coverage. This is reasonable in view of the fact that good hunters have higher reproductive success (Kaplan and Hill 1985; Smith 2004; Gurven and von Rueden 2006). It is also clear that part of their payback may be of a different currency that transforms reciprocal altruism into trade. As they note, this trade for high hunting productivity may range from not traveling when a good hunter's family member is ill (Kaplan and Hill 1985) to feeding the family of a good hunter when the hunter is ill (Sugiyama and Chacon 2000) to greater acceptance of begging from the children of good hunters or to enhanced access to mating opportunities (Kaplan and Hill 1985).

Another way to evaluate whether hunting is parental investment or not is to predict that if males do not hunt and distribute their kills, then the amount of food received by their families will be affected. For the Hadza, Marlowe (2006, 85) reports that "Hadza say that people who do not share are bad people and that they will move away from them." Gurven and Hill provide numerous examples of this dynamic. Ache juvenicide suggests that this interpretation may be correct. Children who have lost their fathers have a higher probability of being killed by men who do not want to support children who lack fathers who can reciprocally support their children. Hill and Hurtado (1996, 434) note that "Among the Ache,

child homicide also seems common when unrelated individuals are being coerced into providing resources for a child who does not receive sufficient parental investment (i.e., orphans)." Further on, they also note that children who have secondary fathers are more likely to be spared such a fate. These secondary fathers, through the Ache ideology of partible paternity (Beckerman et al. 1998), are recognized partial generators of children who may have lost a primary father. Presumably, the continued distributions by secondary to other families ensure unbegrudged returns to their partible children.

Finally, a critical lacunae in Hawkes et al.'s presentation of Hadza data is how resources acquired by men are distributed. A presentation by Wood (Wood and Marlowe 2007) shows that 45% of large game taken by a hunter is distributed to his family compared with an average of 18% to other families. The advantage to their own families is even greater for other resources. While successful hunters may not fully control distributions of large game, distributors clearly bias distributions in the successful hunter's direction. This demonstrates that big game hunting is a mixed strategy even for the Hadza.

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Gurven and Hill offer a sophisticated argument in the debate about the functional roles of men's hunting and their implications for the sexual division of labor. Drawing on socio-ecological factors, they combine elements of provisioning and signaling in their model explaining why men hunt. Their argument, which situates men's hunting in the context of a bargaining game between husbands and wives (Becker 1973, 1974), is an important step toward a more comprehensive understanding of the cultural variants as well as the universal features of the sexual division of labor (Marlowe 2000). However, the ethnographic data reviewed here may not allow pinpointed testing of several key issues in the debate surrounding the motivation for male hunting. There is no doubt that anthropological fieldwork provides richly relevant information on this question. However, such data remain correlational in nature, which makes it difficult to disentangle the competing hypotheses concerning signaling versus cooperative pair-bonding with rigor. We suggest that controlled laboratory experiments may help fill in this gap.

As behavioral scientists with an interest in computational algorithms of the human mind (Kameda et al. 2002; McDermott, Folwer, and Smirnov 2008), we would like to discuss a possible experimental design for one of the hypotheses concerning male-offspring bonding mechanisms suggested by Gurven and Hill's argument. Given that our minds are highly attuned to recurrent adaptive problems via evolutionary (Cosmides and Tooby 1994) and/or cultural processes (Boyd and

Richerson 1985), experimental testing of psychological architectures may shed some new light on the debate. We pursue this exercise by briefly examining related literature on hormones first and then sketching the design of a new experiment.

*Endocrinological responses.* Hormones may provide key information on psychological mechanisms related to male-offspring bonding mechanisms. We have substantive evidence that testosterone is associated with increased emphasis on mating as opposed to paternal effort (“challenge hypothesis”; Archer 2006). Most studies used North American samples, but researchers have begun to study non-Western populations (e.g., Gray, Parkin, and Samms-Vaughan 2007). Muller et al. (2009), for example, tested two neighboring Tanzanian groups (Hadza foragers and Datoga pastoralists). These researchers reported that lower testosterone among fathers than non-fathers was evident only for Hadza foragers; no such difference was found for Datoga pastoralists, where strong social norms against men’s direct interaction with infants apply to fathers and nonfathers equally. These patterns may suggest that, as implied by Gurven and Hill’s model, the two subsistence systems, or the local socioecology of each community, may affect husbands’ and wives’ bargaining power differentially, leading to a different equilibrium of paternal care.

*Toward more direct tests of the “hunting (also) for family” hypothesis: a proposal.* Although rich and illuminative, these data remain correlational. To our knowledge, there are three published studies that have tested the challenge hypothesis experimentally (Fleming et al. 2002; Gray, Yang, and Pope 2006; Storey et al. 2000). In these experiments, endocrine measures were taken from fathers and nonfathers twice, before and after they were exposed to infant-related stimuli (e.g., cries). The results were consistent with the challenge hypothesis. Fathers with lower testosterone levels reported higher sympathy in response to the baby’s cries than fathers with higher testosterone levels and nonfathers. Concerned fathers also had higher prolactin levels than the others, a hormone shown to be relevant to paternal care in animal studies (Ziegler, Washabaugh, and Snowdon 2004).

Both the ethnographic and experimental studies were focused on “direct paternal care,” including feeding infants, showing concerns, etc. However, the current debate is on the specific functional roles of men’s hunting—whether it emerges within the context of cooperative ventures between husbands and wives (Isaac 1978) or whether it is better understood as a costly signal to increase the hunter’s mating value or social status (Bird 1999; Hawkes and Bliege Bird 2002). The experiment sketched below may provide a more direct test for the “hunting (also) for family” hypothesis. As in the previous experiments, fathers and nonfathers would be exposed to infant-related stimuli. The “subliminal stimulus” paradigm (Merikle 2000) might be used here, where the infant-related stimuli are displayed for a period shorter than perceptual threshold to minimize demand characteristics. Then, participants would be asked to work on some rather

tedious (cognitive or physical) task whereby monetary incentives are provided contingent on their performance. Our hypotheses are as follows. To the extent that men are equipped with a psychological architecture to facilitate the “hunting (also) for family” function, (a) fathers, even if not fully aware of the real reasons (subliminal stimuli) will generally be more motivated in the task (e.g., longer persistence) than nonfathers, and (b) this tendency will be more pronounced for fathers with lower testosterone and higher prolactin levels. Of course, this experiment does not deal with a real hunting situation, nor would participants necessarily be hunter-gatherers. However, we believe that along with the ethnographic observations, a laboratory experiment such as this will shed some new light on the debate. As illustrated by the prevalence of family pictures in workplaces, male psychology may be finely tuned to various infant-related cues, which serve the “hunting (also) for family” function.

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23 X 08

Understanding how, when, and why the sexual division of labor emerged is one of the most compelling issues in human evolution. Gurven and Hill present a novel conceptual model that tracks the complexity of responsive allocation decisions between pair-bonds. We agree with Gurven and Hill that monocausal explanations are unlikely to explain the persistence and range of hunting options pursued by contemporary hunter-gatherers. Our reading of the signaling theory is that it provides an explanation for why men sometimes pursue dangerous, inefficient, or seemingly wasteful prey. Current versions of signaling theory emphasize the mutual benefits gained by the signaler and receiver (but see Cronk 2005). These benefits are weighted by socioecological contexts that structure the arenas in which signaling may be effective. Hunting costly prey is but one arena in which men can signal underlying qualities for gaining mating opportunities, status, allies, or political leverage (Bliege Bird and Smith 2005). Thus, the hunting arenas for honest signaling are limited and socioecologically context dependent.

For instance, among central African Bofi and Aka hunters, men invest their effort in cooperative net hunts and individualistic hunting techniques. Cooperative net hunts earn low returns and have highly variable success rates. Men can do better if they use individualistic hunting techniques, which earn higher returns and are associated with a higher success rate. High-status men rely on nets more than any other technique, spend less direct time with their children, and share more meat with people outside their kin group than low-status men (Hewlett 1991*b*; Lupo and Schmitt 2004, 2005). Mothers consistently identified these public foraging events

as opportunities to identify potential future sons-in-law for their unmarried daughters. Other men rely largely on individualistic technologies, spend more time with their children, and share less meat with people outside their kin group. Seasonal precipitation limits the use of nets, and even men who are committed net hunters turn to individualistic methods of capture during the dry season. While it might be argued that high-status net hunters indirectly invest in their children by purchasing material items, our observations show that men often use the money derived from selling meat to purchase items that are shared with other men, not their families (cigarettes, alcohol).

A more compelling question concerns when the current patterns of the sexual division of labor emerged. The recognition that current sex-based patterns of task organization may not represent prehistoric hominins is not new. But recent research suggests a more complicated evolutionary trajectory for labor organization than once imagined. Robson's (Robson, van Schaik, and Hawkes 2006; Robson and Wood 2008) analyses of life-history parameters for extant and fossil hominins suggest that the features of modern human life history are derived and did not emerge as an integrated package. Comparisons among different hominin species suggest distinct life histories that differed from one another. The paradox is further complicated by Lower and Middle Pleistocene paleodemographic data showing high levels of mortality for juveniles and the young, with few individuals surviving into old age (Caspari and Lee 2004; Kennedy 2003). Material evidence from Lower and Middle Pleistocene archaeological sites does not show a marked sexual division of labor or subsistence specialization and implies a high degree of overlap between males and females in labor organization (Kuhn and Stiner 2006). The earliest evidence for significant meat consumption and carcass acquisition suggests hominins engaged in high-risk ventures (O'Connell et al. 2002). Direct evidence for hunting does not emerge until after 500,000 years ago, and the focus was on larger-sized and sometimes dangerous animals (Kuhn and Stiner 2006; Schmitt, Churchill, and Hylander 2003). Smaller-sized prey appear as significant components of the diet in Africa after 140,000 years and in Eurasia 40,000–50,000 years ago.

Cumulatively, these data suggest that we need to start conceiving of multiple and mutable configurations for the sexual division of labor among early hominins that may exceed the range of variability displayed by contemporary hunter-gatherers. Because socioecological circumstances influence the payoffs derived from provisioning and signaling, we can no longer view the sexual division of labor as a static phenomenon. How do these payoffs change when early *Homo erectus* populations colonized different parts of the world? How did these payoffs vary for subsequent in-filling populations? It is only within this context that we can hope to understand the different milieus under which big game acquisition emerged and persisted.

Signaling does not explain all human hunting behavior, but

it might explain inexplicably expensive or costly activities. Clearly, there are a variety of relationships between males and females, from complementary arrangements to those that are asymmetrical in effort (e.g., Quinlan and Quinlan 2007). We agree with Gurven and Hill that future research should examine how the costs and benefits of male mating and parenting investment vary with ecological and social circumstances and how signaling enhances these payoffs.

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Gurven and Hill have done an important reevaluation of a large and valuable literature on foraging societies and the place of hunting in the evolution of human pair-bonding. This paper makes an impressive effort to explain not only the division of labor that results in “man the hunter” and “woman the gatherer” but also how this division of labor supports long-term bonds between men and women past the reproductive prime of both sexes. The data are limited to a few well-studied ethnographic hunter-gatherer groups that no longer rely on foraging throughout the year. Nevertheless, the reasoning is sound, and the multiplicity of pathways to long-term pair-bonds lends credibility to their claims. However, while the authors mention that out-of-household exchanges of meat and plant foods generate a cohesive group (men and women preferred to live in groups with good hunters), neither they nor the literature cited looks beyond the individual. Food sharing among same-sex adults is an adaptive strategy that appears equally important to social cohesion as that of family provisioning. Cohesive social groups reduce the selective pressure on high-risk members of a group, such as children without a parent, old men and women, and women without husbands, and they are important to the survival of individuals as well as the group as a whole.

All human social bonds—except perhaps those intense, short-term, chemically induced bonds between mother and neonate and between mating male and female—appear to be based on exchanges of food and services. Perhaps we are looking at this the wrong way. Bonds between child and mother are strengthened and maintained through feeding and physical contact; pair-bonding is established and maintained through exchanges of food, sex, and coresidence; group cohesion is maintained through cooperative hunting and exchanges of meat between hunters, exchanges of staple foods between women, and residential proximity; and last, men's intergroup exchanges of meat, exotic goods, and women established long-term alliances between individuals and groups throughout a region. Cohesion in the group—as a result of exchanges between men, between men and women, and be-

tween women—increases the survival of the group and all its members and reduces the impact of skill-based repertoires like hunting on fitness. A group bound through many male-male and female-female exchanges of food permits the survival of children of the best and poorest hunters. The modest reproductive advantage of the better hunters extends till their death, and there is no evidence that any evolutionary advantage accrues to a third or more distant generation. The emergence of cooperative food acquisition and sharing may be sufficient to explain the generation of long-term bonds on every level of human society—between mother and offspring, mating pairs, kin groups, community members, and even communities.

Food sharing appears to have emerged as groups of men cooperated to hunt packages of meat too large to be hoarded, the semidependency of human childhood extended, and women cooperated in the feeding and parenting of slowly growing, closely spaced children. Mauss (1990) argued that social bonds established and maintained through gifts between individuals created collectivities and hierarchies of collectivities (Mauss 1990, 5):

It is not individuals but collectivities that impose obligations of exchange and contract upon each other. . . . These total services and counter-services are committed to in a somewhat voluntary form by presents or gifts, although in the final analysis they are strictly compulsory, on pain of private or public welfare.

Perhaps the pertinent social fact is the tension between group- and pair-bonds, an economic trade-off between the bonds that bind the group and those that bind mates rather than that between status signaling and family provisioning. When cooperative group activity increases in importance, exchanges between men increase; as the importance of male cooperation and cohesion lessens, as it does when the Ache are out of the forest, provisioning of the family and pair-bonds intensify. The tension between reproductive pairing and group cohesion—a sociopolitical cost/benefit rather than an individual evolutionary benefit—may result in a more comprehensive understanding of the variability we encounter in the examples. Support for the economics of the facts lies in the flow of meat and plant foods—that is, the relative density and direction of exchanges within and between communities—and the effect of changes in flow from those between adult men to those between men and women. Those male bonds are important way beyond status or signaling benefits; the alliances create and maintain the social group. Gifts of food between women generate a second level of cohesion within the group that reinforces long standing (kin) ties and binds women marrying in from other groups. Direct provisioning of offspring by women is undisputed and a fairly convincing rationale for the division of labor. All these forms of exchange ultimately lead to a more stable existence that enhances the reproductive fitness of everyone in the group.

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Gurven and Hill deliver a battering criticism of the view that status and mating benefits alone explain hunting in extant foragers. Their reevaluation of the hard data used to support signaling theory—namely, data on the caloric yield of big game hunting and on its distribution in the group—should be of major impact, but it is surprising how often they also point out ways in which the criticized theory simply fits badly with commonsensical facts. For example, caloric value alone does not measure nutritional impact; a specific desire for meat, due to nutrients difficult to replace, can explain willingness to risk hunting failure. If you control for size of resources, there are no differences in amounts shared by men and women outside the family, and yet no signaling hypothesis is proposed for women's sharing; men get upset when shares are not returned, but why should they, if they share for mating and status benefits? The signaling theory does not explain marriage; if marriage's only function is to curb the dangerous effects of competition for status, men surely would have devised alternatives (e.g., hierarchies) to the self-imposition of obligations to wives and children. The publicly recognized benefit for good hunters is *marrying* more or better wives, which includes the burdens of marriage. Women do not complain when their husbands go hunting, but they should if it leads to status rather than to provisioning. Women should be indifferent to *marrying* good hunters if hunting were all about status, but they are not; men should abandon their wives as their fertility declines, but few do.

These arguments have the demolishing force of common sense but are in tension with the taste for hard data that dominates the debate. And yet there is a sense in which data are hard only against a background of conceptual assumptions that belong in the domain of common sense. Gurven and Hill demand a measure of contingency in sharing that attends to the particular representations of fair exchange and reciprocity governing each society. To me, this demand is plain common sense. Will colleagues in the other camp accept it?

Some of their arguments assume that the debate is also about the proximate/psychological and not only about the evolutionary explanation of hunting. Although evolutionary explanations are normally not concerned with proximate mechanisms, it is often impossible to analyze *human* behavior abstracting fully from the psychological. Norms and similarly complex sociopsychological structures are here the correct proximate stance. Bliege Bird and Bird (2008) make a recent move in this direction. They analyzed Murta foraging data and concluded that in Murta society, big game hunting is the publicly recognized behavioral signature for magnanimity motives. In Murta ideology, these motives are socially required if men are to climb the social hierarchy and obtain the re-

productive benefits of *marrying* more or younger wives. But then, if competition for status surfaces in male magnanimity at the sociopsychological level and in a normative ideology for upholding the group, the signaling hypothesis loses its teeth. Kirsten Hawkes (2008) urged the Birds to dilute magnanimity motives into “tolerated theft.” Why? Tolerated theft strips sharing from all apparent generosity and from socio-normative motivations. However, this way of adjusting claims about motivations to her preferred evolutionary explanation ignores independent evidence to what those motivations are. Claims about motives should also attend to other research programs that have been producing “hard data” on human motivation. Recall here experimental economics and also a sophisticated experimental research program that addressed an analogous debate: the egoism-altruism debate (Batson 1991).

Hard facts aside, some hypotheses are *prima facie* more plausible than others. Gurven and Hill make an intelligent move when they plead for a pluralism of motives: men want to provision their families but they also want status. If we are interested in evolutionary explanations of human motives, a safe move is to assume that natural selection has long tinkered with the human psyche. The results are probably not neat and are analogous to kludges or Rube Goldberg machines. If men evolved paternal investment from an ancestral state similar to present male chimp mating behavior, we are likely to see a mix of status hunger and genuine concern for offspring, even more so if, as Gurven and Hill point out, status reverts often into benefits for offspring. Pluralism of motives also discloses a disregarded possibility: a polymorphism of strategies as the evolutionary outcome. Plausibly, status motivates (predominantly) some men while provisioning drives others. Changes in the data analysis practiced so far may well be required to tap into evidence for polymorphisms.

Proper development of the interaction between the ultimate and the proximate levels of explanation is a challenge for the evolutionary anthropology of hunting, sharing, and marriage. The bargaining model presented by Gurven and Hill could give readers a wrong idea about purely selfish motivations in married couples. Although they warn about this in a footnote, a more explicit picture of the evolution of genuine emotional concern for spouses and children would be welcome.

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## Reply

We summarize our position: signaling may be important in some socioecological contexts but is unnecessary to explain why men hunt. Provisioning alone can often explain why men hunt and women gather, but additional benefits are common because of the nature of human sociality. Aside from direct offspring provisioning, good hunters who share may gain fitness benefits from contingent reciprocity, social insurance pol-

icies, group augmentation, and costly displays. Displays of generosity enhance a hunter’s reputation, which helps family members indirectly and provides alliance and mating benefits for the hunter (fig. 4). A sexual division of labor in which men hunt and women gather describes specialization based on comparative advantage of complementary activities providing a nutrient-rich diet. Spousal interests will not always converge, and one partner may free ride on the household contributions of the other. We agree that moving beyond simple depictions of the sexual division of labor is a priority for future research. We describe future directions, highlighting themes brought up by the reviewers: (a) the need for diverse methodologies, (b) broader implications for male psychology and behavior, (c) complex sharing arrangements and evolutionary mechanisms, and (d) sexual divisions of labor in our evolutionary past.

*Methodological pluralism.* Kameda and McDermott argue that only experiments can reliably show causality. We agree that inferences based on observational ethnographic methods often face problems of self-selection, bias, and endogeneity. Careful research design and statistical controls can reduce these problems in multivariate analyses. Experiments are another solution but should be designed to have external (and if possible, ecological) validity (Gurven and Winking 2008) for relevance outside the laboratory. By necessity, these will be quasi experiments in field settings because often participants will not be random samples but part of an ongoing study. Experiments employing standardized stimuli or exposure in naturalistic settings can help inform causal relationships. Two examples illustrate our point. The Wood experiments described in the target article—where participants presented with standardized scenarios of hunting parties consisting of hunters of varying skill but with a constant number of reproductive-aged women—showed that Ache and Hadza hunters preferred to hunt in bands of good hunters. Their choice is consistent with a desire to eat well rather than to receive high prestige from being the successful hunter (Wood 2006; Wood and Hill 2000). Only Ache hunters without dependent offspring preferred to join a group of poor hunters, where they might have opportunities for “showing off.” McMillan (2001) investigated whether Ache hunters encountering prey call other hunters within earshot to help with pursuit. Helpers increase the probability of success and can increase caloric return rate but can diminish the direct hunting success of the caller. McMillan’s analysis of calls and responses is most consistent with the goal of maximizing food production for the band rather than for individual prestige.

Hames and Kameda and McDermott comment on our choice of study populations. We focused primarily on the Hadza, Ache, !Kung, and Hiwi because they are well-studied hunter-gatherers and were the original groups cited by Hawkes and colleagues to support the hunting-as-signaling view. Ethnographic data from many other foraging groups lend support to our views on sharing and the sexual division of labor. Hames provides several examples. Our emphasis on

foragers comes from the belief that our long evolutionary history of living as hunter-gatherers has shaped our evolved cognition, emotions, psychological motivations, and decision-making abilities. The best way to make inferences about hunter-gatherer behavior and culture is to develop and test models that predict optimal behavior given variable ecological conditions and other parameters under a set of constraints (Winterhalder and Smith 1992). We agree that no single group represents all foragers and that no definitive statements about trade-offs between parenting and mating effort should be made based only on studies of foragers. A goal of behavioral ecology is to understand how variation in relevant parameters interacts with our evolved psychology to influence what people do. Nonforagers are not irrelevant here; they add additional empirical grist to test theoretical ideas about men's parenting and mating behavior.

*Male psychology, behavior, and hormones.* Certain predictions follow from the premise that men's food production efforts are mainly motivated by a concern for familial welfare. First, men should pay attention to opportunities for advancing offspring welfare. In cases where mating and parenting investment are separable, differential treatment by men of biological children and stepchildren of current and former mates permits further evaluation of investment patterns (Anderson et al. 1999; Anderson, Kaplan, and Lancaster 1999; Marlowe 1999). Second, men should focus production efforts in ways complementary to their mates'. The possibilities for complementary labor allocations among foragers have not been fully explored or appreciated. This is particularly problematic because the fitness implications of nutrient complementarity are not well understood in humans. Nevertheless, several examples suggest that spousal complementarity is widespread. Hadza fathers increase their foraging efforts and diversify their production portfolios when their wives have young infants and forage less (Marlowe 2003). Ache and Hiwi women produce less food per day when their spouses produce more (Hurtado et al. 1992). Tsimane fathers focus on childcare during times when mothers are occupied and unavailable (Winking et al. forthcoming).

Another area of investigation mentioned by Kameda and McDermott is the physiological underpinnings of parental sentiment and behavior. This includes analysis of the hormones prolactin and testosterone and the neuropeptides oxytocin and arginine vasopressin. Prolactin promotes weight gain, lactation, anxiety, and inhibition of reproductive function in female mammals. In species showing significant paternal care, such as cotton-top tamarins and common marmosets, a male's prolactin levels increase in sync with his mate's; an expectant father seems physiologically responsive to his mate's pregnancy and imminent birth (Ziegler et al. 2006). A similar response is found among humans but not other nonpaternal species (Storey et al. 2000). Male couvade pregnancy symptoms are also not uncommon in cultures with high levels of partner intimacy and paternal care (Elwood and Mason 1994). Vasopressin and oxytocin help modulate at-

tachment, support, and pair-bonding behavior in male rodents (Heinrichs and Domes 2008). Studies among humans are just now being done. For example, humans with a certain vasopressin receptor subtype (V1aR) associated with monogamous behavior in rodents were happier in their marriages and felt greater affiliation with their partners (Walum et al. 2008).

Testosterone has also been examined as an endocrine modulator of parenting and mating behavior (Muller and Wrangham 2001). Research in several countries shows that married men and new fathers exhibit lower testosterone levels than single men or those without small children (Gray et al. 2002, 2006), and this same result is found among Hadza men (Muller et al. 2009). Men in relationships but with sexual interest in other women have higher testosterone than those who do not report outside sexual interests (McIntyre et al. 2006).

It is important to recognize (cf. Kameda and McDermott) that most of the results from human studies are correlational, complicating inferences about causality (P. Gray, personal communication). Many of these studies only focus on proximity to infants. In natural fertility societies, married men are likely to have small children for several decades, although men sometimes spend little time in direct proximity to infants and children (Hewlett 1991a). Much of our argument about men's familial contributions implies forms of indirect rather than direct childcare. It is not obvious how the two might be related. For example, Lupo and Kiahtipes argue that Aka Pygmy men seek prestige by net hunting, although Aka men have been ranked as the "Best Dads in the World" by Father Direct, a British organization on fatherhood, based on Aka fathers' very high level of direct proximity to children. The only endocrine study that measured paternal attitudes and actual offspring investment showed no relationship between these measures and testosterone, vasopressin, and oxytocin (Gray, Parkin, and Samms-Vaughan 2007). Storey et al. (2000) did show, however, that men with higher prolactin and lower testosterone levels were more reactive to infant distress. Future research should better link endocrine measures and emotions with behavior using a prospective design in different socioecological contexts.

*Sharing and complex social arrangements.* We agree with Rosas that evolutionary explanations assume functional design and evolved psychological motivation. Ethnographic observations and experimental evidence are more consistent with a psychology of contingent reciprocity and group cooperation than with phenotypic signaling. Sharing patterns among hunter-gatherers appear to imply more than just the evolutionary models of kin selection, reciprocal altruism, and costly signaling (Gurven 2004). Even when contingent reciprocity has been confirmed, good hunters consistently give away more than they receive, and family size or "need" is an important determinant of food transfers (e.g., Gurven 2004; Allen-Arave, Gurven, and Hill 2008). Similarly, small groups of interdependent foragers generally share meat more indiscriminately than those from larger groups of more indepen-

dent foragers. The full suite of possible evolutionary explanations for such highly cooperative patterns has barely been explored. We and Hames mention the health insurance premiums good hunters might pay by extensive sharing to help themselves and their families during periods of sickness and injury. Investing in a reputation for generosity by sharing may be important among foragers with frequent opportunities for cooperation and where reliable and trustworthy partners are in short supply (Gurven et al. 2000a; Panchanathan and Boyd 2003; Smith and Bliege Bird 2005). Aspects of cooperative breeding and between-group competition may also be critical (Bowles 2006). A variety of social norms and sharing rules (e.g., favoring hunt participants, in-laws, pregnant women, coresident non-kin) may spread by cultural group selection (Gintis et al. 2005). Interdependent groups are highly cooperative on a daily basis, and we hypothesize that contingency in these groups is usually based on labor contributions rather than direct tit for tat in food currencies (Gurven, Hill, and Kaplan 2002; Hill 2002). These and other new evolutionary treatments may help bridge the gap between common ethnographic anecdotes of “generalized reciprocity,” as suggested by Ragier, and the standard models of evolutionary biology.

*Sexual division of labor in hominid evolution.* Lupo and Kiahtipes raise questions about the sexual division of labor throughout human evolutionary history. Our discussion of why men hunt assumes a humanlike foraging niche in which peak production is delayed and juveniles are low producers. We recognize that the ability to make inferences requires knowledge about the reliance on hunting, the timing of growth and development, and the dependency of offspring, as revealed by the absence or presence of distinct life-history traits (e.g., childhood, adolescence). But knowledge about hominin foraging patterns is not as clear as Lupo and Kiahtipes describe. For example, recent papers reanalyzing tooth and percussion markings on bone assemblages from Olduvai Gorge highlight methodological difficulties (Domínguez-Rodrigo and Barba 2006, 2007); these authors conclude that early hominids actively hunted and that the “passive scavenging hypothesis is clearly rejected by careful taphonomic analysis of Plio-Pleistocene sites” (189). The portrait of hominid life history is also far from resolved. Data on brain growth and tooth eruption patterns in *Homo erectus* are still somewhat contradictory, but Neanderthals show consistent evidence of a slow, humanlike life history (Ponce de León et al. 2008) despite the fact that they may not show marked economic specialization by sex (Kuhn and Stiner 2006). For these reasons, we made no claims about the timing of the typical sexual division of labor. Definitive statements about the timing of a gendered division of labor await further investigation. Certainly we agree with Lupo and Kiahtipes that the sexual division of labor is not now, nor was it ever, static. Examples of men gathering and women hunting small game in different societies illustrate the flexibility of economic decision-making among foragers.

Human divisions of labor must be considered in a larger evolutionary context. Divergent economic strategies, specializations, and complementarities are recurring themes throughout more recent human history: why did humans ever domesticate animals? An energy-maximizing forager would never pay the high costs of producing meat calories by feeding animals more plant calories than can ever be recovered. Those meat calories, however, consist of proteins, lipids, and micronutrients that are highly valued because of their biological impact. Similarly, honeybees forage for pollen rather than nectar, and primates often forage for insects rather than fruits. No one has ever argued that animal husbandry is a costly signal or a form of mating effort. In groups that practice slash-and-burn horticulture, men usually clear the trees and the brush, whereas women are involved in planting, weeding, and harvesting. In tropical populations of southeast Asia and New Guinea, men cut palm trees and split them before women process the sago palm starch. No one has argued that tree cutting is an honest signal or worthy of prestige. This arrangement is another example of an efficient division of labor that takes comparative advantage into account. Why men hunt and women gather may be no different.

—Michael Gurven and Kim Hill

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