

**Hunting as subsistence *and* mating effort?
A re-evaluation of “Man the Hunter”, the sexual division of
labor and the evolution of the nuclear family**

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Abstract

The role of men in hunter-gatherer societies has been subject to vigorous debate over the past fifteen 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 an inefficient means of obtaining reliable calories; 2) hunted game is a public good and shared widely to others when there is an audience, and without expectation of future reciprocation. If hunters lack the ability to direct food shares, then the ubiquitous observations of male hunting and universal pair bonding cannot be explained from a perspective that emphasizes provisioning and a division of labor. Here we show, however, that there is little direct empirical support for the assumptions of the signaling hypothesis. The ethnographic record depicts a more complex relationship between food sharing patterns, subsistence strategies and the sexual division of labor than has been suggested by recent treatments. We then describe a framework that incorporates trade-offs between mating and subsistence strategies in an economic bargaining context that can help improve our understanding of men’s and women’s roles in hunter-gatherer societies.

Introduction

The traditional perspective of the evolution of the nuclear family is based on a division of labor where men hunt wild animals and women gather plant foods (Lovejoy 1981). The pair bond between men and women is viewed as a cooperative venture geared towards the joint provisioning and care of highly dependent offspring, where women trade paternity certainty for long-term provisioning by men (Washburn and Lancaster 1968, Isaac 1978, Lancaster 1978, Lovejoy 1981, Lancaster and Lancaster 1983). According to this view, “family organization may be attributed to the hunting way of life” (Washburn and Lancaster 1968: 295), based on the notion that “when 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” (ibid: 301). The heyday of the “Man the Hunter” view saw “hunting [as] a way of life, and the success of this adaptation has dominated the course of human evolution for hundreds of thousands of years...our intellect, interests, emotions, and basic social life—all are evolutionary products of the success of the hunting adaptation” (ibid: 293). This hunting-based model for the evolution of the nuclear family and a cooperative sexual division of labor has dominated much of anthropological thinking over the past forty years. Even the occasional protest that highlights the importance of women in subsistence tasks (e.g. *Woman the Gatherer* - Dahlberg 1981), while diminishing the traditional emphasis on hunting, does not deny the central role of cooperative unions among men and women.

Recent proposals concerning the sexual division of labor have painted a different portrait of the hunter-gatherer family and the reasons for its existence. While the ubiquity of men’s hunting among foraging peoples is not contested, the benefits men receive, and presumably the motivations for engaging in hunting activities have been the subject of a lively debate. The

“show-off” hypothesis of Hawkes (Hawkes 1991, Hawkes 1990, Hawkes 1993) initially proposed that men hunt because of the social attention and mating benefits that come from providing game resources that are widely shared. This hypothesis was reformulated using costly signaling theory (Zahavi and Zahavi 1997, Bliege Bird, Smith, and Bird 2001), and hereafter referred to as the signaling model, to suggest that men’s subsistence behavior is designed to provide an honest signal of underlying genotypic or phenotypic quality by targeting large game that are difficult to acquire. This signaling is particularly effective because the transfer of shares of large prey is believed to be outside the control of the hunter and all consumers pay careful attention to men’s hunting results in order to obtain shares for themselves (see Bird 1999, Hawkes and Bliege Bird 2002). Because hunting is viewed as a form of mating effort or status competition, rather than familial provisioning, pair bonds and marriage have been reinterpreted as publicly recognized property rights designed to reduce mating competition among men, rather than as cooperative unions designed to reap gains from the joint production of offspring (Blurton Jones, Hawkes, and O’Connell 1999, Hawkes 2004). The proponents of the signaling model suggest that if men were primarily concerned with familial provisioning their subsistence patterns would mirror those of women, and also that the sexual division of labor will be most pronounced wherever mating yields highest payoffs for men (Bird 1999:72). 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”. Primatologists have considered similar proposals emphasizing male coercion and mate-guarding, rather than provisioning, in considerations of the evolution of pair bonds and monogamous mating systems (Mesnick 1997, van Schaik and Dunbar 1990, van Schaik and Paul 1996). The increasing importance of conflict

over levels of offspring investment among parents has been included in a more general framework of family dynamics in evolutionary biology (Parker, Royle, and Hartley 2002).

These 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 primarily by increased access to resources (Trivers 1972). In contrast to the default case of polygyny among most mammals, human pair bonds have been typically compared to those found among many bird species that generally exhibit high levels of biparental care and high levels of monogamy. However, recent DNA fingerprinting has shown that many species of so-called monogamous birds do show significant extra-pair copulation and that up to 47% of broods (as in the red-winged blackbird) are sometimes 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).

The extent to which men's food production and distribution strategies serve to provision families or display status has enormous implications on our understanding of the evolution of long-term pair bonds (i.e. marriage) and the extent to which the nuclear family is best characterized as a cooperative or competitive enterprise. Whether men are an important source of calories for subsidizing women's reproduction and child growth within the family also impacts our understanding of the evolution of fundamental human life history traits such as delayed childhood, long post-menopausal lifespans and large brains (Hawkes et al. 1998, Kaplan et al. 2000, Tooby and DeVore 1987).

The first part of this paper assesses the empirical and theoretical basis for four critical assumptions of the mating effort model. These include: 1) men often forage for large package

size items even when alternative foraging strategies would yield a higher long term average food value; 2) food acquisition strategies that lead to high daily variance in production cannot effectively provision offspring or be primarily designed to increase offspring fitness; 3) food transfers by males to other individuals are not paid back in food at a later time, nor are they paid back in other currencies which might directly affect offspring welfare; 4) women are not constrained from engaging in male activities (e.g. hunting) if they desired, but rather prefer to engage in other activities because of the lower reliability and productivity of hunting compared with alternative provisioning options.

The second part of the paper attempts to extend the original trade-off framework for understanding men's and women's foraging and reproductive decisions by incorporating insights from bargaining theory in economics. This perspective recognizes potential for cooperation due to shared fitness interests of men and women and for conflict due to changing conditions and disparities in bargaining power, where one party may benefit at the expense of the other. While Washburn's and Lovejoy's original depiction of the nuclear family was overly simplistic, and perhaps erroneous in its assumptions and evidence, we see no reason to abandon the notion of a complementary and advantageous sexual division of labor. Using our modified framework, under-provisioning, defections and partner desertions are also possible outcomes.

Part I. Assessing empirical evidence for assumptions of Mating Effort Model

1.1 Mean productivity of hunting

Do men opt for food production activities that provide lower mean nutrient return rates but higher variance than those obtained by women in the same society? The empirical evidence

from foraging societies is weak but suggests that among at least three groups typical male activities provide both higher average energy returns and higher nutrient value than typical female activities. In other foraging and tribal agricultural societies men's activities may provide a lower mean rate of energy gain but nonetheless high nutrient value per unit time.

Studies in only three modern foraging populations provide hourly return rates for men's and women's foraging in groups nutritionally dependent on wild foods. These groups have therefore played an important role in debates about foraging strategies. The Ache of Paraguay formed the first critical test case used by Hawkes in her original article on male show-offs (Hawkes 1991) and so we reconsider them here. An early report that Ache men could gain energy at a higher rate by foraging for palm products rather than by hunting (Hill et al. 1987) suggested that men hunt because meat is nutritionally more valuable. However, that analysis was incorrect due to laboratory error in assessing the edible portion of palm fiber and failure to measure the time necessary to find patches with good palms that might contain starch as well as the fraction of all cut palm that have extractable fiber (only 1 in 35 encountered palms has exploitable starch). Ache men gain approximately 1,300 calories per hour by hunting and extracting honey (*ibid.*). New data now show that male or female groups foraging only on palm products (starch and hearts) would obtain between 850-1,200 calories per hour (mean 1,050 cal/hr), not counting time spent in camp processing the palm products. With in-camp processing time the return rate from palm products drops to about 870 calories per hour on average (all data from Burger et al 2006). Thus, Ache hunting produces substantially more calories per unit time than searching for, exploiting and processing palm fiber, the main subsistence alternative to hunting.

The Hadza of Tanzania is another hunter-gatherer population that has been cited to provide support for the signaling view of hunting. It has been argued that Hadza hunters mainly focus on large game but could gain more food by hunting small game or by gathering (Hawkes, O'Connell, and Blurton Jones 1991, Hawkes, O'Connell, and Blurton Jones 2001). However, the published data contradict that claim. Hadza men acquired about 1 kg meat/hr (~1,500 calories per hour) hunting large game and only 0.25 to 0.78 kg meat/day (~375-1,170 cal/hr) hunting small game or trapping (ibid). Hadza women obtained only about 900 calories per hour foraging on either roots or berries in the wet and dry seasons (Hawkes, O'Connell, and Blurton Jones 1989). It is now evident that these estimates of women's gathering efficiency are too high because new laboratory analyses examining the nutritional composition of edible tuber portions show that the caloric density for typical plant foods used by the Hadza are much lower than previously estimated (Schoeninger et al. 2001: Table 2). Thus, Hadza men by hunting large game acquired energy at least as twice the rate as did Hadza women by gathering and close to ten times the rate that they could have achieved by focusing only on small game. Nevertheless, men diversify their production portfolio by opportunistically hunting small game when deemed worthwhile and by collecting non-meat foods such as honey, in addition to large game (Marlowe 2004b).

The third foraging population often cited in the hunting debate is the Hiwi of Venezuela. Hiwi data clearly show that hunting is more productive than gathering (Hurtado and Hill 1990). In the late wet season, when women's foraging returns are highest, Hiwi men acquired 2,700 calories per hour hunting. Pregnant and nursing women obtained 1,500 calories per hour and post-reproductive or non-nursing women obtained 1,300 calories per hour (ibid: Tables 6 and 8).

In the other three seasons of the year the sex differences were even larger and Hiwi males obtained almost twice as many calories per hour by hunting as females did from gathering.

The above comparisons, while revealing, tell only part of the story about nutritional gains from hunting because the return rates above were expressed only in terms of caloric energy. The macronutrients from hunted game are nutritionally more valuable than the carbohydrate starch obtained from palms, roots or fruits. Lipids and proteins derive primarily from meat, while much of the energy from plant products consists of carbohydrates and micro-nutrients. Several independent lines of evidence suggest that meat is more highly valued than plant products under a wide range of conditions. Nutritionally, 1 gram of carbohydrate and protein each contain 4 calories, while a gram of fat contains 9 calories. On Ache reservations meat sells for about 3 Guaranies per calorie and rice for about 0.5 Guaranies per calorie, suggesting that meat calories are worth 6 times as much as carbohydrate. Similar ratios are found elsewhere (Hill 1988). These prices should roughly reflect the relative utility of each food to a consumer relative to its supply. Additionally, protein-lipid resources and additional animal source micronutrients are likely to be more nutritionally valuable than carbohydrate in most human societies (see section 2.1). We suggest that 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.

1.2 Risk-prone hunters?

Are high variance food production strategies mutually exclusive with provisioning of offspring? Hunting is usually characterized by significant day to day variation in returns, with even good hunters often returning to camp empty-handed. One extreme may be big game hunters

like the Hadza, where any particular hunter is likely to make a large game kill only 4% of the time (Hawkes, O'Connell, and Blurton Jones 1991). Other societies that focus on very large game, such as those dependent on whaling, also experience tremendous daily variation in meat production (Alvard and Nolin 2002). The Ache and Hiwi, on the other hand, target smaller game and make kills 35% and 60% of the time, respectively. There is little doubt that under most circumstances hunting returns are less predictable than those from gathering activities. However, many economic activities that yield variable returns are nonetheless viable ways of providing income (e.g. selling real estate where commission from a sale often comes after long intervals without a sale). In modern societies where “kills” are made infrequently, there are economic mechanisms to ameliorate income variance. Individuals have found many ways to adapt to such situations in order that the high variance in production does not result in high daily consumption variance.

In foraging societies the primary cultural mechanisms for reducing daily variance in consumption are food sharing, storage and foraging specialization. We believe that these are common and have allowed many foragers in hominin history to survive on highly variable food sources. Indeed, without sharing, no large game hunting strategy ever would have been viable for our hominin ancestors. For this reason, it is not surprising that sharing breadth (number of families that receive a share) and depth (percentage of food given away) have both been shown to be greater for resources characterized by higher variance in acquisition (Kaplan and Hill 1985, Hames 1990, Gurven et al. 2001). Anecdotally, this is the case for many other foragers as well (see Gurven 2004).

Although on average hunting is a more risky method of food acquisition than gathering, it is important to recognize that considerable (although predictable) variation exists in acquisition

of plant products. Major plant resources are often highly seasonal and foragers may experience long periods when no edible plant foods are available. Among the Hiwi, for example, the primary carbohydrate staple, roots, is only available for about 4-5 months during the year, after the floods recede from the savanna and before the ground becomes too hard to dig and above ground plant parts wither and are no longer visible. Because metal digging tools are significantly more efficient than traditional wooden ones, it is likely that the productive carbohydrate season was shorter prior to the introduction of metal tools (Hurtado and Hill 1989). Similar and often more extreme seasonal plant shortages characterize many foraging societies in high latitude locations (e.g. Balikci 1970). Because of the not uncommon seasonal shortages in carbohydrate-rich plant foods, there was a debate in anthropology fifteen years ago concerned whether tropical foragers could ever have lived without engaging in trading relationships with farmers or by cultivating swiddens (Headland and Bailey 1991, Stearman 1991). Ironically, during seasonal plant shortages most foragers probably depend mainly on game animals despite the daily variation in their acquisition.

It is also important to note that many well-studied hunter-gatherer groups are primarily small game hunters, as opposed to large game hunters like the Hadza. As mentioned above, even Hadza hunters, who have been described as specialists of large game, hunt small game. In fact, they almost always pursue small game that they encounter on hunts (Marlowe, personal communication). While the faunal remains of large game in archaeological assemblages of early *Homo* are open to interpretations of hunting or scavenging (e.g. Binford 1981, Blumenshine, Cavallo, and Capaldo 1994), the small game component of those assemblages is likely to have been hunted. There is evidence that small game hunting has been an important component of human diets for at least 200,000 years (Stiner 2002). The importance of small game hunting for

provisioning family members cannot be understated. Because the pursuit of small game has a much higher success rate than the pursuit of large game, reliance on small game is a more predictable subsistence strategy. Furthermore, in all documented hunter-gatherer societies, shares from small game are preferentially consumed within the family. Thus, small game hunting is likely to be an important strategy for provisioning family members in many hunter-gatherer societies.

Bliege Bird et al. (2001) present the best data available to date suggesting that among the Meriam of the Torres Strait island of Mer, men opt for high variance but lower average return foraging when faced with the same alternatives as women. They also show that the sex difference is not explained by macronutrient composition of the acquired foods. This is an important finding and suggests that more research needs to be done in order to determine under what conditions the sexes might choose different means of acquiring food that are sub-optimal for family provisioning.¹

1.3 Sharing and reciprocity

The main reason that high variance hunting is argued to be a poor family provisioning strategy is because it is believed that food transfers (sharing) associated with male food production are not paid back at a later date (Hawkes 1993, Blurton Jones et al. 2000, Hawkes and Bliege Bird 2002, Bird 1999, Bliege Bird and Bird 1997). Food that is shared to others is also viewed as lost because men supposedly have little to no control over the distribution of their production. Men's food production therefore must be discounted such that only the portion that remains in the family contributes to family provisioning. But, an extensive recent review concludes that there is little support for the notions that acquirers have no influence over

resource distribution, and that food is not conditionally shared (Gurven 2004). Instead, every food sharing study to date shows some type of bias in categories of individuals that receive shares, or the size of share given to individuals, and their relationship to the giver. Kin, neighbors and cooperative partners are three particular categories of individuals who almost always receive greater quantities of food in quantitative sharing studies. These results suggest at least partial control over distribution by acquirers, even when distributions are performed by individuals other than the hunters. Most importantly, all food sharing studies that we are aware of, except for the Ache during forest treks, show that the nuclear family of the hunter obtains considerably more from his kill than any other family. The assertion that game species are undefendable, and hence public goods, is not supported by data from quantitative studies. It is also inconsistent with the observation that the same resources are shared differently across societies or in different contexts (Ache forest vs. reservation - Gurven, Hill, and Kaplan 2002, e.g. Huaroni - Franzen and Eaves n.d.), which suggests that game can be defended if necessary.

A growing body of data also shows that food shared with others is indeed often paid back to male producers or their families. This type of conditional sharing has been referred to as contingency (Hill and Kaplan 1993, Gurven 2004, Gurven 2006). Receipt of food that is contingent on having given food is a common casual observation in the ethnographic literature on foragers (e.g. Marshall 1976, Holmberg 1941). Even non-human primates have been observed to engage in contingent reciprocal food exchange (de Waal 1997, Hauser et al. 2003). Studies among Hiwi foragers show that the amount of meat given by any nuclear family to another nuclear family is the single strongest predictor of how much meat will be returned by that other family over a four-month sample period (Gurven et al. 2000b). The statistical association between amount shared and amount received suggests that on average 35-45% of game and fish

shared by men over a six month sample period was returned by the recipient nuclear family because it was shared (i.e. when other factors like kinship are controlled). We may conclude that much higher percentage is returned by consumers of male foraging products if we take into account that kinship and residential proximity also have independent positive effects on amount shared (ibid).

The amount of meat received by a nuclear family during a sample period was also significantly associated with the amount of food given to potential donor families among the Pilaga (Henry 1951, our analysis), the Yanomamo (Hames 2000), Dolgan and Nganasan (Ziker and Schnegg 2005). Even among the Ache, meat given to a nuclear family is highly contingent on the amount received by that family at current reservation settlements, but not on forest treks (Gurven, Hill, and Kaplan 2002). In both contexts, forest and reservation, all non-meat foods show the pattern that nuclear families give more to those families from whom they receive more, even when other factors that also produce these correlations (kinship, proximity, visibility, family size) are controlled. Furthermore, close kin on Ache reservations share much more with kin who provide large amounts of food to them, than with kin who provide little food (Gurven et al. 2001, Allen-Arave, Gurven, and Hill in press). In all societies we are aware of in which contingent food sharing has been tested statistically, it is found! Only Ache forest meat sharing shows no relationship between amounts given and amounts received by nuclear family pairs (Kaplan and Hill 1985, Gurven, Hill, and Kaplan 2002). However, as has been argued elsewhere, even meat on Ache forest treks may be shared in a ‘contingent’ fashion (Gurven, Hill, and Kaplan 2002, Hill 2002). Ache informants in interviews stated that a man must hunt and attempt to kill something in order for others to willingly give him a share in the band’s daily meat production. Teenage boys are warned that if they do not attempt to hunt they will not be fed.

Men who fail to hunt, or fail to help in cooperative hunts are generally not invited to participate on future forest treks. If these statements correctly illustrate the Ache meat sharing rule, then meat sharing is contingent on expected future production and sharing, even when all meat is pooled. Even anthropologists, who provide no meat but share in the kill, can feel the pressure of the contingency sharing system and offer gifts and other services to groups such as the Ache and Tsimane in exchange for accompanying them on forest treks.

The Hadza meat sharing pattern has been described as one in which no contingent sharing is possible because individuals go out to a killed prey and take a portion for themselves. However, Hawkes et al.'s (2001: Table 3) recent data show that a hunter's family does get a larger portion of his kill (29.9 kg per kill) on average than do other families (13.5 kg per kill) for the largest animals. Other biases in meat distribution (to close kin, nearest neighbors, sharing partners, etc.) have not been examined yet among the Hadza, but Marlowe (1999) does show that men who live with biological children rather than with stepchildren produce more food. Presumably this means that Hadza men acquire food partially to feed their families, and have some control over food redistribution. But what about the large amount of Hadza meat transferred to others? Hawkes et al. (2001) report that there is no relationship between the amount of meat a hunter provides to others and the amount he receives in return from all others. This is not a valid test of contingency but rather shows that some men pay a higher premium for their 'insurance coverage' than do other men. Perhaps the right of a man or his family to 'take a portion of the kill' is dependent on that man participating in large game hunting (and sharing the results), as we suggest it is among the Ache. If so, obtaining a share of meat among the Hadza may also be contingent on sharing meat. Nevertheless, a reanalysis of the Hadza data does indeed show a significant positive relationship for contingency among pairs of hunters (Gurven

2004). 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).

Additional contradictory evidence for the mating effort view of food sharing comes from an examination of women's sharing patterns, a frequent feature of hunter-gatherer social and economic life that is rarely examined. It has been 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 false for the Ache, Hiwi and possibly Hadza as well, although information on Hadza women's sharing has not been documented. Instead women generally bring back packages of palm fiber or roots larger than their family can consume and widely share these packages with individuals outside their nuclear family. Indeed, Ache and Hiwi women share all foraged plant foods extensively, giving away about 55% of all collected food in both cases (Kaplan and Hill 1985, Gurven et al. 2000b). Ache women at reservation settlements give away an even higher fraction of their collected resources (76%). Importantly, as package size increases, Hiwi women keep a smaller percentage for their nuclear family (about 40% kept for non-hunted resource packages over 15 kg). The same is true for Ache women in the forest (women keep only 20% of fruit, 25% of larva, 25% of palm heart and 30% of palm starch packages over 2,000 calories). This suggests that men's sharing patterns are not unique and it suggests a payoff for food sharing that is not limited to mating opportunities.

In all these studies men share more than women on average because they more often bring in large packages of food. Multivariate analyses, among the Hiwi (Gurven et al. 2000b), for the Ache at reservation settlements (Gurven et al. 2001) or for the Ache on forest treks (Gurven, Hill, and Kaplan 2002) show no sex differences in amounts given to members of other

families for resources obtained by both men and women after controlling for resource package size. Both men and women bring in large packages that are widely shared and small packages that are not so widely shared.

This is an important point that we elaborate further. Plant foods come in small increments and any woman could stop working whenever she had enough food for her family. Ache women, for example, extract palm fiber starch one handful at a time, yet generally produce between 3,000-6,000 calories in each extraction session (Burger et al 2006). Anecdotal reports suggest that the same is true for Hadza root and berry collection and that Hadza women share food to 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 something from the food they transfer to others. Theory suggests that those gains cannot be an increased number of copulation partners. Instead, the gains from food sharing must be in some form that impacts on women's or their offspring's well being. If women share food according to patterns identical to those of men, and if the production of large packages and subsequent sharing by women is paid back in a form useful for parental investment, a parsimonious conclusion is that the same may be true for men.

In addition to the empirical evidence on contingency, there are abundant ethnographic reports of complaints concerning failures to meet sharing obligations or expectations, particularly in the context of pairwise exchange (see Gurven 2004). Part of demand sharing as described ethnographically may reflect obligations based on expectations of repayment. If hunter work effort is motivated by status signaling and concomitant mating benefits, then men would not be so concerned with receiving conditional shares from those previous recipients. They should not complain or get upset when shares are not returned. Our experience and 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. Fehr and Gächter 2002, Henrich et al. 2006). While the desire to retaliate or express discontent may be stronger for direct defections on ego, there is increasing evidence that some percentage of people are willing to punish those who defect on others as well (e.g. strong reciprocators - Henrich et al. 2004).

Empirical estimates of contingency show that producers receive back on average at least a third of what they give away to others outside their family. We have argued elsewhere that these estimates may be biased by measurement and by sampling error, and that the estimates are only imperfect windows into a complicated set of cooperative exchange relations among individuals (Gurven 2006). There are good reasons for suspecting that cooperation is unlikely to result in complete exchange balance. Each of two parties may have minimal thresholds for acceptable exchange rates (or time delays for return resources). This is based on the value to each of a food “insurance policy” that guarantees food availability from reciprocators on days when they fail to obtain anything. An acceptable “bargain” is any that results in higher utility for each party involved than the alternative of no bargain (Ståhl 1972, Sosis, Feldstein, and Hill 1997). In understanding the exchange of individual *A*’s present production for individual *B*’s future production, there will be a set of potential exchanges where both *A* and *B* can benefit, although they may not benefit equally. This region is usually referred to as a “bargaining zone” and is illustrated as the oval region in the classic Edgeworth box diagram (Figure 1). Concave ‘indifference’ curves radiating from the lower left and upper right corners represent the utility *A* and *B* derive from consuming some combination of *A*’s (or *B*’s) present and *B*’s (or *A*’s) future production. These are called indifference curves because decision makers receive equal benefits

from any combination of current and future production and thus are “indifferent” to the combinations that define the curve. Where the final bargain is struck should be influenced by the relative bargaining power of the two parties, which reflects the expected cost from giving and benefit from receiving a specific quantity of food. These costs and benefits could vary with the amount of existing wealth, influence, production ability, status, or number of dependent offspring (see Boyd 1990 for a similar argument about the viability of unequal exchange). We develop and discuss these ideas with respect to household production in Part II.

[INSERT FIGURE 1 HERE]

1.4 Why don't women hunt?

According to the signaling model of the sexual division of labor, women do not engage in male economic activities only because those activities provide low and unpredictable payoffs. We have already shown that male activities give higher returns than female activities in several foraging societies. In each case, men hunt and women gather. The case of the Agta of the Phillipines is often cited as evidence that women can hunt if they choose and can be as proficient as men despite any encumbrances due to childcare constraints. In fact women in many foraging groups hunt regularly, including both Ache and Hiwi. However, women rarely make kills. They instead engage in activities that help men to hunt successfully. Agta women are notable because they hunt with bow and arrows and kill the same prey types that men hunt. We believe that the Agta data are important because they indicate conditions under which women may kill prey rather than indicating that women experience no constraints that limit hunting. Less than 100 Agta women claimed to hunt at some time in their lives from a population of about 9,000 Agta on the Island of Luzon (P.B. Griffin and T. Headland, personal communication). Most Agta in the late 20th century had never heard of women hunters. Time and production data exist for a

sample of only 6 women hunters (Goodman et al. 1985). Available data suggest that several patterns were relevant to Agta women's hunting during the 1970s-80s: 1) The wild carbohydrate resources in the Agta area provided extremely low returns and were rarely encountered or exploited; 2) Meat was often traded for carbohydrate and other useful items at a very favorable rate; 3) Agta fertility was low, and the ratios of dependents to adults were low, leading to high availability of childcare helpers; 4) Many of the women who hunted most actively were sterile or post-reproductive; 5) Virtually all women's kills resulted from hunting with a team of dogs that generally immobilized prey before it was killed; 6) Women's hunting always took place less than 5 km from camp and on short forays that allowed rapid return to camp (Estioko-Griffin 1985 , Goodman et al. 1985 , Estioko-Griffin 1986). We believe that the first three points also partially explain why African Pygmy women commonly participate in hunting activities. The fact that dogs immobilize Agta prey may explain why they make kills whereas Pygmy women, and Hiwi and Ache women rarely do. Unfortunately no study of Agta women hunters examined whether active hunting during a sample period was related to reproductive parameters during that sample period. But, anecdotes suggest that women hunted less frequently or not at all when pregnant or lactating (Estokio-Griffin 1986:42).

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 thirty years of fieldwork with the Ache KH has seen women actively attempting to kill prey a couple dozen times (only once with bow and

arrow) and heard stories of two women who hunted regularly prior to 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.

Hurtado et al. (1992) proposed that women in foraging societies generally do not hunt because hunting is often an activity incompatible with random interruptions from childcare demands (see also Mukhopadhyay and Higgins 1988). They do not propose that women could not hunt because of strength or other physical constraints such as endurance or spatial abilities. Keeping their offspring alive is the highest priority for women in foraging societies, and this priority is incompatible with effective hunting in most ecologies. Nursing women behave accordingly, by adjusting their gathering return rates depending on the age of the youngest child with them at the food patch. As the age of the infant increases, collection rates increase significantly (*ibid*).

Mothers obligatorily care for infants because lactation on demand takes place frequently throughout the day. If women were to interrupt hunting pursuits to meet immediate childcare demands they would often lose prey. One cannot choose the moment that an active pursuit of mobile prey will begin. If women did not interrupt their hunting pursuits when their infants insisted, their infants would likely suffer. Infants cry and fuss many times a day for good reasons. Failure to react to those distress calls would probably lead to lowered viability. The situation is very different for sessile collected resources whose pursuit can be easily interrupted at any time.

We also believe that hunting per se is dangerous to infants because of long distances traveled under arduous conditions, and the dangers inherent in occasional rapid pursuits. Not surprisingly males experience a higher accident death rate than females among Ache foragers

(Hill and Hurtado 1996) and higher death rate from animal attacks and snakebite among Tsimane men (Gurven, Kaplan, and Zelada Supa 2007). If a mother is killed or severely injured the consequences to the infant are more detrimental than a loss of the father (Hill and Hurtado 1996, Sear and Mace n.d.). Thus, females may be more averse to risk of injury than are males.

Finally, we believe that successful hunting requires at least 15-20 years of experience to obtain maximum return rates (Kaplan et al. 2000, Walker et al. 2002, Gurven, Kaplan, and Gutierrez 2006). Indeed the steepest gains in hunting return rate for males take place exactly during the years when women have highest fertility and are constrained from hunting and other energetically taxing and risky activities. A long learning curve to reach proficiency may explain why older post reproductive women, otherwise free from most childcare constraints, do not begin to hunt in most societies.

Part II: Cooperative pair bonds revisited: a bargaining perspective

2.1 Why the sexual division of labor?

We attempt here to build a conceptual framework for understanding male and female roles in a division of labor that incorporates private and shared fitness interests across the life course. We borrow from neoclassical economic models of marriage markets and household time and resource allocation, including Becker (1973, 1974), Manser and Brown (1980), McElroy and Horney (1981) and Lundberg and Pollak (1994). In these models, rational individuals gain more utility as a joint economic unit than from remaining single; utility derives from a combination of household (including offspring) and market production. An evolutionary analogy would posit that men and women engage in pair bonds (i.e. marriage) to achieve *fitness* benefits through the

joint production of offspring, and that joint production may produce an economy of scale such that the production of the pair is greater than the summed production of individuals working by themselves. In describing the framework, we emphasize four critical aspects of hunter-gatherer socioecology that lead us to expect the observed sexual division of labor among foragers: 1) high dependency of individual offspring over a long time period that results in compound dependency of multiple offspring; 2) an adequate diet requires macro-nutrients that are typically found in mutually exclusive types of foods; 3) delayed productivity for efficient foraging due to time-dependent learning in subsistence activities; 4) sex-differentiated comparative advantage in tasks. We believe that these conditions are common to all foraging groups and that this is the reason that men alone hunt in 166 of 179 hunter-gatherer societies examined, both men and women hunt in 13 societies and in no societies do women alone hunt (whereas women are the main gatherers in two-thirds of these societies) (Ember 1978).

In order to understand the sexual division of labor we must first consider the costs of producing the joint product, i.e. offspring. The average hunter-gatherer woman can expect to have an average of five children over her lifetime (Hewlett 1991), with some groups like the Ache showing much higher fertility (Total Fertility Rate=8). Human children grow and develop very slowly and have been shown in a range of forager and forager-farming environments to consume more food than they produce well into their mid- to late-teens (Kaplan 1994, Kramer 2005). Throughout a woman's reproductive life, she is therefore likely to have multiple offspring of various degrees of dependency (Figure 2). Even at peak ages of adult production, few female or male adults would be able to feed themselves and all of their children without assistance from others (see Gurven and Walker 2006 for estimates of age-specific dependency for low- and high-

fertility foragers). Even when foragers are at the age of peak food production, they are likely to be in a net deficit due to the composite net caloric demand of all their children.

[INSERT FIGURE 2 HERE]

Offspring need alone, however, is insufficient to cause specialization in subsistence activities by sex or age. We must also examine the macro-nutrient composition of foods and the separate strategies used to acquire these. Although there is still no consensus over the optimal combination of lipids, proteins and carbohydrates that should be consumed daily (or if even one exists) given a specific activity profile, there is little doubt that all three are necessary for healthy growth, development, body maintenance and reproduction (see Milton and Demment 1988 and citations therein). A great deal of evidence suggests that protein-lipid resources and additional animal source micronutrients are often limiting components of peoples' diets and hence more valuable than carbohydrate in most human societies. Many studies show that increases in proteins and lipids lead to improved growth and health in a variety of human societies (Larsen 2003, Carpenter 1994). High protein-lipid foods are also critical in brain growth, immune function development and female reproductive function (Milton 2003, Neumann et al. 2003, Murphy and Allen 2003). Experimental manipulation with isocaloric diets shows great 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). The human gut appears obligatorily designed to eat a mixed macronutrient diet (Aiello and Wheeler 1995), and biochemical evidence suggests that several essential amino acids (e.g. taurine, 20- and 22-carbon fatty acids) are only obtained from consumption of animal tissue (Cordain, Watkins, and Mann 2001). Food choice experiments on rats and humans confirm that without income constraints the

typical diet is higher in protein and lipid than most human societies ever achieve (Drewnowski 1997, Hill 1988). Tastes and cultural preferences cross-culturally tend to favor fatty foods and especially meat. Athletes at free training tables select extremely high protein-lipid diets, as do the wealthy classes among the world (ibid.). All these pieces of evidence point to the fact that the macronutrient composition of foods matter. Economic strategies by men and women must therefore provide complementary amounts of carbohydrates and protein-lipids (and probably other micronutrients).

The requirement for a combination of macronutrients means that foods must be acquired that include sufficient quantities of carbohydrates, lipids and protein. Most roots, fruits, shoots, berries and other plant and vegetable products tend to be high in starchy carbohydrates, sugars and micro-nutrients, but low in fats and proteins. Similarly, meat from wild game, shellfish and other kinds of fish is high in protein, and animal organs, bone marrow and brains are especially rich sources of lipids. Animal meat is also likely to contain more lipids during food abundant seasons of the year and just prior to reproduction. The fact that the separate macro-nutrients tend to be packaged in different foods means that a variety of separate food items must be included as part of the human omnivore diet (see Harris and Ross 1987 volume). Game, fish, roots, fruits, honey, nuts, insect larvae, berries and other items common to forager diets are acquired by very different techniques and each requires specific knowledge. It has been argued elsewhere that much of forager diets consist of foods that are generally difficult to acquire and require substantial learning, hence contributing to the dependency of hunter-gatherer children and adolescents (Kaplan et al. 2000). It is important to realize that not all foraging activities need be skills-dependent. Indeed, productivity in many gathering, shellfish collecting and fishing activities may be more strength- or size-dependent than skills-dependent, and so reaching adult-

level productivity in several of these activities may not be difficult (Bird and Bliege Bird 2002, Bird and Bliege Bird 2005). However, hunting activities have been shown to require long periods of time to develop peak proficiency in several societies. Among Ache, Tsimane and other hunting groups, making direct encounters with animals and killing them during pursuits are the two most difficult components of hunting that require the longest time delays to reach peak levels (Walker et al. 2002, Gurven, Kaplan, and Gutierrez 2006, Ohtsuka 1989). Increasing gains in hunting performance require substantial time inputs, more than in most documented gathering activities.

When utility is provided by multiple foods, and acquisition of these foods requires separate subsistence strategies that may require substantial learning investment, and when increasing returns are gained with increased time investment, specialization is a likely, if not inevitable, outcome. Specialization maximizes household utility among cooperating individuals that divide their labor to obtain complementary objectives. This is essentially Gary Becker's Nobel prize winning argument concerning familial division of labor applied to the hunter-gatherer context (see Becker 1991, Bergstrom 1997).

The fact that specialization is desirable does not imply that men should be the sex that hunts and that women should gather. Without comparative advantage by sex, the sexes need only coordinate on a particular complementary set of economic activities, as in the classic Battle of the Sexes game (Rapoport 1966). Without increasing returns to specialization, both sexes might become generalists and then freely alternate the complementary activities that they engage in. However, in section 1.4 we presented the many reasons that men will hunt and women will tend to gather in societies of human foragers. Childcare constraints may be sufficient to give men a comparative advantage and be the sex that actively hunts. The comparative advantage is further

amplified by men's greater average strength and body size, physical components that were presumably selected for due to a history of contest competition with other men in the context of mild polygyny, and perhaps due to men's focus on more hunting-based subsistence. As Hawkes and colleagues have noted, men may gain additional benefits from hunting that are not included in the household utility maximization approach, and these may further motivate male hunting. However, these benefits are not necessary to explain why most men hunt in foraging societies. Instead, the signaling payoffs to hunting probably just increase the likelihood that men will hunt exclusively or in conditions that might otherwise favor greater male involvement in gathering activities.

2.2 Children as public goods: a bargaining approach

The production of offspring is usually a cooperative act between a woman and man. Children are a shared public good because they represent a fitness outcome of both parents, regardless of the levels of investment each of them provides. In order to model optimal amounts of parental behavior, we construct partner utility or fitness functions that contain shared household (or public) and personal (or private) components. Our task is to determine an optimal set of time budget allocations for each marital partner in the union and the resultant level of efficiency and equity in the distribution of gains. Two extreme possibilities include "symmetrical" marriages where similar gains are realized by each partner and "dictatorial" marriages where only one partner determines the allocations to both (Manser and Brown 1980). The existence of "deadbeat dads", males who contribute little to marriage unions and especially if such unions are dissolved, does not negate the fact that an economy of scale associated with cooperation is an important feature of marriage unions; unstable unions and unequal bargaining

power due to unequal conditions or outside 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 in childcare.

The amount of time that should be spent investing in offspring can be modeled using indifference curves. Each partner decides how much of their daily time budget is to be spent in each alternative activity. For simplicity we group all work activities and label them “household production” and group all activities that yield private gain and label them “leisure”. Here we use two categories for simplicity, but any number of categories could be chosen. Work activities includes those pertaining to direct resource acquisition (hunting, fishing, gathering, etc.), food preparation (butchering, cooking, cleaning, washing utensils, etc.), camp maintenance (constructing houses, making fire, collecting firewood, getting water, etc.), and childcare activities (bathing, feeding, babysitting, etc.). Leisure might include social visits, relaxation and grooming, pursuing extra-pair relationships, play, sleep or any other activity that does not provide utility to other household members.

[INSERT FIGURE 3 HERE]

The budget constraint is defined by the total number of hours available that could be spent in either household production or leisure. If we plot household production on the x-axis and leisure on the y-axis the budget constraint line intersects the two axes at the point where all time would be dedicated only to that activity. Usually a budget is a straight line, although we can imagine that 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. Each partner attempts to maximize fitness gains from a marriage union subject to budget constraints by choosing an optimal set of activities (Figure 3). Next, we can imagine concave isofitness

curves that describe the combinations of public and private goods that provide the same amount of returns in fitness (or some proxy) units. As in Figure 1, 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 curve for: 1) investments of care and food consumption on offspring survival and growth; 2) investments in mate acquisition. 3) investments in status activities that may provide both private benefits (e.g. mating benefits) and public benefits (e.g. deference).

The indifference curve approach is useful for looking at any important tradeoffs, and has been used to model women's optimal time allocation to childcare versus food production, for example (Hurtado et al. 2006). Maynard Smith (1977) was the first to incorporate the trade-off between parenting and mate searching into a model of mate desertion, or divorce. Empirical investigation of the relevance of these two factors has been explored in several forager groups by Hurtado and Hill (1992) and Blurton Jones et al. (2000). When men's activities can have only minimal impact on improving child welfare and when mating opportunities are high (e.g. high operational sex ratio), pair bonds are brittle, divorce is likely and expected male parental investment is low. This theoretical model has been tested to some extent, however, the impact of men's parental investment have been measured mostly in extreme circumstances and using crude fitness measures, such as examining infant and child survival when a father dies or in father-absent households. Results show that the presence of a father has a strong effect on children in hunter-gatherer societies where men's contribution to the diet is great (e.g. Ache), but the overall impact cross-culturally is variable (Marlowe 2001). However, the presence of other kin who may

contribute aid during the absence of fathers makes exploration of true father effects difficult (Winking 2006).

Partners do not make allocation decisions in isolation, and so any consideration of optimal behavior for men must consider the decisions of women and vice versa. Attempting to understand time budget decisions of men or women in isolation might lead to the result that both partners should become generalists, which as we argued above is an inefficient outcome. People considering marriage may have certain minimal expectations of household contribution that they expect of potential spouses. These can be considered threat points, which describe a level of expected contributions by the partner and their presumed fitness effects, below which will result in a dissolution of the marriage (Figure 3) (Manser and Brown 1980). Evidence for threat points is suggested by ethnographic documentation of commonly desired characteristics for marriage partners. Data from several tribal societies suggest that while men value physical attractiveness more than women, both partners are concerned that a prospective long-term mate display positive character traits, be hard-working, generous, and a high producer (Hill and Hurtado 1996, Marlowe 2005). These traits only make sense if partners subscribe to the notion that the major gains from marriage are both productive and reproductive. If women did not gain from marrying men and were instead only gene-shopping, then we would expect much more polygyny than observed among foragers and only brittle de facto pair bonds.

[INSERT FIGURE 4 HERE]

In the conceptual model, an initial allocation decision is made by one partner, a reactionary allocation is made by the other partner to this allocation, and so on until one of the following outcomes is reached: 1) both partners arrive at a stable equilibrium of contributions to the household; 2) the equilibrium is unstable and eventually one of the partners will contribute

everything, or 3) it is always in the interests of one partner to defect and contribute nothing (Chase 1980). These three outcomes are illustrated by the use of utility response curves (Figure 4). The second scenario may represent the downward spiral of a marriage heading for divorce, where each lowering of investment by one partner results in an increase in the partner's investment. The third scenario should also result in divorce, except under the limiting case where the contributing partner has no other options. At the equilibrium, the second and third scenarios may result in the same unequal distribution of in-pair contributions among partners. Usually it will be the case that the optimal time allocation for the male partner (point A in Figure 3) will not match the solution which would be optimal from the female point of view. Instead there is a region between the optimal male and female solutions (as in Figure 1) which defines a set of time allocations for each sex that is open to bargaining.

This process of declaring expectations and responding to a partner's level of commitment may be an implicit part of the logic behind matrilocal residence and brideservice patterns commonly found among new couples 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 of in-laws. The important point here, as we argued in section 1.3 with respect to sharing, is that the bargaining outcome does not have to insure equal levels of contribution by men and women in marriage, but rather need only insure that men and women both gain more from these unions than they would from alternative options.

It might be expected that marriage commitments are highest when children are young and partner reproductive value is high. Dwindling male investments may therefore be expected some years after the initiation of marriage. As shown in Figure 2, however, the high caloric demands

of children in a foraging environment can last well into parents' mid-forties and fifties, until the youngest child is independent. Insuring survival through the high mortality period of infancy and childhood (about 50% on average for hunter-gatherer populations) is only one way that fathers can contribute to the welfare of their existing children. Improved growth and nutrition, teaching foraging skills, proficiency in hunting, facilitating alliances and providing social support during conflict, and direct protection from violence are several other avenues for fathers to positively impact child welfare and fitness. Defection during the mid-forties, for example, might be costly in terms of lost fitness relative to the potential gains from starting a new union with another woman². This is especially true if a man's mate value decreases with his expected productive lifespan. Empirical evidence suggests that in at least two societies men are more likely to engage in extramarital sex near the beginning of marriages rather than later on when their wives have little reproductive value (Winking ms; Hurtado and Hill 1996). Some high status men may be able to reap gains from defection when spouse mate value declines, or support two wives, but these are likely to be the exceptions rather than the rule for most men. It's not surprising then that socially-imposed monogamy is the dominant marriage pattern for hunter-gatherers (Murdock 1967, Marlowe 2004a), even if actual paternity patterns may sometimes resemble that of effective polygyny (Low 1993). Individual attractiveness, status, wealth, specialized skills or abilities, and other potential bargaining chips can vary across men and within men over their own lifetimes. We might expect, for example, that attractive men by virtue of their 'good genes' invest less in children than less attractive men who need to compensate with more long-term investment (Waynforth 2001). Aka men who are recognized as high status spend less time with their children than lower status men (Hewlett 1992). Features of the local ecology, such as the number of available fertile females relative to the number of male competitors, payoffs to male

coalition building, difficulty and productivity of different foraging activities, etc., can also affect the opportunity cost of men's time spent in subsistence tasks that provision family members. To the extent that people marry others of similar mate value (e.g. Schoen and Weinick 1993), we might expect that differences in bargaining power should not be so great for a majority of couples.

One implication from the conceptual exercise presented here is that even if mating effort were a priority for men, this does not imply that the sexual division of labor will be more pronounced in societies where mating effort gives the highest payoff (cf. Bird 1999). The sexual division of labor may not be impacted much at all, although the observed level of contribution by males to their own offspring may be lower under contexts of greater payoffs from investing in mating effort. For example, the Hiwi have a more pronounced sexual division of labor than among the Ache (Hurtado et al 1992), but Ache men have much higher availability of mating opportunities (ibid) and higher divorce rates. Factors other than mating displays probably explain why both of these societies show sex differences in resource acquisition patterns. It is likely that men engage in whatever activities give highest nutritional utility after accounting for economic choices likely to be made by women, and more so when these activities also provide social or mating benefits. Women may also maximize nutrient gain rate subject to the constraints of lactation and childcare, and then adjust their behavior if men provide certain types of foods. In such a scenario, men might still face decisions about whether to use the resources they obtain in mating or parenting investment. In either case they should acquire foods of highest utility to women and children. This would result in a division of labor regardless of whether mating or parenting provided highest payoffs to men.

Discussion

Hunting ability is a common route to high status among foragers cross-culturally (Wiessner 1996). Good hunters have been shown to display higher reproductive success everywhere the relationship has been investigated (Smith 2004). Women show higher average total fertility in forager societies the more that men contribute food to the diet (Marlowe 2001) and women produce less food when their husbands produce more (Hurtado et al. 1992). On average, men contribute about 65% of the calories, and 85% of the protein, in the diet among foragers (Kaplan et al. 2000, Marlowe 2001). There are multiple pathways by which hunting ability can increase reproductive success, as illustrated in Figure 5. We separate proximate level motivations from ultimate level benefits that determine fitness. In this model, the economics underlying time budgets allocated to hunting must take into account the sum of all proposed pathways. In contrast, the status signaling or mating effort model commonly posits that extra-pair mating benefits due to partner choice for good genes (rather than for production ability or for willingness to provide resources) explain the correlation. 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 within the current relationship. Thus, taken to the extreme, any form of provisioning can be interpreted as a form of mating effort (van Schaik and Paul 1996). Figure 5 offers alternative routes by which mating effort or social status striving can produce benefits typically attributed only to direct provisioning (Gurven and von Rueden 2007).

[INSERT FIGURE 5 HERE]

Our proposal is that status enhancement need not only improve the hunter's extra-pair mating success, but can have short-term and long-term impacts that ultimately affect in-pair reproduction via improvements in child survivorship, reduced interbirth intervals and marriage with younger, or more fecund partners. High social status from hunting may also yield non-reproductive benefits, either through direct or indirect reciprocity (Smith 2004, Alexander 1987) or via the costly signaling of cooperative intent (Gurven et al. 2000a, Frank 1988, Smith and Bliege Bird 2005).

We conclude that the view that hunting is largely mating effort is incomplete and stems from a conflation of psychological motivations underlying men's time budgets and the fitness effects that are a result of men's subsistence choices. If men desire status and hunting is a primary route to status because of the valuable currency of meat, then we need to focus attention on how higher status contributes to higher fitness among foragers. Indeed, despite a number of correlations between hunting ability and reproductive fitness measures, the relative contribution of the different pathways in Figure 5 has not been quantitatively estimated in any forager society. Mating benefits are only one component of higher male status. Apart from the household benefits of hunting described in section 1.3, male food sharing of production in a public forum may have important signal value about the qualities of the producer male, thereby increasing male status. One recent study, however, among a forager-horticulturalist society does bring important insight here. Among Tsimane hunters, we found that much of the reproductive benefit associated with hunting and social status is realized *within* and not outside marital unions (Gurven and von Rueden 2007). Proficient Tsimane hunters are also more likely to share meat and be regarded as hard workers—qualities that are especially important to mates and existing and potential social partners (ibid). Although good hunters tend to also share meat generously we

find that meat sharing is associated with an increase in in-pair fertility, but bears no strong relationship with extra-pair mating in the Tsimane sample. Cross-culturally, good hunters may marry early, marry younger or more attractive and fecund wives because their higher production ability and generosity gives them leverage in the mating market. Once they are married, good hunters and their families may benefit from the many pathways suggested by Figure 5.

Apart from the household benefits of hunting outlined in Figure 5, male food sharing in a public forum may also have important signal value regarding the qualities of the producer male. The costly signaling of high phenotypic quality could then result in more favorable treatment by any or all members of the social group (Hawkes 1990). For example, as described above for the Tsimane, successful hunters might gain sexual access to more and higher quality females or obtain more and better male allies, and competitors might be more reluctant to confront them in a variety of arenas. Although some of these payoffs impact only on male fitness through mating success, many of the imagined payoffs might also benefit offspring (e.g. father having more allies and fewer competitors). Indeed we believe that some examples of food sharing by women foragers might also best be understood as costly signaling, yet the payoffs to that sharing are clearly not in mating opportunities. Women as well as men compete for status (Hrdy 1999, Campbell 2002, Rucas et al. 2006), presumably because this benefits their offspring. In modern societies wealthy females engage in public philanthropic activity, and post-reproductive 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. There is no reason to suspect that all male status display should be motivated by mating gains. Indeed, male status acquisition may be a form of paternal investment.

The gains of cooperation from repeated interactions with valued partners is believed to make the costs of signaling cooperative intent worthwhile over the long term (Frank 1988, Gintis, Smith, and Bowles 2001). Presumably these repeated interactions will involve some level of dyadic and indirect reciprocity. Such possibilities are only beginning to be investigated. For example, do men receive other goods and services from those who obtain portions of their production? Do other individuals who eat from men's kills give them other food types (honey, collected foods), make tools for them, bring them firewood, babysit their children, feed their children more often and care for their families more often when they are ill? Among the Ache children of high-return hunters experience higher survival (Hill and Hurtado 1996) despite the fact that they receive no larger portions of father's game than do other children in the foraging band. Ache children also experience higher mortality after paternal death or 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. Ache orphans tell detailed stories of the hunger they experienced after their father's death (ibid), and a recent study shows that Ache families who share more on reservation settlements are more likely to receive food from others when they are ill or injured (Gurven et al. 2000a).

Hunting may be a ubiquitous enterprise for men cross-culturally precisely because of the multiple pathways by which it can impact fitness via both private and public household gains. The early historical focus on the impact of good hunters on child survivorship and the recent emphasis on the benefits from extra-marital mating are both incomplete explanations for why men may hunt. The fitness that accrues to hunters is likely due to the summed direct and indirect pathways shown in Figure 5 and discussed above. We believe that current evidence suggests that the provisioning pathways alone probably favor hunting in most societies, but the commitment to

hunting is reinforced further by the signaling payoffs that aid in mating success and coalition building. Why else would women desire marriage, and with good hunters, if the products of male hunting were public goods that led only to increased mating opportunities for men? If the gains of hunting were purely personal, we should expect women to discourage their husbands from hunting. Instead we have observed just the opposite. Ache, Hiwi, Tsimane and Machiguenga women often vigorously encourage their husbands to hunt³, and men who don't hunt often have poor mate choice (because women don't want to be married to men who only gather vegetable foods).

Conclusion

We have presented a model of the sexual division of labor where men hunt and women gather in most societies because of maternal constraints, the long learning period for many foraging activities, and male comparative advantage combined with the goal of providing a diverse, multi-nutrient diet. Furthermore, men's game production through hunting is not lost through sharing but instead tends to be biased towards family provisioning and channeled to others strategically via contingent reciprocity, social insurance and costly display. We agree with Marlowe (1999) that current data support a "parenting and mating effort hypothesis" of men's tendency to hunt while women gather and to forming long term pair bonds with a small number of reproductive partners.

Long-term pair bonds between men and women cannot adequately be explained by costly signaling or mating effort alone because these imply that there should be little incentive for women to "marry" good hunters and that men should divorce their wives as their fecundity drops to very low levels. Even on the psychological level of men's motivation, we do not feel that men

in foraging societies are driven primarily by mating interests. In the societies that we have observed, men voice obvious, overt, and sincere concern over spousal and offspring welfare, and were involved in numerous activities throughout the day that indicated such concern. Among the Ache, Hiwi and Tsimane, men often take custody of children after maternal death or divorce and provide extensive parental support. Several hypothetical scenarios conducted with Ache and Hadza men further show that they prefer residing in groups with good hunters who will yield high returns for provisioning, rather than residing in groups of poor hunters where family provisioning benefits will be low but status signaling opportunities will be high (Wood and Hill 2000, Wood 2006). Only Ache hunters without small dependents were more interested in signaling, while level of dependency showed no effect on Hadza hunters' preference for being in groups of good hunters. We suspect that new physiological data on male-female and male-offspring bonding mechanisms and hormones that promote such bonding (e.g. oxytocin, vasopressin, dopamine, norepinephrine, phenylethylamine, serotonin, decreased testosterone) will demonstrate that human males were designed by natural selection to increase cooperative sentiment with female partners over time and to help raise highly dependent offspring (Hrdy 1999, Gray et al. 2004). These mechanisms may set humans apart from other primates. Undoubtedly some spousal conflicts arise because of male mating goals and these conflicts may sometimes modify men's behavioral patterns. New data can help address the question of the extent to which the sexes cooperate or compete in reproduction. New studies among foragers and non-foragers (e.g. Sherk 2005) should test how the costs and benefits of male mating and parenting investment are likely to vary with ecological circumstance, partner status and value, condition and level of need of offspring, and availability of substitutable aid.

FIGURE 1. Edgeworth Box of Food Exchange. The underlying bargain is the quantity of A 's current food production exchanged for B 's future production. Food consumed in the future has less value than food consumed today but both contribute to ego's utility as represented by the concave indifference curves radiating outward from A 's and B 's respective origins. The oval region in the interior is the bargaining zone (see text). While points C and F yield high utility (although higher for B and A , respectively), point E represents the intersection of A 's and B 's highest indifference curves. Adapted from Gurven (2004).

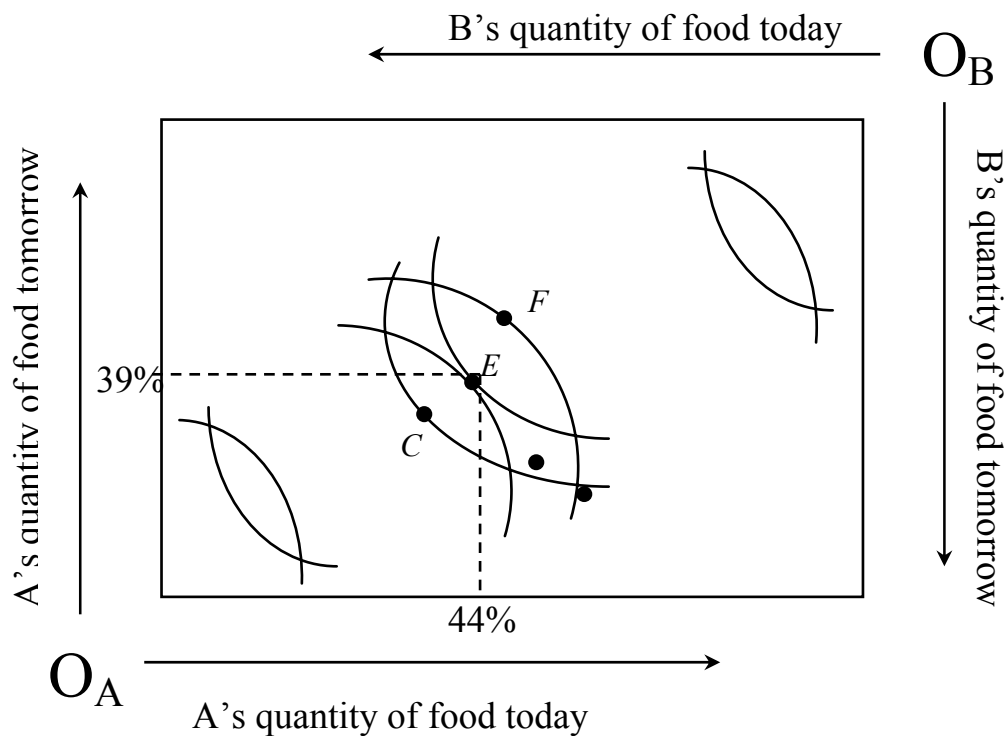


FIGURE 2. Number of dependents by age for Ache and Dobe !Kung (inset) females based on age-specific fertility and mortality measures for these populations. Ache women have high fertility over their lifetimes (Total Fertility Rate, TFR = 8) and !Kung women have low fertility (TFR=4). Adapted from Gurven and Walker (2006).

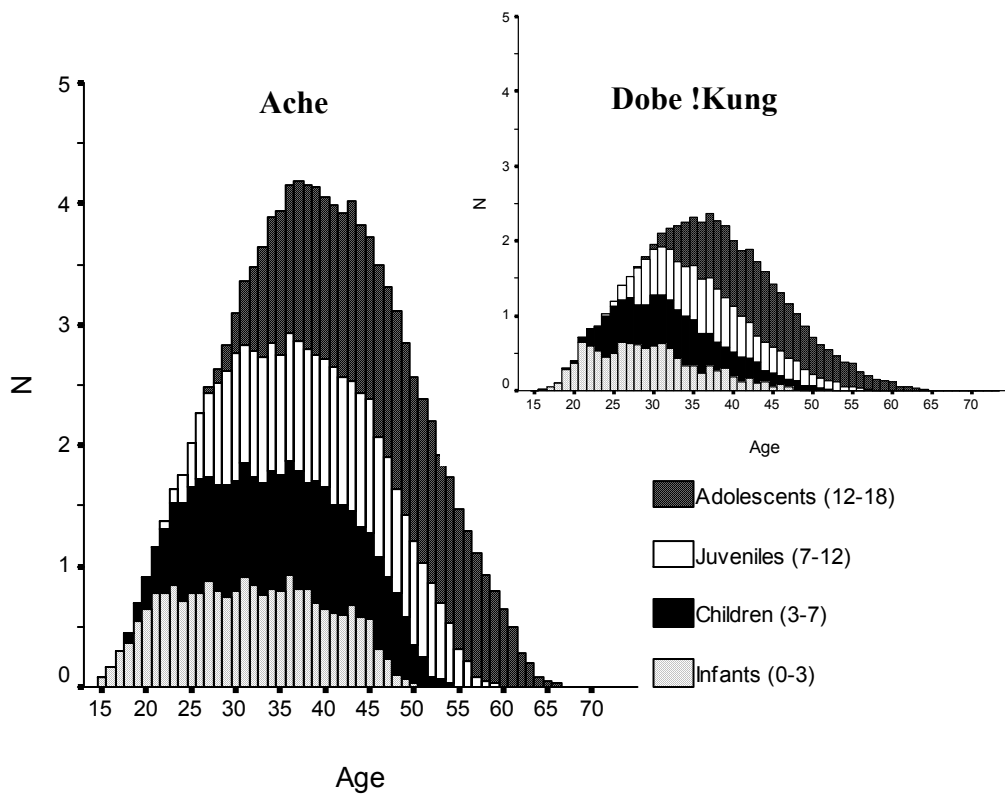


FIGURE 3. Isofitness framework underlying a man's optimal mix of household contributions and private gains. Straight diagonal lines represent budget constraints underlying a man's use of time. The point A is the optimal allocation of a man's time to household goods and private gain, but this point lies below the woman's minimum acceptable level of household contribution. Therefore a man will choose the sub-optimal allocation at point 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 is illustrated by point C.

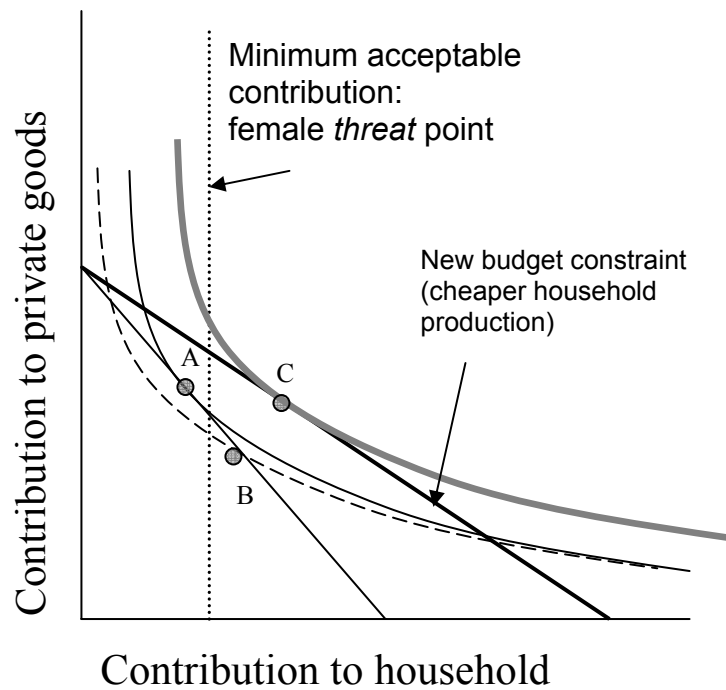


FIGURE 4. Reaction curves for husbands (dashed curve, H) with respect to wives (solid curve, W) and vice versa. An initial level of W's contribution on the x-axis invokes a reaction by H that defines H's contribution level on the y-axis. H's contribution invokes a response by W based on her reaction curve, which then maps back to the x-axis. 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 contributes more than the equilibril amount in b), she will contribute everything to the household and H will contribute nothing. If W contributes less, the reverse outcome will hold where H contributes everything and W nothing to the household. Adapted from Chase (1980).

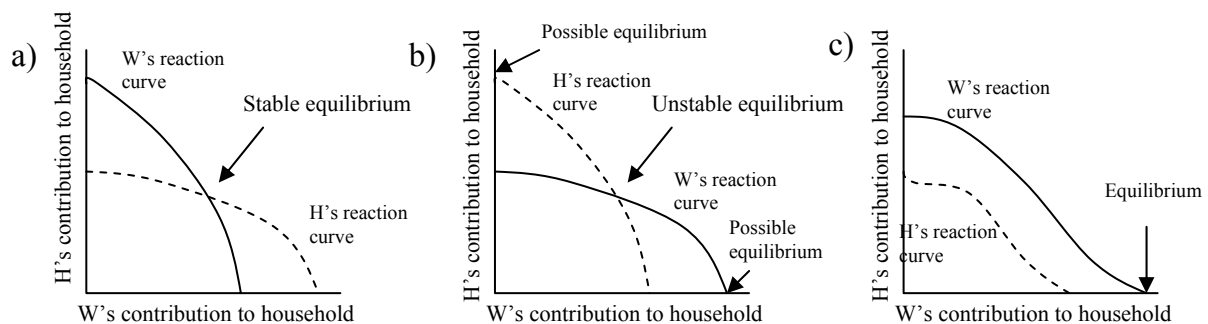
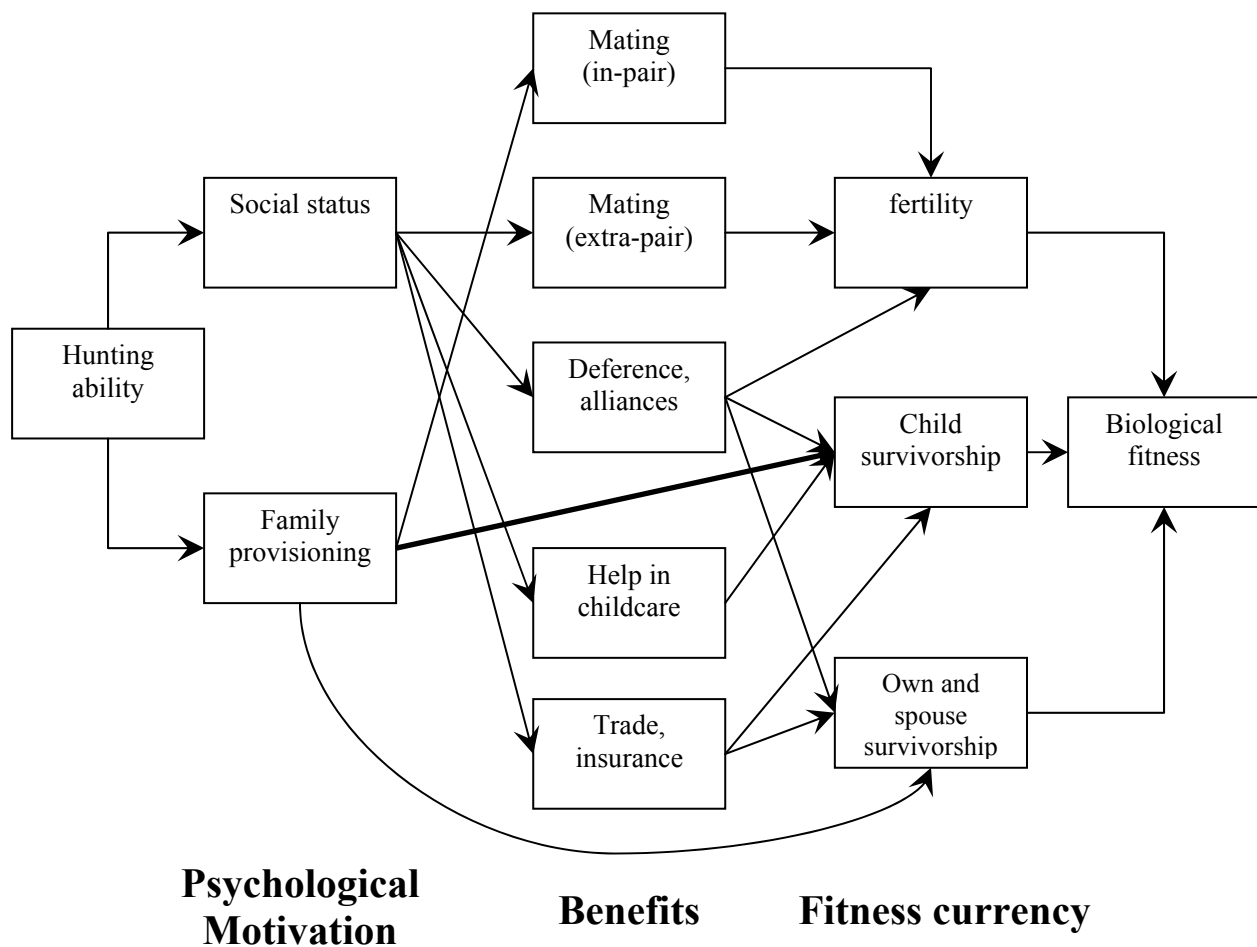


FIGURE 5. Causal pathways mediating relationship between hunting success, social status and biological fitness. The pursuit of social status from hunting can provide many benefits in addition to in-pair and extra-pair mating access, including deference, coalitionary support, aid in childcare and social insurance. The path between provisioning and child survivorship is made bold to emphasize direct and indirect routes; with an efficient division of labor, men's provisioning allows women to engage in high quality childcare, such that provisioning provides direct and indirect benefits to child survivorship. Overall impacts of hunting ability on fitness are mediated by increases in fertility and survivorship of self, spouse and children. Adapted from Gurven and von Rueden (2007).



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¹ A substantial literature in economics has investigated gender differences in risk-averse financial decisions. A recent review (Schubert, R., M. Brown, M. Gysler, and H. W. Brachinger. 1999. Financial decision-making: Are women really more risk-averse? *American Economic Review, Papers and Proceedings* 89:381-385.) concludes "...we find that female subjects do not make less risky financial choices than male subjects". Instead well designed experiments have shown that neither sex has a consistently higher certainty equivalency (preference for high variance income) on typical financial tasks such as investment decisions and insurance purchasing, but that either males or females sometimes show higher risk preference on pure gambling tasks depending on whether gains or losses are at stake.

² 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 (see Fessler, D. M. T., and K. J. Haley. 2003. "The strategy of affect: Emotions in human cooperation," in *The Genetic and Cultural Evolution of Cooperation*, vol. Dahlem Workshop Report. Edited by P. Hammerstein, pp. 7-36. Cambridge, MA: MIT Press.).

³ 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".