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# Hunting and Nuclear Families

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## Some Lessons from the Hadza about Men's Work<sup>1</sup>

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Hadza hunter-gatherers display economic and social features usually assumed to indicate the dependence of wives and children on provisioning husbands and fathers. The wives and children of better Hadza hunters have been found to be better-nourished, consistent with the assumption that men hunt to provision their families. Yet, as is common among foragers, the Hadza share meat widely. Analyses of meat-sharing data confirm that little of the meat from large prey went to the hunter's own household. These analyses also show that neither a man's hunting success nor the time he spent hunting made any difference in how much meat his family got from the kills of others. Here we address questions posed by this set of observations. What explains the better nutrition of the children of better hunters if they did not get differential rations of meat? If better hunters got no more meat for their effort and poorer hunters were not punished with less, what incentive could account for the continuing disproportionate contribution that some men made to the group's nutrition? If women were not dependent on their husband's hunting success for meat, an obvious incentive for women to marry hunters disappears. We briefly consider the implications of these patterns for the evolution of marriage and nuclear families.

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Among most ethnographically known hunter-gatherers, hunting is men's work, women marry hunters, and spouses establish households in which, among other things, all sometimes eat meat. This constellation of features is widely assumed to show that nuclear families are units of common economic interest, with labor divided by sex to serve familial welfare (Murdock 1949, Sahlins 1972). Meat sharing beyond the household is viewed as exchange, successful hunters insuring against the unpredictability of hunting to provision dependents by trading surplus meat when they are successful for shares to be repaid when fortunes are reversed. This model underpins the most influential scenario of human evolution, in which an array of distinctively human features is presumed to evolve as a consequence of males' hunting and sharing meat to support their mates and offspring (Washburn and DeVore 1961; Washburn and Lancaster 1968; Isaac 1978; Hill 1982; Lancaster and Lancaster 1983, 1987; Ridley 1996; Pinker 1997; Kaplan et al. 2000).

Hadza foragers, living in the tropical savanna along the East African Rift, face many of the ecological constraints assumed to favor reliance on hunters for household provisioning. They exemplify aspects of social and economic organization widely attributed to domestic or familial production (Sahlins 1972). Nuclear families are socially distinct, occupying separate household structures. Women gather plant foods. Men hunt. Meat is a highly valued component of everyone's diet. In the classic *Man the Hunter* volume, Woodburn (1968:52) underlined the importance that Hadza attach to meat. While "vegetable food makes up the bulk" of the Hadza diet, people "think of themselves and describe themselves as hunters. From informants' assertions, one would gather that little but meat is eaten. . . . Moreover the Hadza place such emphasis on meat as proper food . . . that they are apt to describe themselves as suffering from hunger when they have less meat than they would like."

Here we explore some of the payoffs to Hadza hunters for their work, testing hypotheses drawn from the proposition that men hunt to provision their families. We use data on meat sharing reported elsewhere (Hawkes, O'Connell, and Blurton Jones 2001) to estimate the marginal nutritional gain a hunter could expect to earn for his own household from big-game hunting and compare it with incomes from alternative foraging choices. We investigate whether differential meat consumption can explain why, as reported earlier (Hawkes 1993b), the children of better hunters are generally better nourished and find that, within the limits of our data, it cannot. Instead, the link is through mothers. Better Hadza hunters are married to women who are more successful at solving their own nutritional problems and those of their chil-

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TABLE 1  
*Seasonal Conditions, Number of Days Observed, Number of Camp Scans, and Number of Large Animals Taken by Members of the Focal Camp during 1985–86 Time-Allocation Sample Period*

Season	Condition	Number of Days Observed	Number of Camp Scans	Number of Large Animals Taken
1. September/October	Late dry	47	195	30
2. November/December	Early wet	18	173	2
3. December	Early wet	9	85	3
4. January	Early wet	5	52	0
5. March/April	Late wet	14	383	1
6. May/June	Late wet	21	359	2
7. July/August	Early dry	30	460	5
		[144]	[1,707]	[43]

dren (Blurton Jones, Hawkes, and O'Connell 1997, Hawkes, O'Connell, and Blurton Jones 1997).

Most of the meat that women and children eat comes from hunters other than their husbands and fathers. In light of a similar pattern among Ache foragers in the forests of eastern Paraguay, Hawkes (1990) hypothesized that the pressures of sexual selection might play an important role in the evolution of human hunting and developed a model emphasizing female choice. The model assumed that, when game was widely shared, women concerned to feed their children would prefer that men other than their own husbands supply it. A preference among women for better hunters as extramarital sexual partners was then an incentive for hunters. This is an alternative to propositions about hunting to provision families, but it shares with the traditional view an assumption that hunting is fundamentally about "meat for sex" exchanges. When meat is widely shared and the hunter does not control the distribution of meat, this assumption is wrong. A hunter cannot direct differential shares to lovers any more than to his wife. If women get as much meat whether or not they favor the hunter, they have no subsistence incentive for preferring better hunters as sexual partners.

In the Hadza case the members of the successful hunter's household (his wife and resident children) do sometimes get a larger share than other men's households, but most of the time they do not (Hawkes, O'Connell, and Blurton Jones 2001). Consequently women gain little extra meat for themselves and their children by marrying better hunters. Nor, as long as meat is shared in this way, could women gain larger portions of meat by favoring better hunters as lovers. To the extent that meat distribution is not controlled by hunters, expectations of meat-for-sex exchanges (within marriage or without) are unlikely incentives for either hunting men or hungry women. Yet men hunt and women marry hunters. If neither of these is explained by family provisioning, they remain to be explained in some other general way.

Here we report previously unpublished data and new analyses that further specify the payoffs Hadza men get for hunting. Our analyses add more challenges to the assumption that marriage is fundamentally a bargain in

which women enlist provisioning husbands. After presenting our findings, we consider alternative explanations for pairing and link status-rivalry incentives for big-game hunting to hypotheses about the evolution of nuclear families.

## Research among the Hadza

A population of about 750 hunter-gatherers, the Hadza live in savanna woodland southeast of Lake Eyasi in northern Tanzania (Woodburn 1968, Blurton Jones et al. 1992). The data reported here were obtained in the course of several periods of fieldwork beginning in the mid/late-1980s among the 200–300 Hadza commonly found in the 600–800 km<sup>2</sup> district known locally as Tli'ika.<sup>2</sup>

### COLLECTING TIME-ALLOCATION DATA

During 1985–86, Hawkes and O'Connell followed a single group of roughly constant size (generally about 35–50 people) but changing composition through a series of five sequentially occupied camps, collecting data on time allocation and foraging (see Hawkes, O'Connell, and Blurton Jones 1997 for details). The study period can be divided into seven "seasons" defined on the basis of changes in camp location and diet (table 1). Men hunted daily, usually alone or in pairs. In addition to encounter hunting and scavenging, they also used blinds to ambush game near waterholes at night during the late dry (season 1). Women and children gathered plant food. They usually traveled in large groups, often accompanied by a man or older boys who provided protection, especially from local pastoralists. Tubers in all seasons, berries throughout the wet (seasons 2–6), and baobab most often in the early dry (season 7) were the main targets of foraging women. Small parties of men, women, and children (often single families) took honey intermittently from early

2. For additional information, see Blurton Jones, Hawkes, and Draper (1994), Blurton Jones, Hawkes, and O'Connell (1989, 1996, 1997), Hawkes, O'Connell, and Blurton Jones (1989, 1991, 1995, 1997) Lupo (1994, 1995, 1998), Marlowe (1999), O'Connell, Hawkes, and Blurton Jones (1988, 1990, 1991, 1992).

wet through early dry. The sharpest seasonal contrast was between the late dry, when hunting returns were best (largely because of nighttime ambush hunting success), and all other seasons, when hunting was relatively poor but plant foods more widely available.

Data on time allocation were gathered throughout the 1985–86 study period by means of “instantaneous” camp scans, focal-person follows, and observations of departures and returns summarized in daily logs of residents’ activities. Scans were spot checks on the activities of all individuals present in camp. They were distributed throughout the 12 daylight hours, never more than 2 an hour on any given day, with an average of 13 scans per day, each one recording the location and activity of all individuals present at that point in time. Running totals were kept of the number of scans completed during each daylight hour to ensure even distribution across the day. This work produced a large sample, roughly 1,700 scans.

The activities of residents absent during a scan were determined from follows and daily activity summaries. Follows provide detailed records of the behavior of one or more individuals accompanied by Hawkes or O’Connell on day trips away from camp. Data collected included the identities of all individuals in the party, routes followed, persons encountered en route, prey types seen and quantities taken, and a detailed time schedule. Activity summaries were compiled at the end of each day. Data from scans and follows were collated and any gaps in the records for particular individuals identified. These were sometimes filled simply by inquiry. When a resident’s location during a particular scan could not be ascertained, he/she was recorded as “not seen.” The data set so produced includes more than 50,000 records, each identifying a person, time, place, and activity.

This time-allocation database was partitioned for analysis by season. Nonresidents were excluded, since we caught them only during visits to our study camp. Those who were camp residents only briefly during a season and present for only a few scans were eliminated from that subset. Although the scans across a season sample all hours of the day fairly evenly, they do not do so every day, so time budgets calculated on small numbers of scan times may be distorted accordingly. This adjustment results in an underrepresentation of unmarried men, who are unlikely to stay many days in the same camp, and therefore we cannot use these data to compare married and unmarried men. Time budgets were then calculated for each camp resident for each season, resulting in a sample of 243 individual time budgets on a total of 90 different individuals, each time budget based on an average of 114 (s.d. 78, s.e. 5) observations. Total observations in time budgets vary because the number of scans varies by season, as does the number of days any particular subject was resident in each camp. Because our topic here is hunting, we focus initial attention on the 23 time budgets for 11 adolescent boys and 35 for 14 married men. For some analyses here we also use 35 time budgets on the wives of these men (see Hawkes, O’Connell, and

Blurton Jones 1995, 1997 for data and analysis of women’s and children’s activities).

#### ASSESSING SUBJECTS’ NUTRITIONAL CONDITION

Changes in subjects’ nutritional condition were assessed by weighing all camp residents periodically. We use weights taken at the beginning and end of each season to evaluate nutritional welfare by season. Bracketing weights are unavailable for seasons 3 and 4 (which spanned short periods); therefore these seasons are eliminated from any analyses that use body weights.

#### CONTROLLING SEASONAL VARIATION

Because activity patterns and diet vary by season and so does the pool of subjects, seasonal variation could obscure other relationships. For example, since nighttime hunting in the dry was accompanied by less daylight time allocated to hunting,<sup>3</sup> a subject absent in the dry would *for that reason alone* show more daylight time allocated to hunting. For analyses of variation in men’s daylight time allocation overall, including several seasons, we used z-scores. These normalize a man’s effort in a season to the seasonal means for other men in that season, indicating his relative effort compared with the effort of other resident men in that season.

#### GATHERING DATA ON MEN’S HUNTING SUCCESS

Data on men’s hunting success are drawn not only from the 1985–86 study period but from others as well. Estimates of average overall hunting success rates are based on camp resident records and records of all large-animal prey hunted or scavenged during 1985–86, the 1986 and 1988 late-dry seasons, and parts of the 1989 wet season. Data on individual hunters’ success rates are based on observations in 1985–86 plus late-dry 1988. Foraging patterns and data collection routines in other field periods were similar to those summarized above for 1985–86 (see Blurton Jones, Hawkes, and O’Connell 1989, 1996, 1997; Hawkes, O’Connell, and Blurton Jones 1989, 1991, 1995, 1997; O’Connell, Hawkes, and Blurton Jones 1990, 1992).

#### MEASURING MEN’S FORAGING EFFORT

Hadza men emphasize big-game hunting but also take other resources. On most days, they collect plant food snacks and (less often) small game for themselves. They occasionally bring home small game and sometimes baobab fruit. When accompanying women’s foraging parties, they may spend time collecting small amounts of the target resource (Hawkes, O’Connell, and Blurton Jones 1995). In some seasons they search specifically for honey, often in nuclear-family parties. In short, not all time spent foraging is devoted to hunting. At the same

3. Daylight hunting time for men and adolescent boys combined: late dry,  $n = 7$ ,  $2.2 \pm 0.36$  hrs/day; other seasons,  $n = 51$ ,  $5.39 \pm 0.42$  hrs/day;  $p = 0.002$ .

time, away from camp for any reason, men are always armed and alert to hunting and scavenging opportunities. Since counting foraging time as hunting time errs in both directions but attempts to increase the precision of the estimate are likely to introduce other biases, we use foraging time as our best approximation of daylight encounter hunting and scavenging effort. Honey collecting time is a subset of this, extracted for separate analysis. Nighttime ambush hunting in the late dry season is tabulated separately.

## Hadza Hunting

### OVERALL TIME ALLOCATION

Table 2 shows average yearly (1985–86) daylight time-allocation patterns for married men and teenage boys (see also Hawkes, O'Connell, and Blurton Jones 1997). Distribution of effort is similar, except that married men spend less time on food acquisition and more on tool manufacture and visiting other camps. As is apparent from the "not seen" category, we were less successful in monitoring the whereabouts of the boys.

Elsewhere we have shown that boys spend more time foraging than do girls, the difference increasing as they grow older but disappearing after marriage (Blurton Jones, Hawkes, and O'Connell 1997; Hawkes, O'Connell, and Blurton Jones 1995, 1997). This does not mean that boys bring in more food. Two sex differences emerge among Hadza juvenile foragers. First, while boys and girls spend similar amounts of time with women's foraging parties and *can* earn similar return rates, girls carry home substantially more food (Hawkes, O'Connell, and Blurton Jones 1995). Second, boys spend more time away from camp with other boys (Hawkes, O'Connell, and Blurton Jones 1995). We count this as foraging time even though the amount of food acquired may be negligible. Follows show that foraging boys look for the small honey stores produced seasonally by some insects and practice shooting at small birds from which they earn very low return rates (Blurton Jones, Hawkes, and O'Connell 1997). Limited attention to food gathering in mixed company and more time spent with peers could indicate the priority boys give to activities that establish their standing relative to each other, including attempting to build and enhance their reputations as enthusiastic hunters (Blurton Jones, Hawkes, and O'Connell 1997).

Time spent foraging by married men matches that spent by women of childbearing age (Hawkes, O'Connell, and Blurton Jones 1997). While this might suggest that men curtail their foraging after marriage in order to spend more time directly monitoring their wives, frequent physical separation of spouses is the Hadza norm (Woodburn 1968). Hadza husbands and wives usually spend several hours of the day apart, foraging separately. Even in camp, men and women occupy different public activity areas during the day (O'Connell, Hawkes, and Blurton Jones 1991).

TABLE 2  
*Time Allocation (Mean Hrs/Day) to Various Daytime Tasks by Hadza Teenage Boys and Married Men*

Task	<i>n</i>	Mean	S.E.	<i>p</i> <sup>a</sup>
Food acquisition				
Boys	23	6.34	0.37	
Men	35	4.13	0.47	0.001
Food processing				
Boys	23	0.58	0.19	
Men	35	0.60	0.10	0.916
Household maintenance				
Boys	23	0.41	0.11	
Men	35	0.46	0.10	0.745
Equipment manufacture				
Boys	23	0.33	0.05	
Men	35	1.14	0.22	0.004
Visiting other camps				
Boys	23	0.15	0.12	
Men	35	0.69	0.17	0.023
Honey collecting <sup>b</sup>				
Boys	14	1.52	0.44	
Men	19	1.57	0.36	0.924
Not seen <sup>c</sup>				
Boys	23	1.01	0.11	
Men	35	0.40	0.06	0.000

<sup>a</sup>Two-tailed.

<sup>b</sup>Seasons 2, 6, and 7, when mean honey collecting effort was > 10 min/day.

<sup>c</sup>So recorded when we could not determine their whereabouts.

### OVERALL HUNTING RETURNS

Meat is an important part of Hadza diets. Over 256 days of observation (2,076 hunter-days, 1985–89), Hadza living in study camps took 71 large animals, roughly 10,115 kg (live weight), 4.9 kg (live weight)/hunter-day, or about 0.7 kg/consumer-day (Hawkes, O'Connell, and Blurton Jones 1991). In the 1985–86 time-allocation subset of that sample (144 days) they took 43 large animals (table 1) totaling 5,900 kg, an average of about 40 kg/day for slightly more than 40 resident consumers or just under 1 kg (live weight)/consumer-day.

These high meat averages result from the large size of Hadza prey. By contrast with average *kilograms* of prey/hunter/day, hunting success rates measured in *catches* of prey/hunter/day are low. Successful encounters are uncommon. With 71 large animals acquired by resident hunters over the 2,076 hunter-days, the average is 0.034 prey/hunter-day, 1 *per hunter-month*. This is a direct consequence of specialization on big game: the larger the animal, the fewer there are, and hunting of course requires perseverance, patience, and skill. Successful encounters are a small fraction of total encounters, themselves in turn a small fraction of visual contacts. In Hadza country, large animals are seen frequently, their tracks even more so, but potential prey are usually too distant for a man to raise his bow. Hunters took action in pursuit only about once or twice a day, and all but a very few of these pursuits failed.

Most sightings of small game were not encounters either, in the foraging modeler's sense (Stephens and Krebs 1986), and when hunters did act on promising chances for small game, most of those pursuits failed as well. Still, potential success rates were much higher for small prey. In an experiment designed to quantify the rates that hunters could get if they took small animals (Hawkes, O'Connell, and Blurton Jones 1991), the average success rate for encounter hunting was 12 times the rate for big game. The rate was 40 times higher if they set snares. That much higher rate in catches does not mean that hunters would increase their long-term rate of meat acquisition by ignoring big game. Mean rates in meat for big game were about 5 kg/hunter/day, while the measured rates for specializing in small game were much less than 1 kg/hunter/day.

#### VARIATION IN HUNTING TIME AND SUCCESS RATES

All Hadza boys and men hunted. Most men spent a few hours in the morning and/or afternoon, sometimes all day, in search of large game. This varied by season and from day to day among individuals. The major seasonal difference in hunting effort was associated with the late dry, when men added nighttime ambush hunting to their daily routine. Men and boys hunted the same fraction of nights during that season ( $0.29 \pm 0.08$  and  $0.29 \pm 0.04$  respectively). While there was a general shift to less daytime encounter hunting in this season, this did not reduce effort differences among individuals. For both men and teenage boys, daytime foraging was positively correlated with fraction of nights spent in ambush ( $n = 8$ ,  $r = 0.79$ ,  $p = 0.02$ ). Those who spent more time ambush hunting at night also hunted more during the day.

Some men were much more successful at hunting than others. For the 14 married men on whom we have a minimum of 21 observation-days in 1985–86 and 1988, the range in large prey taken/day was 0–0.118, the mean  $0.042 \pm 0.04$ . Women's nominations of good hunters closely corresponded to our measured rates (Blurton Jones, Hawkes, and Connell 1997), a result consistent with the supposition that our short-term measures reflect a long-term difference and one of which people took note. In our sample, hunting success was not correlated with a man's age or with number of children in his household but did vary with average foraging time. As noted above, better hunters spent more time hunting (Hawkes, O'Connell, and Blurton Jones 2001). Partial correlations show that long-term success rate (skill) predicts seasonal success rates even when differences in time spent hunting are controlled. But the converse is not true, implying that skill makes a larger difference in a man's chances of capturing large prey than does the time he spends hunting (Hawkes, O'Connell, and Blurton Jones 2001).

#### COMPARISON WITH OTHER FORAGING OPPORTUNITIES

If men's foraging goal is to provision their families, they should employ the strategy that earns the highest rate of household food income.

To test this hypothesis, we estimated the gains that a man should expect to get for his own household from alternative resource choices. About 10% of the meat from the very largest prey and about 5% of meat from prey under 180 kg went to the hunter's household (Hawkes, O'Connell, and Blurton Jones 2001). If the portions that went elsewhere were repaid in shares from the recipients' kills, then the exchange value of the shares that went elsewhere would properly be counted as part of the household income a man earned from hunting. This explanation for meat sharing, consistent with Trivers's (1971) model of reciprocal altruism, has been widely favored among behavioral ecologists and evolutionary psychologists (Cashdan 1985; Kaplan and Hill 1985; Winterhalder 1986, 1997; Smith 1988; Cosmides and Tooby 1992). In this meat-for-meat exchange model, individuals trade benefits over time, each taking a short-run cost to net long-run gains from trade. If getting shares is contingent on giving them, with the result that hunters continue to share only with those who repay and exclude defaulters, then those who share do better than those who don't (Axelrod and Hamilton 1981). But contingency is crucial: without it, sharers are vulnerable to free-riders, who take benefits but do not pay them back (Trivers 1971, Cosmides and Tooby 1992).

Woodburn (1998) claims that Hadza meat sharing is not exchange, and analysis of our sample of household meat shares (Hawkes, O'Connell, and Blurton Jones 2001) supports his view. We did not find evidence of contingent sharing. The size of shares that went to a man's household was unaffected by his hunting success or the relative time he spent hunting. As is common among ethnographic foragers, Hadza meat distributions were not controlled by the successful hunter. Even if a hunter had been "keeping score," he had no opportunity to direct shares to some recipients and away from others. The meat was more like a public good than the hunter's private property. Others got shares whether or not they had provided them in the past, and a man's household got shares from the large prey taken by others whether he hunted much or not. Therefore most of the meat from a kill had no effect on the marginal nutritional gain a man could expect to supply to his own family. What he earned for his household by specializing in big game was the 10% or less of the meat from any big game he captured. These results provide the basis for calculating an expected rate that can be compared with the rate of household income he could earn from adjusting his foraging practices to target other resources.

The overall daily average acquisition rate for big-game hunting of 4.9 kg/hunter-day (table 3) includes nighttime ambush hunting in the late dry season. In our sample, there is marked year-to-year variation in the rate of meat acquisition by nighttime hunting across dry seasons, the

TABLE 3  
Hunters' Average Acquisition Rates

Type of Hunting	Kg (live wt) per Hunter-Day	Failure Rate per Hunter-Day
All big-game hunting and scavenging, 1985-89	4.88	0.97
Late-dry nighttime ambush hunting		
1985	5.24	0.96
1986	1.98	0.98
1988	0.46	0.998
All daylight encoun- ter hunting and scavenging, 1985-89	3.17	0.98
Experiments with small game		
Encounter hunting	0.25	0.77
Snaring	0.78	0.43

SOURCE: Hawkes, O'Connell, and Blurton Jones (1991).

1985 rate being notably high (table 3). Here we focus on *daytime* encounter hunting and scavenging, a year-round activity that trades off against the daylight hours men could otherwise spend taking small game or plant foods. The overall average *daytime* take for big game is 3.2 kg/hunter-day. Men spent just over 4 hours of daylight hunting (table 2), and therefore a big-game hunter could expect a daytime acquisition rate of 3.2 kg/hunter-day, divided by 4.1 hrs/day, or 0.78 kg/hunter-hour. In our household sharing sample, the successful hunter's household (and those of other men) got 5% of the meat on average from prey weighing less than 180 kg. This is the size-range of 68% of the prey in our full large-animal sample (48 of 71 animals). The hunter's household got 10% of the meat when prey were larger. Using this more optimistic figure, his expected *household* return rate would be 10% of 0.78, around 0.08 kg/hr.

Although Hadza hunters generally ignored small animals, experimental data (Hawkes, O'Connell, and Blurton Jones 1991) indicate minimum return rates of about 0.25 kg/hunter-day for encounter hunting small game and 0.78 kg/hunter-day for snaring. Small animals taken as prey draw little attention and so are easily kept by the hunter or, if brought home, by his household (Woodburn 1968, Barnard and Woodburn 1988). If the meat of small animals is mostly consumed by household members, then the whole acquisition rate for these prey is the marginal gain that a man could earn for household meat consumption by taking small animals.

The average acquisition rate a man could expect to achieve for his own household was 0.08 kg/hr if he specialized in large prey and 0.04 kg/hr if he specialized in small (table 4). By these calculations, a hunter seeking to maximize his household income should not specialize in small animals *instead of* large, but he *should include small animals* among the prey he takes (Hawkes,

O'Connell, and Blurton Jones 1991). Each time he encounters a small animal, he can expect to earn its average postencounter acquisition rate while he pursues it. The measured postencounter rates for small animals ranged from 0.23 to 1.5 kg/hr (Hawkes, O'Connell, and Blurton Jones 1991). This means that each time a hunter encounters a guinea fowl and passes by in order to continue earning 0.08 kg/hr searching for big game, he is reducing his household income. Even if neighbors made claims on small animals, a man who pursued them and kept less than half of the *lowest-return* small prey would still earn a greater nutritional benefit for his own household than he would get from specializing in big game.

Measuring return rates in kilograms per hour for large and small prey allows approximate comparisons, since both are composed of meat. Macronutrient differences are unlikely to be large. Hunting and plant-collecting comparisons involve a complication. While both can be evaluated in Calories/hour, a calorie of carbohydrate may be worth less (or more) in nutritional value than a calorie of protein (Hill 1988). Assuming 1,500 Cal/kg of prey (Lee 1979), the expected household income from big game is about 120 Cal/hr. This is lower than the rates that all but the very youngest children earn from plant collecting (Blurton Jones, Hawkes, and O'Connell 1989, 1997). Men could earn rates similar to those women earn from gathering (Hawkes, O'Connell, and Blurton Jones 1995). Even if calories of fat and protein were four or five times more valuable than calories of carbohydrate (Hill 1988), men could earn higher rates of nutrient gain for their families by gathering plant foods than they earn as big-game hunters.

These comparisons are based on mean rates. They ignore the most important reason that big-game hunting is an ineffective strategy for provisioning a family: *It does not provide a reliable nutrient stream*. The daily risk of failure for a Hadza big-game hunter is consistently  $\geq 96\%$  (table 3). Big-game encounter hunters can expect to fail 45 days for each success, while small-game encounter

TABLE 4  
Comparison of Daytime Big-Game and Small-Game Hunting

Resource Target	Average Acquisition Rate (kg/hunter-hr)	Average Rate for Forager's Own Household (kg/hunter-hr)	Average Number of Days Between Successes
Daytime big-game	0.78	~ 0.08	45
Small-game			
Overall	0.04	0.04	1-3
Postencounter	$\geq 0.23$	$\geq 0.23$	1-3

SOURCE: Hunting acquisition rates from Hawkes, O'Connell, and Blurton Jones (1991); percentage to hunter's own household for big game estimated from meat-sharing data in Hawkes, O'Connell, and Blurton Jones (2001).

hunters would go only 1–3 days between successes (table 4), and plant collectors would rarely if ever come home emptyhanded (table 5).

Two points should be stressed: (1) the strong inverse relationship between prey size and success rate and (2) the fact that the low success rate for large prey among the Hadza is actually high by comparison with other modern foragers. The Ache, for example, hunting in the forested Neotropics of Paraguay, capture an average of 0.66 prey/hunter-day in the size-range under 10 kg. For prey in the 20–40 kg range, the Ache rate falls to 0.06 prey/hunter-day. Two prey species larger than 40 kg (tapir and capybara [Hill and Hawkes 1983]) are taken so rarely that no captures occurred over observations of 674 hunter-days (Hawkes, Hill, and O'Connell 1982). Lee (1979) reports that among traditional !Kung-speaking Bushmen in arid southern Africa “few hunters kill as many as five big animals a year” (p. 216) and estimates that “over the long run a hunter averages only two or three large antelope a year” (p. 242). During the 83 hunter-days covered by his 1964 !Kung work diaries, no large antelope were taken. Only 4 of the 18 prey captured during that period weighed more than 10 kg (p. 266), and those were warthogs taken by the best hunter using his “excellent dogs.”

The differences in success rates for large prey reflected in these numbers are mostly due to differences in animal densities (Damuth 1981) and consequent encounter rates. Hadza encounter large animals much more often than do Ache or !Kung hunters. Yet, even though the big-game hunting is relatively good in Hadza country, it generates an income much too unreliable to support a family. A Hadza hunter sees animals often and is close enough to try a shot almost daily, yet he still goes *weeks* without making a kill or acquiring a large carcass by scavenging. Then, when he *is* successful, most of the meat goes to others. Even though the long-term overall average he supplies to the group with this foraging strategy is high, the marginal increase in his own family's nutrition is less than he could earn in other ways. These data are inconsistent with the hypothesis that men's hunting is a strategy for family provisioning.

#### CHILDREN'S WEIGHT CHANGES

If hunters are provisioning their families, the children of better hunters should be better nourished.

Hawkes (1993b) reported more positive weight changes for the weaned children of better hunters. While this finding directly supports this second hypothesis, it is puzzling in light of the preceding observations, arguments, and analyses.

The 1993 report was based on a cursory tabulation of a subset of the 1985–86 weights. Small sample sizes and strong seasonal variation in weight changes (Hawkes, O'Connell, and Blurton Jones 1997) sharply limit the resolution of these data, so conclusions must be tentative. Those same factors also make strong patterns especially impressive. For the full set of weights, there is no relationship between father's hunting success and children's

TABLE 5  
*Comparison of Daytime Big-Game Hunting and Plant Gathering*

Resource Target	Average Acquisition Rate (Cals/forager-hr)	Average Rate for Forager's Own Household (Cals/forager-hr)	Average Number of Days Between Successes
Daytime big-game	1,650	120	45
Plant foods	≥ 1,000	> 1,000	0

SOURCE: Hunting acquisition rate from Hawkes, O'Connell, and Blurton Jones (1991); percentage to hunter's own household for big game estimated from meat-sharing data in Hawkes, O'Connell, and Blurton Jones (2001); plant acquisition rate from Hawkes, O'Connell, and Blurton Jones (1995).

weight changes ( $n = 54$ ,  $r = 0.007$ ), but the circumstances of the late dry season, in which ambush hunting was so successful (table 1, season 1), require special attention. Hunters were much more successful in the late dry of 1985 than at any other time. In this season, which accounted for 33% of the observation days of the time-allocation sample, hunters took > 60% of the total amount of meat acquired during that period (table 1). Perhaps small additional portions had negligible value when meat was generally available—in fact, this relatively heavy meat-eating season was the only one in which children generally lost weight. The children of better hunters may have gained more weight (or lost less) in the *other* seasons because even small additional amounts made a large difference when meat was usually scarce. When the late dry season is excluded from the analysis (fig. 1), there *is* a positive relationship between father's overall hunting success rate and children's weight changes.

For the largest prey, the hunter's share is significantly larger than the shares to the households of other men (Hawkes, O'Connell, and Blurton Jones 2001). While better hunters do not take relatively more of the largest animals,<sup>4</sup> they take everything more often. If the children of better hunters are better nourished because they get more meat from their fathers' hunting, then their weight changes should be related in time with their fathers' kills.

A weak test of this third hypothesis appeals to seasonal differences in individual hunting successes. If more positive weight changes are due to the father/husband's holding a larger share more often, then variation in his success by season should predict the relative weight changes of his children. It does not. Excluding the late dry, there is no correlation between child's seasonal weight change and father's seasonal hunting success (large prey that season/days observed):  $n = 40$ ,  $r = -0.086$ .

4. For the 43 large prey taken by men for whom we have enough observation days to estimate success rate, the correlation between success rate and estimated carcass size is  $-0.0303$ .

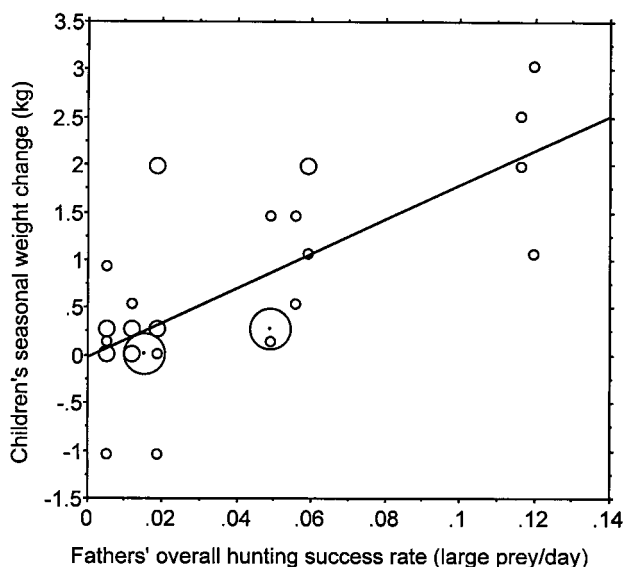


FIG. 1. Children's seasonal weight change (kg), excluding the late dry season, by fathers' overall hunting success rate (large prey captured when resident in study camp/total days observed as study camp resident). Circle size indicates the number of cases with the same coordinates. The line is the best-fit linear regression:  $n = 39$ ,  $r = 0.677$ ,  $p < 0.001$ .

While the second hypothesis is supported, this one, its correlate, is not. Combined, these analyses do *not* support the proposition that better hunters' children gain more weight because they eat more of their fathers' kills. Yet, as shown in figure 1, *something* appears to connect children's nutritional status to husband/father's hunting success rate. One possibility is that better hunters are better foragers generally, supplying more other foods to their households.

#### THE CONTRIBUTION OF HONEY

Some resources taken by men are more predictable than big game. If more foraging time means more nongame food to a hunter's household, then the co-resident children of men who spend more time acquiring it may be better nourished. One food besides meat that is routinely acquired by Hadza men is honey. When foragers return to camp with loads of honey, people present cluster around to claim shares. Any honey visible is widely distributed. However, unlike foraging groups targeting other resources, honey-collecting parties are often composed of nuclear-family members. All members of the party consume large amounts of honey as it is taken throughout the day. This could provide an opportunity for men to channel nutrients differentially to the members of their own household. Better hunters' children may be better nourished because their father provides more honey for them.

On average, men spent 1.5 hrs/day collecting honey in seasons 2, 6, and 7 and  $< 10$  min/day in other seasons. Considering only the high-effort seasons, the relationship between the time a man spent honey collecting and the weight changes of his co-resident children does not support this fourth hypothesis:  $n = 32$ ,  $r = -0.269$ , one-tailed  $p = 0.068$ . It borders on statistical significance but in the direction opposite to the prediction. Still, in the honey seasons, as in the rest of the year outside the dry season, the children of better hunters gained more weight ( $n = 31$ ,  $r = 0.608$ ,  $p < 0.001$ ). Since this variation appears to be unrelated to differences in the amount of food provided by fathers, *something else* may link men's long-term hunting success rates to children's weight changes.

#### THE CONTRIBUTION OF WIVES AND MOTHERS

If men are hunting to provision their families, the wives of better hunters, receiving more support, may be able to work less themselves.

When women's average daily foraging hours (indexed by the fraction of 12 daylight hours allocated to foraging away from camp in the seasonal time budget) are plotted against husbands' seasonal hunting success (fig. 2), it is apparent that women do *not* forage less when their hus-

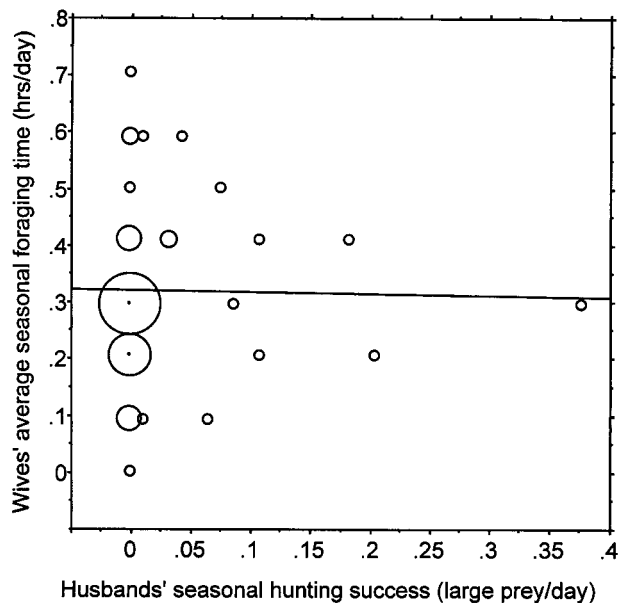


FIG. 2. Wives' average seasonal foraging time (hrs/day) by husbands' seasonal hunting success rate (large prey captured when resident in study camp that season/days observed as study camp resident that season). Circle size indicates the number of cases with the same coordinates. The line is the best-fit regression:  $n = 36$ ,  $r = -0.014$ , one-tailed  $p = 0.468$  (excluding late dry:  $n = 30$ ,  $r = 0.059$ ).



bands' seasonal hunting success rates are high.<sup>5</sup> Excluding the late dry, when large amounts of meat in camp may have reduced any provisioning advantage associated with holding larger shares, does not change this result. High variability in seasonal success rates could mean that much larger samples are needed to reveal significant relationships, but it is just this variability that makes hunting a poor provisioning strategy. The mismatch with common expectations about hunting as provisioning is underlined by the *positive* relationship between a man's overall hunting success rate and the foraging effort of his wife (fig. 3). The pattern remains when the late dry season is removed. Better hunters have harder-working wives.

Elsewhere we have reported results that link the foraging efforts of Hadza women to the nutritional welfare of their children and grandchildren (Hawkes, O'Connell, and Blurton Jones 1997). Hadza women tend to target similar resources within a season, their foraging return rates have low day-to-day variation, and the plant foods they acquire are not much shared beyond their own children and grandchildren. On those grounds, we used time spent foraging as an index of the amount of food that women supplied to their households. We found a positive correlation between mothers' foraging time and the weight changes of their weaned children as long as mothers were not nursing. Mothers foraged less with the arrival of a new baby, but increased efforts from grandmothers provided the nutrient stream to support their weaned grandchildren (Hawkes, O'Connell, and Blurton Jones 1997).

Could it be women's work that accounts for the correlation between hunters' success rates and their children's weight changes? The earlier report of the association between fathers' hunting success rates and children's weight changes (Hawkes 1993*b*) listed four possible pathways by which a hunter's success rate could differentially affect nutrition in his household: (1) the household of the hunter responsible for a kill might hold larger shares of the meat; (2) the families of better hunters might be better treated by neighbors; (3) better hunters' households might have the nutritional advantage of constant co-residence with that hunter; or (4) the children of better hunters might be better foragers themselves.

Data reported in Hawkes, O'Connell, and Blurton Jones (2001) show that the first of these is not usually the case. The hunter's household gets no more than others when prey are less than 180 kg. Although the successful hunter's share *is* larger for the very largest carcasses, the distribution of a hunter's kills over time (his seasonal success rate) is not related to the differential weight changes of his children (as reported above) and so is a poor candidate to account for them. In light of the associations between the foraging of mothers (and grandmothers) and children's nutrition, we have added a fifth possibility to the list: If better hunters tend to have harder-working wives, their children's nutritional

5. Number of weaned children in the household has no effect on Hadza women's foraging time.

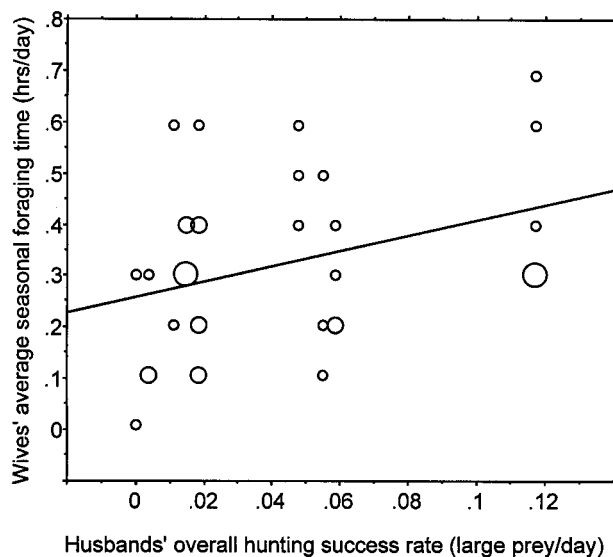


FIG. 3. Wives' average seasonal foraging time (hrs/day) by husbands' overall hunting success rate (large prey captured when resident in study camp/total days observed as study camp resident). Circle size indicates the number of cases with the same coordinates. The line is the best-fit regression:  $n = 35$ ,  $r = 0.345$ , one-tailed  $p = 0.021$  (excluding late dry:  $n = 29$ ,  $r = 0.407$ ,  $p = 0.014$ ).

advantages may be the indirect reflection of the direct effect of mothers (and grandmothers) (Blurton Jones, Hawkes, and O'Connell 1997).

Hawkes (1993*b*) reported that a man's hunting success was correlated not only with his children's weight changes but also with those of his wife. Both results were based on a subset of the 1985–86 data. As with the children (detailed above), the correlation with wife's weight changes disappears when all the data in the 1985–86 sample are included ( $n = 22$ ,  $r = 0.293$ ,  $p = 0.186$ ) but emerges when the late dry season is removed (fig. 4). Children's weight changes are positively related to those of their mothers in all seasons (fig. 5) as well as in the subset that excludes the late dry.

These overlapping associations among household members raise suspicions about indirect effects. Are the associations between children and their mothers only indirect, resulting (by pathways as yet obscure) from the common effect of the same husband/father's overall hunting success rate on both his wife and his children? Or is the association between children's nutrition and fathers' hunting success rate an indirect result of better hunters' marrying women who are better able to manage their own nutrition and that of their children?

Our investigation of women's trade-offs (Hawkes, O'Connell, and Blurton Jones 1997) showed that mothers reduced their foraging effort and their contribution to weaned children on the arrival of a new baby. When

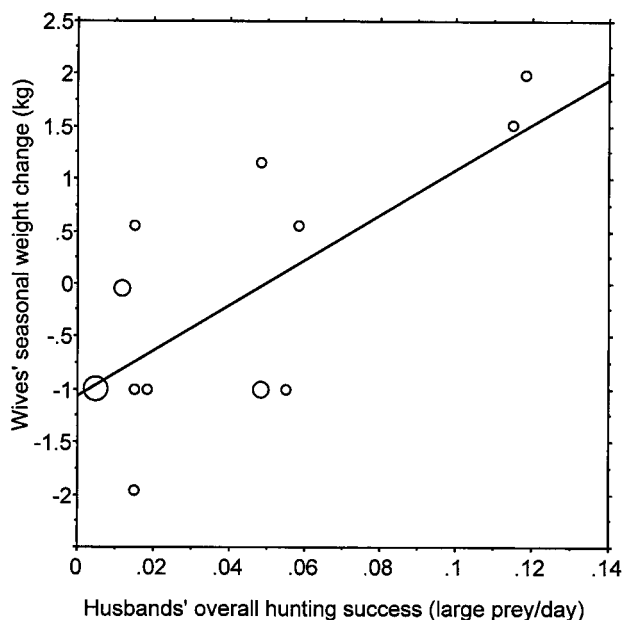


FIG. 4. Wives' seasonal weight change (kg), excluding the late dry, by husbands' overall hunting success rate (large prey captured when resident in study camp/total days observed as study camp resident). Circle size indicates the number of cases with the same coordinates. The line is the best-fit regression:  $n = 16$ ,  $r = 0.696$ ,  $p = 0.001$  (if late dry were included:  $n = 22$ ,  $r = 0.293$ , one-tailed  $p = 0.093$ ).

women were not nursing, their children's weight changes were more positive the greater their own foraging effort, but this relationship disappeared when they had a nursing infant.

Since mothers allocate so much effort and attention to a nursing infant, provisioning from fathers would be especially important to weaned children whose mother is nursing another infant. If hunters are provisioning their households, they should make a greater difference in their children's nutrition when their wives have a nursing infant. Under those circumstances the children of better hunters should have more positive weight gains.

Figure 1 showed that, outside the late dry season, children's weight gain is predicted by their fathers' overall hunting success. Figure 6 plots only the cases in which mothers were nursing new infants. Here, when children are generally assumed to be most in need of father's provisioning, the relationship is a bit weaker (compare figures 1 and 6), but it remains significant.

Children's weight gains are most strongly linked with their fathers' hunting success outside the late dry season when their mothers are *not* nursing (fig. 7). These same weight gains are also correlated with the children's mothers' foraging effort (fig. 8), a correlation that holds across all seasons (fig. 9). To investigate whether the relationship between children's weight gains and their

mothers' work is an indirect reflection of their fathers' hunting success (by some as yet undiscovered pathway), we calculate the partial correlation. Controlling father's hunting success, the partial  $r = 0.847$  (versus  $r = 0.804$  when husband's hunting success is not removed). The relationship between mother's effort and child's weight gain is *not* a reflection of father/husband's hunting success.

The differences in children's welfare that initially appear to result from the hunting success of their fathers are largely reflections of the foraging efforts of their mothers (and grandmothers). We have no direct consumption measures. The limits of the data are considerable. Within those limits, positive relationships between a man's hunting success and the nutritional welfare of his children are due not to advantages in meat eating but to differential effort from the women to whom better hunters are linked by marriage.

## Discussion

### THE HUNTING HYPOTHESIS

Hunting has long been viewed as the keystone innovation that propelled the evolution of other behavior that distinguishes hominids from other apes (e.g., Washburn and Avis 1958, Washburn and DeVore 1961, Lee and DeVore 1968, Isaac 1978, Kaplan et al. 2000). According

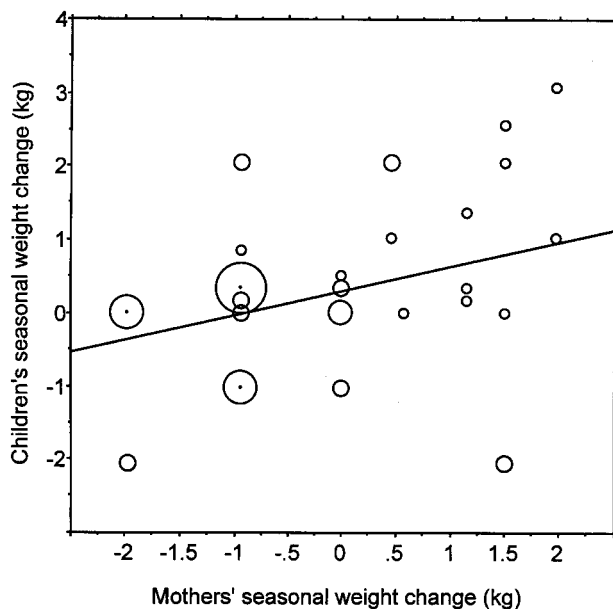


FIG. 5. Children's seasonal weight change (kg) by mothers' seasonal weight change (kg). Circle size indicates the number of cases with the same coordinates. The line is the best-fit regression:  $n = 45$ ,  $r = 0.34$ , two-tailed  $p = 0.022$  (excluding late dry:  $n = 34$ ,  $r = 0.559$ ,  $p < 0.001$ ).

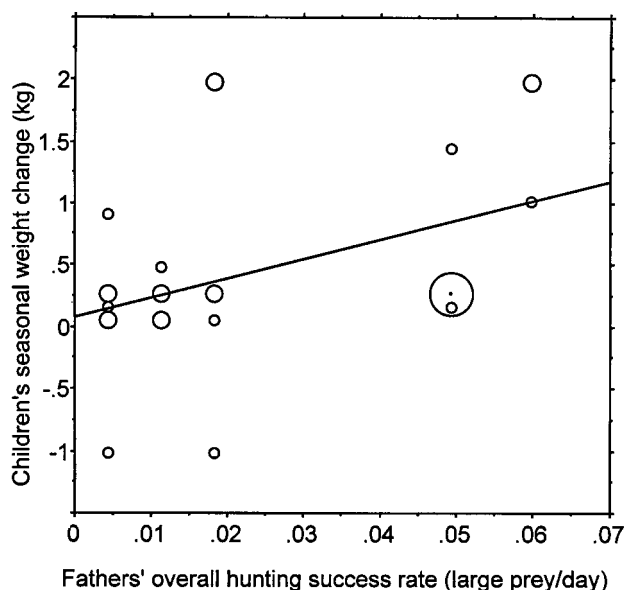


FIG. 6. Children's seasonal weight change (kg), excluding late dry, by fathers' overall hunting success rate (large prey captured when resident in study camp/total days observed as study camp resident), when mothers are nursing new infants. Circle size indicates the number of cases with the same coordinates. The line is the best-fit regression:  $n = 28$ ,  $r = 0.413$ , one-tailed  $p = 0.014$ .

to this argument, the spread of savanna environments reduced the availability of plant foods and increased opportunities for predation. Hunting males acquired packages of valuable nutrients large enough to share with their mates and offspring. Women chose husbands whose support allowed them to bear and rear more offspring, the children themselves being more dependent on their parents. Not only nuclear families, the sexual division of labor, and monogamy but also other distinctively human patterns of cooperation arose because game animals are large enough to allow sharing beyond the household and hunting is risky enough to require it. Hunters reduced the family subsistence risk by sharing meat with other hunters in exchange for recipients' obligation to repay it later. This remains the most widely used foundation for ideas about human evolution, even though challenges to it, especially in paleoanthropology and hunter-gatherer behavioral ecology, have continued to mount.

Influential syntheses in the 1960s and '70s linked hunting for family provisioning with the use of stone tools, expanded brains, and the appearance of bipedal locomotion (e.g., Washburn and DeVore 1961, Isaac 1978), making paternal hunting a fundamental trigger of the hominid radiation. Subsequent fossil discoveries showed that hominids were bipedal before 4 million years ago—millions of years before the appearance of

stone tools and expanded brains (Johanson and White 1979). At the same time, the claim that hunting was indicated by the appearance of stone tools in association with large animal bones at Plio/Pleistocene archaeological sites came under strong challenge (Binford 1981). Subsequent work inclined researchers to the view that the hominids associated with the formation of the early sites had only scavenged residual meat and marrow after remains were abandoned by other vertebrate consumers (Blumenshine 1987, 1991). Others surmised that Plio/Pleistocene hominids at least occasionally acquired large animal carcasses with meat still attached, possibly by aggressive scavenging (e.g., Bunn and Ezzo 1993, Capaldo 1997, Dominguez-Rodrigo 1997). Even if fully fleshed carcasses were sometimes appropriated by the early Pleistocene hominids, many lines of evidence indicate that this would have happened much too rarely to provide the subsistence foundation for the radiation of genus *Homo* (O'Connell, Hawkes, and Blurton Jones 1988, O'Connell et al. 2001, Lupo and O'Connell 2001). Regular hunting of large-animal prey is now generally seen to date no earlier than the late Middle Pleistocene (within the past half-million years) (e.g., Mellars 1995, Stiner 2001, Klein 2000). Over the past few decades, those working directly with the paleoanthropological record have found less and less archaeological foundation

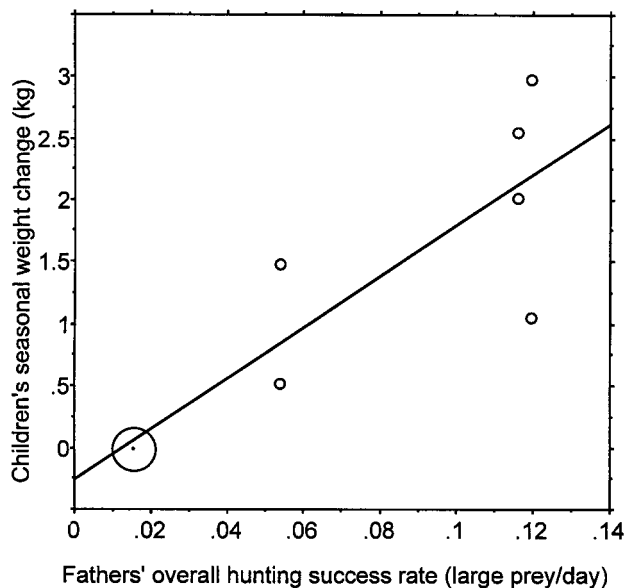


FIG. 7. Children's seasonal weight change (kg), excluding late dry, by fathers' overall hunting success rate (large prey captured when resident in study camp/total days observed as study camp resident), when mothers are not nursing. Circle size indicates the number of cases with the same coordinates. The line is the best-fit regression:  $n = 11$ ,  $r = 0.885$ ,  $p < 0.001$ .

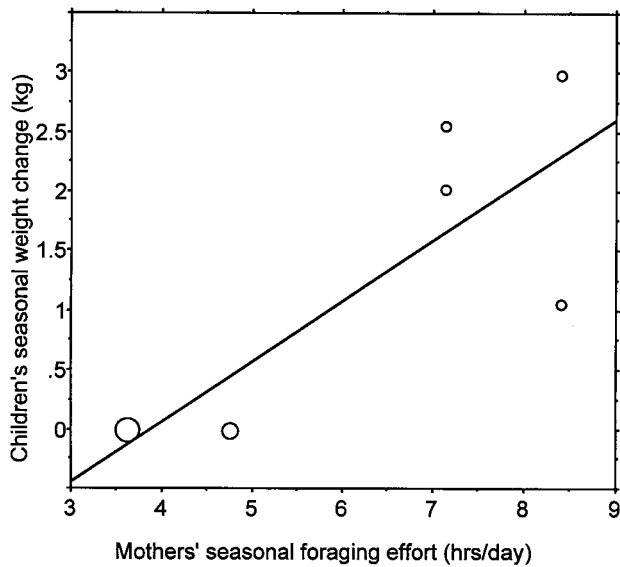


FIG. 8. Children's weight change (kg), excluding late dry, by nonnursing mothers' foraging time (hrs/day). Circle size indicates the number of cases with the same coordinates. The line is the best-fit regression:  $n = 9$ ,  $r = 0.848$ ,  $p < 0.001$ .

for inferences that hunting fueled the initial hominid radiation or the subsequent radiation of our genus.

Meanwhile, the view that among more recent hunter-gatherers men usually hunt to provision their families was challenged by ethnographic studies in modern foraging communities. A record of the food-sharing patterns among Ache foragers (Kaplan 1983, Kaplan and Hill 1985) provided quantitative documentation of two patterns previously observed among other hunter-gatherers (e.g., Lee and DeVore 1968). Most of the food adults and children ate was acquired by someone outside their own nuclear family, and meat was so widely shared that the hunter's own nuclear-family members got no more than others did (Kaplan and Hill 1985). Aspects of the quantitative Ache record were consistent with the possibility that some foods were more widely shared because the cost of *not* sharing resources with certain characteristics was especially high (Blurton Jones 1984, 1987). Ache men preferentially targeted just those foods that (whoever acquired them) were most widely shared (Hawkes 1991). Since a wide range of consumers could expect nutritional benefit from the hunter's effort, with relatively less going to his own family, it was suggested that men's foraging strategies might be better understood as mating competition than as paternal effort (Hawkes 1990, 1991).

This show-off hypothesis was subsequently modified and elaborated to highlight the similarities between public goods and large-animal carcasses that are widely shared and the collective-action problem entailed in their supply (Hawkes 1992, 1993a; Hawkes, O'Connell, and Blurton Jones 1991). Selective incentives for sup-

pliers are generally required to motivate the continued contribution of collective goods (Olson 1965). Preferential attention, status advantages, and prestige can be effective incentives. The hypothesis that hunting is often more an arena of male status rivalry than paternal effort has been contested (e.g., Hill and Kaplan 1993, Kaplan et al. 2000, Gurven et al. 2000). Recent applications of costly-signaling theory (Veblen 1899; Zahavi 1975, 1977, 1990, 1995; Zahavi and Zahavi 1997; Boone 1998; Neiman 1998; Frank 1999; Smith and Bliege Bird 2000; Miller 2000) expand the domain of the debate, underlining similarities between show-off explanations for hunting and explanations for other kinds of costly displays. Bliege Bird (1999; Bliege Bird et al. 2001) has shown the promise of costly-signaling models for explaining not only men's hunting but also an array of other differences in the foraging choices of men and women.

Different kinds of hunting practices and different ecological and ethnographic settings pose different explanatory problems. Day-to-day hunting differs from communal surrounds or drives that involve more participants, different scheduling, and perhaps different incentives for participation. Sometimes such group hunting has been suggested in evolutionary scenarios (e.g., *Time-Life* representations), but at least as often solitary hunters are described, each seeking captures for his own family (e.g., Ridley 1996). Descriptions of traditional hunting among !Kung-speaking Bushmen of the Kalahari have been especially influential in these scenarios (Isaac

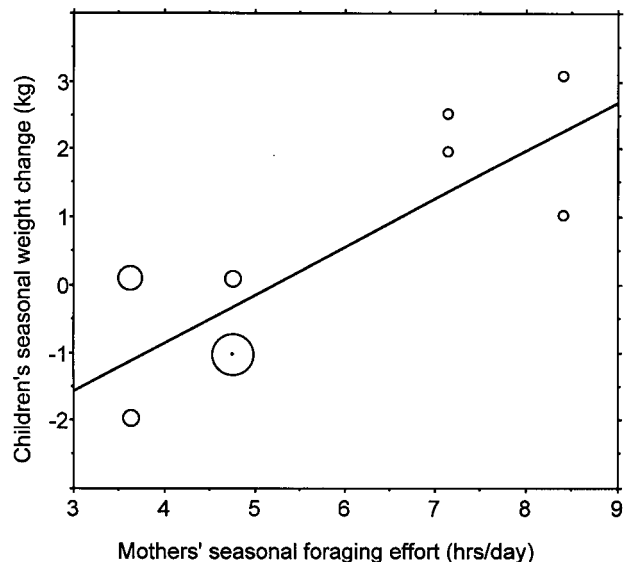


FIG. 9. Children's weight change (kg), all seasons, by nonnursing mothers' foraging time. Circle size indicates the number of cases with the same coordinates. The line is the best-fit regression:  $n = 16$ ,  $r = 0.804$ ,  $p < 0.001$ . (When husbands' overall hunting success rates are controlled, the partial correlation is  $r = 0.847$ ,  $p < 0.001$ ).

1978). Among the !Kung, as among the Hadza, men usually searched for big game alone or occasionally in pairs (Lee 1979). Because the most prominent statements of the hunting hypothesis refer to daily encounter hunting in or near the arid African tropics, the payoff to hunters and the fate of the family-provisioning assumptions in such cases is of special interest. The data and analysis reported here are further challenges to the view that hunting is family provisioning. Differences in nutritional welfare of women and children are not linked to differences in meat rations from the kills of their hunting husbands/fathers. Women married to better hunters work more rather than less.

Yet, among the Hadza, as in most foraging communities, people form nuclear families. An important source of the resilience of the view that human hunting is mainly family provisioning is that it would so simply account for marriage and the nuclear families that distinguish modern humans from the other great apes (Boyd and Silk 1997, Deacon 1997, Lewin 1998, Pinker 1997, Ridley 1996). "Husband" and "father" are socially recognized roles in virtually all human societies (Murdock 1949). In hunting-and-gathering economies, the meat that men acquire is a highly prized and usually a quantitatively important component of local diets (Lee 1968, Hill 1982, Kaplan et al. 2000). The challenges to the hunting hypothesis that are extended here do not dispute the generalization that meat is often an important and highly valued human food. Instead, the issues in contention are whether human hunting is largely paternal effort (i.e., a hunter's investment in his own children), whether marriage is essentially a bargain women rely on for subsistence support, and whether human "divisions of labor" by sex are outcomes shaped to serve the common economic interest of nuclear families (Bliege Bird 1999).

#### EXPLANATIONS FOR PAIR BONDING

Pairing for reasons other than paternal provisioning has emerged as important in studies of other primates (Wright 1990, Smuts and Gubernick 1992), in mammals generally (Komers and Brotherton 1997), and—where it is the most frequent mating system—in birds (Gowaty 1996). Male attempts to control female sexuality (Smuts 1992) and female responses to the dangers that males can pose (Hrdy 1979, 1999) are recognized to play an important role in human as well as other primate mating systems (Mesnick 1997, van Schaik and Dunbar 1990, van Schaik and Kappeler 1997, van Schaik, van Noordwijk, and Nunn 1999, Wrangham 1979, Wrangham et al. 1999).

Since monogamy almost never occurs in nonhuman mammals unless females are dispersed (Komers and Brotherton 1997), the patterns among birds, where it is common in the absence of dispersion, are of special interest for possible human implications. More than 30 years ago, in his definitive review of avian breeding patterns, Lack (1968) explained the extremely high frequency of monogamy as the result of the large payoff to nuclear families from paternal provisioning. Subse-

quently the focus on conflicts of interest among males and females sharpened considerably among students of animal behavior (Williams 1966, Trivers 1972). Those studying birds were further alerted to other costs and benefits as techniques for detecting genetic parentage came into use, showing that social pairing often does not imply genetic monogamy (Birkhead and Møller 1992).

Ornithologists have the advantages of measuring large demographic effects over relatively short time spans, as well as wide latitude in treatment of their subjects. In addition to uncontroversial paternity testing, they can experimentally manipulate pairs and broods and evaluate the assumption that paternal care is crucial to offspring survival over a single field season. Reviewing the data from removal experiments, Gowaty (1996:489) concluded that "for many females male parental care has small or negligible effects on female reproductive success, suggesting that as a general explanation for social monogamy, the Male Care is Essential Hypothesis is inadequate."

For birds the paternal provisioning side of Lack's classic hypothesis is under revision. The effects of mating competition on persistent pairing are increasingly evident. Davies (1991:283) surmised that "the predominance of monogamy in many birds arises not, as Lack proposed, because each sex has greatest success with monogamy, but because of the limited opportunities for polygyny. . . . Strong competition among males makes it difficult for a male to gain another female." Investigations of mate-guarding are fairly recent among ornithologists, but the topic has a longer history of attention in studies of mating patterns in humans. Researchers with diverse theoretical orientations have emphasized the mate-guarding aspects of marriage (Goodenough 1970, Broude and Greene 1980, Flinn 1988, Wilson and Daly 1992). In humans, however, this has been attributed to an assumed species habit of high paternal investment, with mate guarding a consequent strategy to improve the chance that the effort is not misdirected (Daly, Wilson, and Weghorst 1982, Daly and Wilson 1987, Wilson and Daly 1992). No such habit need be implied (Hawkes, Rogers, and Charnov 1995). Widespread evidence that males display jealousy in species where they make little or no parental effort shows that male competition for paternity by itself is enough to favor male jealousy and coercion (de Waal 1982, Smuts and Smuts 1993, Clutton Brock and Parker 1995).

#### THE EFFECT OF FATHERS ON CHILDREN'S WELFARE

The monogamy typical of hunter-gatherers has usually been attributed to a hunter's inability to support more than one wife (e.g., Alexander et al. 1979), an explanation that depends on the paternal-provisioning assumption. Among modern humans, both those who depend on foraging and those who make a living in other ways, fathers sometimes do supply substantial parental care. But often they do not.

The Ache of eastern Paraguay are an especially well-studied case (Hill and Hurtado 1996) and one in which

foraging men worked unusually long hours (Hill et al. 1985) to make an especially large contribution to overall subsistence (Hill et al. 1984). As we also found among the Hadza, foraging Ache mothers with nursing infants spent less time gathering food for themselves and their weaned children than women who were not lactating (Hurtado et al. 1985). If wives relied on *husbands* for subsistence, a husband's help would be especially important following a new birth. Hill and Hurtado's (1996) extensive interviewing provides an account suggesting that, in contrast, nursing women were *less* likely than other women to have their husbands' help. They report (pp. 275–76):

A good number of men admitted abandoning a female partner during her pregnancy, only to return several months after the birth had taken place (or sometimes not returning at all). . . .

The temporary abandonment of new mothers was commonly observed by us and is probably a traditional pattern. [An Ache man reported]: "In the forest we didn't marry [stay married to] new mothers. Their bodies smell, the old men said. . . . The smell of milk was the only reason we were afraid [to be married to them].

In the case of the Hadza, the limited data reported here show little or no direct effect of fathers on children's differential nutrition. Blurton Jones et al. (2000) found no effects of Hadza fathers' presence on children's survival. Using demographic data from four hunter-gatherer societies including the Ache and the Hadza, they looked at the varying effects of co-resident fathers on children's survival and the relationship between these effects and the stability of pair bonds. They found, as Hurtado and Hill (1992) had noted in a comparison of two foraging societies, that marriages did not last longer where fathers' continued co-residence had larger effects on children's welfare. Instead, pairing was more stable when men faced more intense mating competition.

#### MATING COMPETITION AMONG MEN

Again the Ache record is especially rich. In the forest, marriages were quite fragile, women averaging ten marriages by age 30 (Hill and Hurtado 1996:231). At any one time, most Ache adults were monogamously married, but most also had experienced shorter-term polygamous unions. "Virtually every adult woman over the age of thirty-five" had been polygynously married, and of the men interviewed in detail about their marital history 60% (11 of 18) had been *polyandrously* married (Hill and Hurtado 1996:229). Plural marriages usually dissolved because of "fighting between co-spouses." Notably, women admitted more jealousy in such relationships than did men. Hill and Hurtado quote a polyandrously married man who insisted: "When we husbands slept with our wife we could see each other have intercourse

at night. We weren't annoyed. We men weren't bad-tempered." The ethnographers say (p. 230):

These denials of male jealousy are similar to conversations we have had with many Ache men who claim that when their wives have affairs with other men they are not angry at the man who cuckolded them, but they are upset with their spouse. Ache men often beat their wives under such circumstances, but they never directly confront her lover. We believe that such denials provide more information about the character of male alliances and confrontation than they do about differences between the sexes with regard to jealousy.

The importance of male competition is further underlined by the problems that Ache boys confront as they grow into men (p. 227):

Although young women seemed generally willing to experiment with early trial marriage (they could always break it off the next day), young men were more reticent. Older men discouraged the young men from marrying or having sex, and boys would become targets in club fights when they began to "have" women openly.

Hill and Hurtado's conclusions about the importance of male competition deserve emphasis: Negotiating and maintaining fragile relationships of sociability with other men who are competitors for the same paternity plays a central role in Ache mating and marriage.

Blurton Jones et al. (2000) have suggested that mating competition among men could lead to conventions in which a man's claim on a wife, once established, was (more or less) recognized by other men. The advantages of settling contests by convention are especially great when contestants are armed with lethal weapons. In addition, because humans are more like birds than other primates in the dependence of the young on provisioning, human females would have a special interest in supporting conventions among men that reduced interruptions and danger from contestants for mating. Since human mothers must provision their children well past weaning, attention from sexually interested males could impose especially troubling interference costs on foraging women. A husband who reduced that interference would be an asset (Smuts 1992, Mesnick 1997, Wrangham et al. 1999).

Yet, among many modern hunter-gatherers, including both the Ache and the Hadza, husbands and wives spend much of the day apart. As Woodburn (1968) noted, the separation of the sexes is especially notable among the Hadza. Usually men and women not only forage separately but part on leaving the house in the morning and join different social groups even when both are in camp. The extreme mate-guarding patterns observed in some human communities (e.g., Flinn 1988, Wilson and Daly 1992) are absent here. Yet, there is no anonymity and no privacy. Gossip is the main entertainment. In intimate communities, language may remove any need for a

guarding mate to stand constant vigil. With marriage a publicly acknowledged relationship known by all, gossip may reveal (and expectation of it reduce) threats from any man on another's claim. If a woman gained some protection from the publicly recognized claim of her husband, a husband with higher standing among other men might be a more effective protector. Female choice could thus reinforce the status competition among men (Blurton Jones et al. 2000).

#### BIG-GAME HUNTING AND COMPETITION

If storytelling allows husbands to guard their mates without personal vigilance, it also allows hunting reputations to be known and compared by an audience that need not observe any kills directly (Hawkes 2001). Among the Hadza, as with the foraging Ache, hunters spend most of their time away from their wives. Hunters often make kills when no one is watching. Others have a keen interest in hunting nevertheless, and not only in the successes of their own husbands/fathers. Most of the meat that anyone eats comes from captures made by men in other households. Wide meat sharing makes the successes of all hunters a matter of direct interest to everyone. Both wide sharing and great emphasis on the desirability of meat have long been highlighted by ethnologists (Wiessner 1996), but the processes underlying both and their implications for men's foraging goals have been disputed. Many assume that hunters share to provide insurance against the risk of hunting failures, exchanging meat for obligations to repay it later. Quantitative observations in some ethnographic settings show food being distributed to repay past debts (e.g., Hames 2000, Gurven et al. 2000), but this is not so in other cases, especially for meat (e.g., Kaplan and Hill 1985, Hawkes 1993a, Bliege-Bird and Bird 1997, Hawkes, O'Connell, and Blurton Jones 2001).

Among the Hadza, the very high daily probability that a hunter fails combined with the very large piles of meat when one succeeds makes any hunter's success a matter of interest to an especially wide audience, even including people in other camps. It takes more time to butcher and consume large carcasses. They are an attractive bonanza that allows concurrent use by many consumers. With any hunter's success a matter of general interest, hunting is an especially attractive arena for male competition. Hunting skill can be among the most important determinants of men's social standing, much more important when big animals are taken than when they are not.

This is a basis for the hypothesis that an important benefit a man earns for himself by hunting big animals is favorable audience attention that affects his social standing relative to other men (e.g., Dowling 1968; Hawkes 1993a, 2000). Among the Ache, men with better hunting reputations have much higher fertility than other men (Hill and Hurtado 1996). The pattern shown here—that better Hadza hunters have harder-working wives—suggests that better hunting reputations make Hadza men more successful competitors for mates. Elsewhere we report that Hadza women who are producing

surviving children faster are married to men with better hunting reputations. Better hunters between the ages of 40 and 65 are more likely to have wives younger than 45, implying that they are more likely to desert their first wives in mid-life and start new families with younger ones. These patterns suggest that better hunters are more likely to out-compete suitors for both first and second wives (Blurton Jones, Hawkes, and O'Connell 1997).

Women may prefer to marry better hunters for an array of reasons. Men of higher status may be better protectors, and other benefits may flow from association with them (Blurton Jones et al. 2000). The subsistence benefits claimed by the hunting hypothesis, however, are much less important than widely assumed and perhaps even absent altogether. Wives and offspring receive little or no more meat than others from the hunting of their husbands/fathers. They do, however, benefit from the hunting of all men who target big animals. To the extent that men are drawn into hunting big animals through mating competition, this form of competition has distinctive consequences. Unlike the kind of showing off that gives an audience only information, such as peacocks' tails or other costly displays that signal hidden qualities (Veblen 1889, Zahavi 1975, Grafen 1990, Johnstone 1997), hunting brings in material benefits for many (Hawkes and Bliege Bird 2001). In fact, in some cases like the Hadza, men may contribute more food to the collective when their foraging goal is not family provisioning. The modern Hadza example, with parallels among other recent hunter-gatherers, offers empirical support for the hypothesis that men's work is often driven by male competition. This hypothesis may be an especially useful tool for developing evolutionary scenarios about the initial emergence of men's work as a substantial source of human subsistence.

## Comments

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This is another wonderful paper from Hawkes and company. I am particularly delighted by their demonstration that sharing among hunter-gatherers is not an exchange process. This is no minor issue, given the depth of the concept of reciprocity in contemporary bourgeois thought and particularly among their colleagues in evolutionary biology. At the same time, the meat of hunters is not a public good, either. Scarce goods are never there for the taking; there are always mechanisms that structure the allocation of shared goods. The more appropriate analogy is *entitlement* on the basis of social position (among those present at the distribution). Hawkes et al. have found that there is no special entitlement for the family of the hunter. It is possible that

there are no differentials in entitlements among Hadza families, leading to the suggestion of a “public good.” We know that the reward for the hunter comes in the form of prestige, often realized by his conspicuous role in the distribution of meat or, indirectly, by his being able to confer the same privilege on a structural superior.

The paper proceeds much like a crime novel, taking a desultory course toward the discovery of a solution; and as it is with many a good mystery, the culprit is quite unexpected. To my mind, the solution is also most improbable. A point of controversy that other observers will raise is that men choose women for their talents as wives and lovers, not for their ability to provide food for future children. The latter factor can be only an unpredictable downstream bonus. Unfortunately, Hawkes et al. cannot argue that women work harder in order to retain better hunters as husbands, given the presumed lack of any inducement for doing so.

So, why do better hunters have healthier children? The answer to this question requires a fuller appreciation of the rewards of being known as a good hunter.

For many hunter-gatherers there are times of great plenty and times of great hunger. At these extremes there is a tendency for available supplies to be distributed broadly (Ingold 1980:146–47). However, during periods of modestly reduced availability, there is a tendency for the camp to disperse into smaller units, often single-family units, foraging for smaller patches of gathered foods and smaller prey. As Ingold makes plain, better hunters are desired as leaders of these smaller groups, given their prestige for competence.

The families of the better hunters are clearly advantaged during periods of dispersal not only because of the superior abilities of the particular hunter but also because men of prestige are better able to select companions whose presence would be most advantageous, creating thereby more effective teams. In the African context, the focus of attention at such times would be on gathering, and we would expect the wives (and other family members) of better hunters to be advantaged by optimal aggregations in their gathering activity.

However, seasonal variations in the levels of social aggregation are not prominent in the discussion by Hawkes et al. We are told that “in some seasons they search specifically for honey, often *in nuclear-family parties*” (my emphasis). This tells me that there is an unexplored variable here. Can that be where the true culprit lies?

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Hawkes and colleagues present us with a rich set of data and carefully argued analyses to address long-standing anthropological debates about the evolution and maintenance of human social arrangements. They have demonstrated that among the Hadza (1) men’s specialization in hunting and sharing *only* big game does not maximize

household meat income, (2) while children and infants of better hunters are better nourished, this is not correlated with the amount of meat and honey acquired by their fathers, and (3) the wives of better hunters spend more time foraging and have better-nourished children, but these are not a product of increased advantages supplied to them with meat from better hunters. These results allow them to question further the notion that human families are units of common economic interest maintained when hunting and sharing are designed to support offspring and mates. Along the way, they are able to supply us with provocative, often elegant suggestions concerning nuclear-family formation and mate pairing for reasons other than paternal provisioning.

The Hadza data reflect a common cross-cultural theme that suggests that household incomes are not always pooled, that men and women often have divergent goals for the income they produce, and that under certain circumstances men may direct their income in ways that do not benefit children directly. In settings as different as Ghana, Bangladesh, Guatemala, and India, the *proportion* of income that a father directs to his household is consistently correlated with increases in children’s health, but increases in father’s overall income do not predictably translate into enhanced welfare of his children. In contrast, women’s absolute income and the trade-offs they face in production and child care do have a direct effect on children’s well-being (see reviews in Bennett 1990, Dwyer and Bruce 1988, Khandker 1998, Wilk 1989). For example, a 10% increase in borrowing from the Grameen Bank by Bangladeshi women resulted in a 6% increase in arm circumference and an 11% increase in height of their daughters. No effect or occasional negative effects on a household’s children were observed when loans were made to fathers (Khandker 1998). In the United States and South Africa, proportional spending on alcohol and tobacco is lower when a child’s birth mother is present in the household and when she has control over resource distribution (Case, Lin, and McLanahan 2000), and mothers also allocate more resources toward ensuring positive health outcomes in their children than do coresident stepmothers or birth fathers (Case and Paxson 2000). The observation that fathers do not automatically distribute their incomes to their households does not mean that fathers are not significant: the presence of fathers can often reduce child mortality (e.g., Hill and Hurtado 1996), and fathers do contribute food and direct care to their children, even among the Hadza (Marlowe 1999). What seems clear is that absolute income is not a good predictor of a father’s level of investment in offspring, though it is of a mother’s, and that even though mothers may often earn less than fathers they may direct that income in ways that more efficiently invest in children than in some other alternative arena. While Hawkes and colleagues do not specifically investigate alternative foraging goals, they suggest that intrasexual competition (for prestige, social attention, mates, and allies) may be a critical component of men’s subsistence strategies.

The more general implication, that pair-bond stability



may be less about paternal provisioning per se than about men's concerns over competition for paternity and women's concerns for harassment protection, should encourage new attention toward testing some alternative predictions about how these might structure socially recognized contracts and pairing arrangements. Recent research investigating the causes of pair bonding and social monogamy among nonhuman primates suggests that protection may be one important function (Van Schaik and Kappeler 1997, Palombit 1999) but that it may not be sufficient to explain all instances of social monogamy (Fuentes 2000). Among chacma baboons, males and females commonly form long consortships that seem to be due to the payoffs for mate guarding and protection from infanticide—these form within multimale/multi-female groups and are not associated with social monogamy (Weingrill 2000). Tamarins are now suspected to form pair bonds for reasons other than raising offspring: helpers that are not male mates more significantly affect the number of offspring raised in both new and established groups (Bales et al. 2000). This may be not because of protection from predators or aid in transport but rather because all group members (not just males) provision juveniles and such support may allow mothers to wean offspring earlier. Among humans, pair bonding and social monogamy may have equally disparate causes, and there are likely to be circumstances of pairing where women do not benefit from protection or male provisions directly affect women's decisions to marry and have children (e.g., Borgerhoff Mulder 1990). Recently Schoeninger et al. (2001) have suggested that Hadza's women's return rates from tubers would be much too low to support others, the implication being that the calories provided by the successful male hunters in the group may be making up for shortfalls in women's foraging. These issues and the more general ones that Hawkes and colleagues raise will undoubtedly require continued attention to resource characteristics and factors that influence time allocation, income, and distribution patterns in various social and ecological settings.

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Hawkes, O'Connell, and Blurton Jones's sophisticated analysis of Hadza hunting, women's labor, game distribution, and child weight changes provides strong evidence that big-game hunting is not a form of paternal investment. The issue I wish to address is whether the Hadza provide a general model for hunter-gatherers or the evolution of the nuclear family.

I think it might be more profitable to subsume the hunting hypothesis under a model of the evolution of biparental care. Humans differ fundamentally from our closest ape ancestors in that human males invest in their offspring (or the offspring of the women with whom they are currently consorting) to a degree unmatched by apes.

This investment can range from direct and indirect infant care (Hewlett 1992) and food provisioning to protection of children from coresidents. The hunting hypothesis is a particular instantiation of the evolution of biparental care. In its most extreme form, males specialize in big-game hunting as a form of parental investment. In return they acquire paternity certainty and increase their fertility and the survivorship of offspring. To a large extent, this is the model evaluated by Hawkes et al., and it is found to be wanting. I think they are correct in suggesting that big-game hunting is overemphasized in evolutionary scenarios as the primary mechanism for the creation of nuclear families. Nevertheless, males do more than hunt big game; they gather, acquire small game, and care for offspring. Thus it may be the case that big-game hunting is not the mechanism through which biparental care evolved but other economic and investment activities are sufficient to create families through biparental care.

As Hawkes et al. note (Dowling 1968), in many foraging societies that specialize in hunting the general rule is that men share game, especially large game, with the entire community. However, there are a number of societies in which widespread sharing is a seasonal phenomenon. For example, in Damas's (1972) comparative analysis of sharing among the Iglulik, Netsilik, and Copper Eskimo we find that that widespread sharing occurs largely when large camps occupy the sea ice during winter seal hunting. During the part of the year when caribou and anadromous fish are sought, there is little or no sharing outside of the nuclear family. In both of these cases men, sometimes cooperating with one another, are the primary producers of fish and caribou for their own families. Internuclear-family sharing is not expected unless one family has been unlucky. A closer look at the Netsilik case reveals that male hunting and fishing are designed to provision families for most of the year (Balicki 1963:117–19) and sharing is the exception rather than the rule. Other examples of foragers who share hunting resources in a restricted manner are described by Kelly (1995:166). These examples demonstrate that big-game hunting is sometimes a form of paternal investment and men can seasonally play the role of "show-offs" or paternal investors.

In providing these counterexamples where males' hunting of large game (caribou clearly qualifies) is designed to provision their own families, my goal is not to counter Hawkes et al.'s generalization with negative evidence but to try and untangle the ecological factors that may promote or inhibit the general sharing of large game. One factor that seems important is camp size. Among the Netsilik winter sea-ice camps sometimes contain up to 150 individuals. At this time they hunt ringed seal, and it is shared through partnerships which ensure that the share received by the successful hunter's family is no greater than the shares given to partners and their families. However, in the summer group size falls to as few as one to three families during the inland pursuit of caribou and fish, and sharing is rare. Men are expected to provision their own families. Significantly, perhaps,

hunting success is strongly synchronized between hunters (the caribou herd is either present or absent) and there is no utility in sharing. In contrast, hunting seal at breathing holes is a very chancy business, and hunting success seems not to be synchronized. A useful model of whether resources will be shared which is independent of resource size is presented by Winterhalder (1986). It seems to me that to answer the question of whether big-game hunting played a significant role in the evolution of the nuclear family would depend on whether resource acquisition patterns of men matched those specified by Winterhalder.

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Humans are, in biological terms, cooperative breeders. Mothers depend on others to rear young successfully; however, variation in who provides assistance within and across groups is remarkable in light of the completeness and duration of juvenile dependence. Hawkes, O'Connell, and Blurton Jones have made key contributions motivating anthropology to revisit the recipe for human life-history evolution, elucidating the role of postreproductive female aid, the value of extracted tuber resources to the human diet, and the foraging efforts of children as factors affecting maternal reproduction. Here they take on one presumed constant in human parenting effort: the role of fathers and their investment interests in provisioning young. Hawkes et al. suggest that the children of better hunters are better nourished not because of paternal effort but because their mothers are more successful foragers. The results demonstrate that Hadza men are not maximizing daily caloric returns to their families by participating in big-game hunting.

As is the case for all null findings, the interpretation of null associations between father's hunting success and children's weight deserves further scrutiny. Several possibilities exist: (1) there is no association between father's hunting success and his children's weight; (2) individual variation in income between hunters after primary meat distribution is insufficient to account for variation in children's weight; (3) father's hunting success is not directly related to the dosage (intake) of meat children consume (e.g., meat is shared across varying numbers of individuals at multiple points in the distribution chain); (4) children's weight is a poor outcome measure because of confounding effects of age, sex, and variation in caloric intake from other sources; (5) the temporal relationship between paternal returns and children's weight does not capture the true latent period of meat intake; (6) statistical power is low because of small sample size; (7) some third variable remains unmeasured. Most of these alternatives can be evaluated only with food-sharing data and other measures of children's nutritional status (Willett 1990) and reflect the difficult (but ultimately rewarding) challenge that behavioral ecologists

experience in quantifying behavior and biological outcome in small and dispersed populations.

The hypothesis that male economic behavior is better explained as mating effort is important and warrants additional analyses, but posing these strategies as mutually exclusive underestimates the potential sophistication of male fitness calculus and the costs of coordinating action in groups. Big-game hunting and the food-sharing patterns it promotes constrain individual males' ability to direct captured resources differentially to mates, potential mates, offspring, or other kin. Optimizing trade-offs between mating, parenting, and alloparental (inclusive) fitness opportunities does not necessarily imply divergent productive behaviors. While it is true that calories are depreciable (food consumed by one's lover cannot be consumed by one's children), by targeting highly valued foods and sharing them widely human males can simultaneously invest in multiple fitness avenues and reduce the risk of failure of any one path to reproductive success. In this way, group hunting and sharing may have become a stable strategy for males across highly variable environments with changing access to mates and payoffs to offspring quality, even if competitors gain as well (i.e., mutualism [e.g., Alvard and Nolin 2001, Sosis 2000]). Such benefits suggest that Hawkes et al.'s delineation of data constituting paternal provisioning is unnecessarily narrow. While Hadza children often consume meat acquired by other men, do children without fathers (or without hunting fathers) fare as well? Human males provision young both directly through their own efforts and indirectly by participating in a cooperative (or competitive) economic behavior whose outcome is shared food.

Meat is not the daily bread but is irreplaceable as a key source of protein, fats, and important nutrients (Hill 1988, Kaplan and Hill 1992). Protein intake affects immune function (Chandra and Chandra 1986) and maintenance and growth (Bogin 1999), including that of brain tissue (Mann 2000), and is associated with life-history parameters of body size, growth velocity, and age of menarche (Ahmed et al. 1998, Berkey et al. 2000), fecundity, pregnancy (King 2000, Kalhan 2000), lactation (Motil et al. 1989), and child development (Bhargava 2000; Winikvist, Habicht, and Rasmussen 1998). Indeed, protein requirements are highest early in life when growth is rapid (Marquis et al. 1997, Ulijaszek 1995). Tubers, upon which the Hadza depend, are notoriously poor sources of nutrients. While children, adult female, and postreproductive female Hadza are demonstrably quite productive (Blurton Jones et al. 1997, Hawkes et al. 1997), maternal reproduction still appears to depend on the nutritional support of a mate (Kaplan et al. 2000). It is unclear why males, while valuing the reproductive payoff of meat as mating currency, would be insensitive to its reproductive payoff as parental investment. Testing assumptions of such importance strengthens our understanding of the evolution of human reproduction and behavior.

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Hawkes, O'Connell, and Blurton Jones force us again to rethink the idea that the purpose of human male hunting behavior is family provisioning and consequently to rethink the evolution of mating systems and social organization in *Homo sapiens*. The focus on men's hunting as either parental investment or mating effort seems rather artificial to someone whose early training was in ornithology. In a broad array of birds males procure food and offer that food to females in a courtship context as well as in the context of parental investment. Men's hunting behavior is unlikely to serve only one evolutionary purpose or to serve the same purpose(s) irrespective of ecological setting. Hawkes et al.'s documentation of the distribution, benefits, and costs of hunting is important to understanding the evolution of human social organization. That said, I remain unconvinced that male provisioning of relatives (and particularly offspring) is unimportant.

Hawkes et al. show that bringing down quite large game (> 180 kg) results in larger proportional distributions to the hunter's household—roughly double the proportion received from small game. Since fitness is a measure of relative reproductive success, this proportional increase might, under conditions of deprivation, be significant. That the hunter's household receives 5% or 10% is of interest, but we need to know how per capita distributions differ. If 5–10% within the household results in a per capita distribution substantially greater than that to *individuals* in other households receiving some share of the kill, then there is a marginal benefit to the hunter's household members. Material fitness benefits to kin through large-game hunting mitigate the argument that large-game hunting is primarily a means of showing off and gaining matings and is therefore mating effort rather than parental effort.

Given large-game hunting, the fitness costs of the distribution of large proportions of game outside of the hunter's household are potentially mitigated in two ways. First, in a storage technology, what cannot be consumed quickly is likely to be unusable. Once a large prey item is obtained, sharing what can be neither used immediately nor stored incurs little actual fitness cost. Natural selection occurs among existing alternatives, and therefore how much meat can be consumed before it becomes inedible is relevant. Secondly, the individual fitness cost of meat distributed outside the hunter's current household must be discounted by the relatedness of individuals receiving this bounty. Hawkes et al.'s statement that good hunters of middle age have younger wives because of serial monogamy suggests that some children outside the current household may be offspring of those same hunters (from previous wives). Thus, some proportion of the meat being distributed outside the household may well be supporting a hunter's own offspring. If hunting is mate attraction (and I have no quib-

ble with the idea that this is one component motivating hunting behavior), then one would expect good hunters to have more children outside of marriage. Sharing should increase out-of-wedlock and out-of-household offspring's well-being. This would tend to reduce the observable nutritional effects of being in the household of a good hunter versus that of a less successful hunter and may explain the lack of significant differences in weight gains between children within and outside the current households of good hunters. Hawkes et al. say that "the data and analysis reported here are further challenges to the view that hunting is family provisioning." Rather, I think they challenge the view that hunting is solely (or perhaps even primarily) family provisioning when "family" is defined as the current household. The data clearly indicate that large-game hunting is not solely parental investment but do not clearly indicate that it is not, in part, family provisioning.

Information on the reproductive success of good hunters of large game both within and beyond their contemporary households and on the per capita (rather than per household) distributions of meat may allow Hawkes et al. to apportion large-game hunting into mating effort, parental effort, and, potentially, kin investment components. One might expect that the relative importance of each component would vary with ecological circumstances. A broad comparison across hunting and gathering societies of detailed hunting success and resource distribution is critical for understanding the economic workings of human families faced with various levels and distributions of resources in traditional subsistence economies. This work emphasizes again that the "nuclear family" or a household is not a monolithic interest group. To the extent that resources pursued by men are allocated not only to current offspring but also to acquiring additional mates and providing for those mates and any resulting offspring, the fitness interests of husbands and wives will be in conflict.

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The essence of Hawkes et al.'s hypothesis, as I see it, is that Hadza males' orientation toward hunting big game was based on considerations of mating competition rather than family provisioning. The hunting strategies would, however, look different if we regarded the effort of any single Hadza hunter as part of a joint effort to meet the meat-provisioning needs of the whole band. Big-game hunting (unlike the combination of big- and small-game hunting), then, would appear to be the best strategy for maximizing returns ("Mean rates in meat for big game were about 5 kg/hunter/day, while the measured rates for specializing in small game were much less than 1 kg/hunter/day"). Such a strategy seems in full accord with the egalitarian hunter-gatherer ethos,

and the system of resource distribution inherent to such a strategy can be called “generalized meat distribution” instead of “meat sharing.” Hawkes et al., however, tend to view big-game hunting as one of many possible strategies for family meat provisioning, and therefore they contrast the two factors which might have led to the choice of big-game hunting, mating competition and effectiveness in family provisioning.

I would argue instead that big-game hunting resulted both from mating competition and from the effectiveness of big-game hunting as a joint effort of the whole band’s hunters. In other words, Hadza males preferred to hunt big animals not only out of a desire to win more diligent and sexually attractive marriage partners but also in an attempt (according to the conventional wisdom) to ensure the meat-provisioning needs of the whole band in the most effective and least risky (in terms of average returns) way. In support of this line of argument I would point to Deacon’s paper on the shift in some parts of South Africa around 9,000 years B.P. from mobile big-game hunting to more generalized food resource procurement strategies (Deacon 1978:106–7), the causes of which were either ecological or technological (or both) rather than having to do with changes in mating strategies. An additional argument is that the !Kung hunters of the Namibian part of the Nyae Nyae (N//hwa !ai) region in the 1950s concentrated on big antelope hunting, did no snaring (which was the task of aged hunters and youngsters), and rarely hunted small animals (Marshall 1976:295–303), while the Dobe area (Botswana, /Kai/Kai and /Kangwa Valleys) prime-aged !Kung males hunted small local antelopes and set snares regularly (Yellen and Lee 1976:45–54). The reason for this difference is obvious: in the Dobe area the game populations were depleted by the pressures of the pastoralist economy, whereas in the Nyae Nyae region they were not.

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This article presents evidence that, among the Hadza, differential hunting success does not directly affect the relative nutritional status of the hunters’ wives and children but, rather, affects the quality of the wives that hunters acquire. Good hunters, it seems, have wives who are better able to provide for themselves and their children. I can see some weaknesses in the development of this argument. For example, the lack of correlation between weight gain of wives/children and short-term hunting success of the husband/father could equally well be explained by other households’ reciprocating gifts of meat received in the past. While Hadza hunters may have little control over the primary distribution of meat from a kill, I would be surprised if sharing did not continue through secondary and further transfers that allowed more scope for directed giving. A valued household

might thus receive small additional portions of meat from many others when someone else brings in game. It should also be recognized that hunters can choose to move on from a community that does not adequately acknowledge their contribution. Turnover in foraging communities can be high (for example, while the community Hawkes et al. studied averaged 35–50 residents, time budgets were calculated for 90 residents through the year). While hunters may not be able to direct differential shares of their catch to particular individuals, they can certainly direct their contributions differentially between communities.

I would not expect a wife’s foraging effort to be negatively correlated with husband’s hunting success unless needs were limited, and no case is made for this here. A positive correlation with overall hunting success could arise if, as Hawkes et al. propose, successful hunters attract women who are inherently more hardworking and thus better able to provide for themselves and their children. But a positive correlation also could be expected if hunting success affected the extent to which men were able to protect their foraging wives from interference or distraction by other men. It is precisely such ability to protect that Hawkes et al. propose is good hunters’ attraction for women. It may be, then, that hunters are not competing for more productive women but buying their women freedom to be better providers. Success in this would, of course, affect a hunter’s attractiveness to women and thus his ability to acquire high-quality wives. The “quality” being sought, however, may not be foraging productivity. Women, like men, may contribute to quality of children in ways other than providing food.

Hawkes et al. suggest that hunting evolved as a form of paternity competition in which the community at large is co-opted to support the claims of those who provide something of value to all its members, thus reducing the need for constant investment in guarding mates. Since all stand to benefit from any large kill, the movements of all men are monitored, but closest scrutiny is reserved for anything that might affect those who have proved most successful in the past; thus, intrusion on their interests will be least likely to go unnoticed and unreported. This raises a difficulty, however. The variation in hunting success between Hadza men is so high that it is difficult to see why poor hunters would continue to pursue large game, thus consistently demonstrating their lack of quality. Such men surely would do better to seek other strategies for obtaining and defending access to mates and contributing to the well-being of their children. Since they do not, we must consider the possibility that the costs of not pursuing large game are greater, here, than the costs of doing so. It may be that members of the community penalize those whose behaviour precludes contributing valued goods as much as they reward those who succeed in doing so. In that case, hunting—and male work in general—might be seen as the product of coercion as much as competition.

Further analyses might well demonstrate that hunting success among Hadza does not benefit children of the hunter either directly or indirectly through trade or fa-

ilitating production by his wife. It might indeed be the case that, among Hadza, hunting success benefits both the hunter and his mate only through its effect on the degree to which others in the community monitor and inhibit intrusions on the hunter's claims. This in itself, however, would provide no basis for inferring that hunting in other societies is driven by competition for paternity rather than paternal investment. It certainly would not justify an assertion that hunting evolved in response to such competition. An understanding of the functional relationships that maintain a pattern of behaviour today does not necessarily contribute to explaining the origins of that behaviour. Even if hunting and sharing of large game by humans evolved in a physical environment similar to that in which the Hadza now live, the social environment may have been very different. The discussion in the article is predicated on earlier observations that pairing tends to be more stable when competition for mates is intense. The description of Ache pairing behaviour, however, suggests that relationships in that society are far from stable. If competition between Ache men is indeed high and hunting provides a public arena for that competition, then the co-evolutionary link proposed here between hunting, marriage, and nuclear families appears weak.

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Hawkes et al. have contributed yet another important, insightful paper on what the ethnographic data on foraging people can tell us about human evolutionary ecology. They challenge the notion that males' hunting success is aimed at provisioning their families. They test this assumption directly and also indirectly, as manifested in a mother's ability to provide greater parental investment if her mate is an outstanding hunter. Their elegantly tested six hypotheses allow a careful consideration and rejection of the notion that male investment in hunting is all about risk reduction in meat foraging, at least among the Hadza. It seems clear that, at the very least, advocating meat-provisioning as the only purpose of male hunting effort is simplistic. Hawkes et al. use this paper to further their efforts to replace a meat-as-nutritional-package with their own hunting-as-costly-showing-off hypothesis (Hawkes 1990, 1991). They attempt to use this data set to overturn "the hunting hypothesis." I am not quite sure which hunting hypothesis they are talking about; they cite Washburn and DeVore (1961) and Kaplan et al. (2000) in the same breath, without elaborating on the exhaustive data set and multifaceted predictions about life history and other variables that the latter paper is concerned with. In other words, there's a straw man in the paper, and it is Man the Hunter. If we reduce the main issue in the paper to that of the centrality of meat in the human diet and

therefore in human evolution, we find Hawkes et al. challenging a mountain of data on meat eating in the paleoanthropological, archaeological, primatological, and ethnographic record. Their alternative to meat and to the reasons for spending inordinate amounts of time and energy trying to obtain it is not clear. Whether meat is highly sought after for nutritional, political, or reproductive purposes, it is indisputable that it is highly sought after. Even if we posit hunting as costly signaling, the fact that the object of the hunt happens to have prime nutrient and caloric value makes it extremely likely that there is a fitness component to hunting that underlies and enables hunting-as-mating-effort to work. Thus Hawkes et al. find themselves in the paradoxical position of arguing that the point of hunting is not the meat that is captured, yet meat once captured fills a nutritional role that is undeniably important. Given that foragers the world over seem to eat as much meat as they can, in whatever form they can (Cordain et al. 2000), that meat foraging is not linked to fitness via dietary parameters is an exceedingly hard case to make. In spite of my enthusiasm for their skepticism of conventional wisdom about forager behavior ecology, I feel that it is warranted to ask Hawkes et al., "Where's the beef?"

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It is rare to see the kind of theoretical and methodological coherence and continuity of focus that the authors of this paper, together and sometimes in association with others, have maintained through their fieldwork and writing. In this sense alone, their work is always welcome. Firmly centered in and at the center of human behavioral ecology, they have frequently tested conventional anthropological wisdom at all levels. This present work is no exception. I think, however, that it also raises some questions, at least for me, about the degree of ethnological reality that this perspective can incorporate.

I will, however, limit my comment to one specific point. This relates to the obvious detachment of the economic component of hunter-gatherer culture from its social organizational aspect(s). There seems to be a tendency in this literature to focus on the household as the principal unit of domestic economy, despite the centrality of the kin-based band (Kelly 1995) as the affiliative core of hunter-gatherer aggregates. While I am unable to speak specifically to the Hadza, Ache, or many other foraging groups, my own work and that of others on Eskimo societies (see Damas 1972; Nooter 1975; Fienup-Riordan 1983; Wenzel 1995; Bodenhorn 2000) strongly suggests that the extended family forms the effective domestic economic unit as much today as in the past. I continue to see this as critical for understanding Inuit subsistence—despite Smith's (1991) Inujjamiut analysis—and suggest that hunter-gatherer economic relations

are more socially based and complex than behavioral models currently allow.

But kin-relatedness among task group members, while clearly important to the way such groups are composed and paid off, may only be one factor of many. It may also be, and indeed is among Inuit, that within these task groups, which may include unrelated hunters, the efforts of seemingly unsuccessful participants are recognized as contributing to the success of others and it is the investment of time and energy by these "losers" that is acknowledged through sharing.

It is of considerable analytical importance, therefore, that the organization of sharing, as it affects economic events within extended families and between unrelated households or larger village-scale groupings, be considered. Among Eastern Arctic Inuit, while the extended family clearly is of preeminent economic importance, the *nunariit* (those who reside together) is also encompassed within this sharing economy (see Damas 1972; Wenzel 1991, 1995). How these economic arrangements are organized at each of these levels is critical to understanding not only the material flows resulting from these transactions and who are the consequent "winners" and "losers" but, more salient, the importance of subsistence in the social maintenance of hunter-gatherer culture.

## Reply

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We thank the commentators for their attention and stimulating ideas. Among the issues raised by their remarks we take up four: (1) the hunting hypothesis, (2) humans as a biparental or cooperatively breeding species, (3) the importance of nonmeat resources in hunter-gatherer diets, and (4) the generality of lessons from the Hadza.

Stanford chides us for seeing in Kaplan et al. (2000) the same hunting hypothesis articulated by Washburn in the late 1950s. Kaplan and colleagues do claim to propose a novel theory. They include longevity in their list of life-history changes, a characteristic not noted by Washburn, and also offer a formal model to show how some aspects of life history might be interrelated. Their formal model includes no variable that specifically represents brains, no sex (so of course no conflicts of interest between the sexes), and no nuclear families. The verbal argument that they claim the model supports, however, is essentially the same as Washburn's: Hunting is the most productive human foraging activity; hunters procure high-quality food in packages large enough to share; bigger brains improve hunting success but require that children mature more slowly, making them more dependent for a longer time on maternal care; more child care makes hunting unprofitable for mothers, forcing them to depend on provisioning by hunting husbands.

This hypothesis has proven remarkably invulnerable to challenge, despite enormous changes in both evolutionary theory and the empirical record. Washburn initially followed Dart in linking an "obstetrical dilemma" and slower child development to the evolution of bipedalism, which Dart thought allowed our lineage to become effective predators. But fossil evidence later showed that bipedality emerged and persisted for millions of years with no evidence of either big-game hunting or an increase in brain size. Decoupling bipedalism from the model left the rest of it (hunting : brain expansion : life-history changes : paternal provisioning) unchanged. Perhaps it is so resilient because it is essentially correct, but here we have added more reasons to think otherwise.

Stanford says that we have failed to persuade him that "meat-foraging is not linked to fitness via dietary parameters." We have not tried. We continue to think it is the nutritional benefit that consumers get from meat that makes them pay so much attention to hunting success. Kazankov points out dietary benefits for the *group* from big-game hunting. But group benefits are not sufficient incentives to explain the behavior of individuals (e.g., Olson 1965, Williams 1966, reviewed in Hawkes 1992). We are looking for fitness-related benefits for the hunters themselves to help explain why they keep at it. Our hypothesis links the hunters' benefits to the value consumers get from meat. But usually others get just as much from a kill as the hunter's own family gets (Hawkes, O'Connell, and Blurton Jones 2001), and most of the time he catches nothing, forgoing opportunities to bring home food to this own family.

Judge says that, given that hunters take large animals (a "given" we want to explain), they incur little cost in sharing the meat because if not eaten quickly it will rot. As we have reported, meat does not lose its value quickly in the Hadza case. Here people can and do dry meat. Drying can store the meat for later Hadza consumption. Not only that, non-Hadza neighbors are eager to trade highly desired goods for it. It is demand for immediate consumption, not an absence of technological means, that limits storage. The ethnographic shorthand "meat sharing" conjures up a picture of hunters choosing how much to keep, how much to give away, and to which particular recipients. This is not what happens. Instead, hungry people come to the butchering site (and subsequently to any residential base where meat has been transported). Like guests at a buffet, they know who the host is but serve themselves. People get shares no matter what their relationship or state of debt to the hunter (Hawkes, O'Connell, and Blurton Jones 2001).

Hunters know that this will happen yet continue to specialize in hunting big animals, choosing to spend effort trying to be hosts instead of feeding their families. We hypothesize that they do this because successful hunting shows a man to be a desirable ally and formidable competitor and thereby earns him differential treatment from others. Hunting big animals is an especially effective advertisement of these qualities *because* hunters do not control meat from large prey. Since ev-

everyone is eager to eat meat and everyone gets some when a large animal is captured, everyone has reason for close and immediate interest in any hunter's success (see Hawkes and Bliege Bird 2001 for more discussion).

Judge notes that per capita distributions of meat are what matters, and these may favor the hunter's relatives in ways that we have not detected. We think that her hypothesis rests on the mistaken assumption that a hunter controls the distribution of meat, but she is correct that our measures are very imprecise. The imprecision is partly due to the phenomenon itself. People claim shares; hunters do not give portions to each recipient. Judge refers to our finding that the hunter's household share is larger for the very largest prey (>180 kg) (Hawkes, O'Connell, and Blurton Jones 2001). This surprising pattern remains to be explained, but it is suggestive that the larger the prey the bigger the party. When prey are especially large, more consumers come to the butchering site and more visit the residential bases to which household shares have been carried (O'Connell, Hawkes, and Blurton Jones 1990, Hawkes, O'Connell, and Blurton Jones 2001).

Ivey says that it is unclear why men would not use meat as parental investment. Since large carcasses are treated as common goods, men could provide more meat for their own families by taking small game. We hypothesize that the reason they rarely do so is the trade-off between paternal effort and mating effort they face. Attention to trade-offs of this kind and especially the inescapable competition among males for limited paternity has helped explain the variation in male strategies across the range of sexually reproducing taxa (Williams 1966, Trivers 1972, Hawkes, Rogers, and Charnov 1995). Our hypothesis is that Hadza men forgo the small animals that they could keep for their families because they gain (or lose) more fitness from their reputations as big-game hunters.

But what about the poor hunters? Minnegal asks why they don't try something else. This good question should stimulate an array of testable hypotheses about the costs and benefits of possible alternative strategies. Our hypothesis does not, however, make hunting competition a winner-take-all contest. Even in the very unlikely event that one man were to acquire large carcasses two days in succession, someone else would score next. The best hunter *usually* fails. This might help explain why male hierarchies can be so much shallower—more egalitarian—among human foragers than among other living hominoids (Hawkes 2000). Anyone who uses his bow *might* be successful. Moreover, a man's most important competitors are those closest in rank. Even the worst hunter may benefit from staying close to the second-worst, and the second-worst could always fall lower.

Hames suggests that we may be inflating the importance of big-game hunting in the evolution of human social organization, pointing out that even if hunting is not paternal effort, men can invest paternally in many other ways. He claims that recognizing humans to be a *biparental* species is the important thing. But assuming that men are usually paternal investors can obscure an

important role for mating competition in shaping male strategies (Hawkes, Rogers, and Charnov 1995). Among other primates, behavior initially interpreted as paternal effort has often turned out not to be (Smuts and Gubernick 1992; van Schaik and Paul 1996; Palombit 1999; van Schaik and Janson 2000).

Primates are an unusually social order. Continuous year-round associations of mixed-sex groups are common (van Schaik and Kappeler 1997) and most likely characterized our hominid ancestors. Group members are potential sources of both harm and help to mothers. Ivey calls humans "cooperative breeders." Our especially high reliance on allomothers is connected to distinctive features of human life history (Hrady 1999). Unlike our nearest living primate relatives, modern humans bear babies at intervals shorter than the time it takes a newborn to attain feeding independence. We think that this pattern of producing overlapping dependents evolved in tandem with our greater longevity and later age at maturity (Blurton Jones, Hawkes, and O'Connell 1999; Hawkes, O'Connell, and Blurton Jones 1997, n.d.; Hawkes et al. 1998; O'Connell, Hawkes, and Blurton Jones 1999), perhaps in the following way: Late Pliocene climatic change limited the availability of resources important to ancestral hominids, forcing them to make greater use of foods that just-weaned juveniles could not handle for themselves. The consequent increase in mother-child food sharing opened a new avenue to fitness gains for senior females whose own fertility was ending. Without nursing infants of their own, more vigorous older females could increase the fertility of their daughters by provisioning grandchildren. Longer adult life spans (extended postmenopausal survival) would have been favored, making it advantageous to delay maturity and so grow bigger before first birth.

Primates as a whole have slower life histories than other mammals of similar body size. Across the primate order there is fast-slow variation as well, from the fast life histories of small mouse lemurs to the much slower life histories of the great apes (Harvey and Read 1988; Charnov and Berrigan 1993). This fast-slow characterization incorporates a suite of correlated life-history features, including longevity, age at maturity, and annual fecundity. Modern human life histories show values on these variables that would be expected if a great ape ancestor had added grandmothering: even greater longevity and later maturity, with shorter interbirth intervals than the "grandmotherless" apes (Alvarez 2001, Hawkes et al. 1998). The evidence from paleoanthropology is consistent with the hypothesis that this adaptive shift separated the first widely successful members of genus *Homo* from the australopithecines (O'Connell, Hawkes, and Blurton Jones 1999, Smith and Tompkins 1995, Hawkes, O'Connell, and Blurton Jones n.d.).

Underlining how much the fitness of most primate mothers can be affected by the way that others treat their offspring, Hrady (1999) notes that with our life history a human mother must be even more concerned than most about the character and availability of help for her children. The attention she pays to a new infant interferes

with what she can do for her other children still not able to feed themselves. Two other elements are part of the same legacy and provide a source of help: grandmothers themselves and juveniles who remain prereproductive longer (Blurton Jones, Hawkes, and O'Connell 1997; Hawkes, O'Connell, and Blurton Jones 1995, 1997). Sometimes fathers help too; but, as Bliege Bird and Bird point out, they often have other priorities. Ivey's (2000) data on allomothering among the Efe of the Ituri provide a particularly well-quantified example: relatives and nonreproductive individuals, "especially adult females and children" (p. 864), are differentially recruited as Efe caregivers.

Biparental-care models carry the implication that nuclear families are fundamental features of human social life, the evolutionary antecedents of "extended" families. Alternative models such as cooperative breeding reverse this sequence: more exclusive pair bonds may be added to a set of older interdependencies. And, as Bliege Bird and Bird point out, the assumption that nuclear families are units of common interest may hamper our explanations of classic patterns in ethnography as well as of "newly emerging" family forms in the postindustrial world.

Readers might see an echo of Washburn's hypothesis in the argument that human mothers face especially stringent child-care trade-offs. If women are differentially concerned with child welfare, wouldn't they turn to husbands for subsistence support? Ivey cites Kaplan et al. (2000) for evidence that Hadza women depend on the "nutritional support of a mate." Kaplan and colleagues use our data and agree with Ivey's characterization of the implications, but, as we continue to point out, the data *do not* in fact support that conclusion. By hunting big game, a man invested effort that did not favor the subsistence of his own household. If he captured a large animal it was a bonanza for all. Over a year Hadza hunters in our sample captured an enormous amount of meat, but it was not predictably available from day to day. Other resources were the basis for reliable daily provisioning. Within the (considerable) limits of our data, it is the foraging effort of Hadza mothers and grandmothers, *not that of fathers*, that differentially affects the nutritional welfare of children.

Ivey notes the need for more data here, and we agree. She also registers her skepticism about the possible importance of tubers, surmising that "they are notoriously poor sources of nutrients." We think that tubers are only one of many important resources aside from big game, but this suspicion of tubers is supported by the surprising news about Hadza tubers in particular mentioned by Bliege Bird and Bird: Schoeninger et al. (2001) report a very low nutritional yield for the staple *//ekwa* (*Vigna* sp.) (100 kcal/kg in their text, 148 Cal/kg in table 4). We have used an estimate of 850 Cal/kg based on our own samples (Galvin et al. 1990) and a similar value reported by Vincent (1985).

Schoeninger and colleagues infer that the reason for the fivefold difference between their estimate and Vincent's is that Vincent did not exclude the inedible frac-

tion. When Hadza eat *//ekwa* they often spit out a fibrous quid. Schoeninger et al. say that Vincent took no account of this. But our measure is similar to Vincent's, and neither Vincent's two labs nor ours made the mistake of including calories from indigestible fiber. For our estimate of spat-out fractions, we chewed weighed subsamples and weighed the resulting quids. Quids ranged from 0 to 42.7% of the peeled weight ( $n = 33$ ), with a mean of 20%. Schoeninger et al. derived their estimate by using a device for mixing liquids called a "stomacher," in which they combined an aliquot of hydrolyzed tuber with salivary amylase. After three to six minutes of mixing, they extracted, dried, and weighed the fibrous mass that remained. They estimated this to be equivalent to expectorated quid, a mean of 57.5% ( $n = 5$ ), two and a half times our average. That difference and a difference of 27% more dry fraction in our sample than theirs (28.4 g/100 g in our samples [ $n = 34$ ] versus 22.3 g/100 g in theirs [ $n = 4$ ]) are enough to account for about a threefold difference between our nutritional value estimates. Our own data, Vincent's, and observations of Hadza diggers spending long hours collecting this tuber make us skeptical of Schoeninger et al.'s very low estimate. We wonder whether pounding or chopping the sample to mimic mastication before introducing it to the stomacher—something that Schoeninger and colleagues did not do—might have released more nutrients. We hope that those researchers and others will join us in continuing to work on this important topic.

Bell, Hames, Kazankov, and Minnegal question whether this particular Hadza data set can tell us anything general about why men hunt, why nuclear families are such a common feature of modern human social organization, or why big-game hunting and nuclear families initially evolved and spread in ancestral populations. The question of how general any particular set of findings may be has an especially colorful recent history in the field of hunter-gatherer ethnography. Richard Lee's (1968, 1979) descriptions of !Kung foragers around Dobe in the '60s were so field-defining that they came to be regarded as *the* model of the foraging lifeway not just for Dobe in the mid-20th century but for modern hunter-gatherers in general and for humans throughout the Pleistocene (Isaac 1984). This "tyranny" of the !Kung (e.g., Wobst 1978) stimulated Barnard's (1979:142) memorable comment: "The !Kung are not the only hunter-gatherers in the world; they are not even the only Bushmen in the Kalahari." Researchers had barely begun to investigate patterned variation across a broader range of cases when the whole enterprise of using modern hunter-gatherers to build hypotheses about the past was called into question. Perhaps, it was argued, ethnographically observed foragers can tell us little about what people might have done before the Holocene because we are all now embedded in the world system. This "revisionist" critique claims that the !Kung Lee studied in the 1960s were part of a worldwide underclass whose behavior was shaped not by the problems of foraging for a living but by a history of economic dispossession and political sub-



ordination (e.g., Schrire 1980, Wilmsen and Denbow 1990).

The question of how to learn something general from particular observations is, of course, ubiquitous. Every moment, every sequence of events is unique. What about an infinite number of unmeasured other variables? How can we assume that any relationships extend beyond the limits of the particular events observed? What about chance, especially with small samples? Issues like these concern us, too, and in light of them we emphasize the importance of constructing and testing hypotheses. Observations have meaning only in light of hypotheses and become interesting only in relation to those that are theoretically warranted and worth testing. We agree with all the commentators that ecological and historical contexts matter. The Hadza are especially interesting for questions about the evolution of human hunting and its consequences for just those reasons. The behavior of these modern people can help us discover the problems faced by our ancestors as they made a living on wild foods in an ecological setting which represents the best modern analog for the one that witnessed the evolution of the genus *Homo*.

We referred to a few other ethnographic hunter-gatherers in this paper, especially the Ache (who have a quite different recent population history and occupy a very different habitat from the Hadza's), where hunting also seems to be more status rivalry than family provisioning. We argued that the paternal provisioning explanation does not explain pairing in these cases and discussed the alternative hypothesis that mate guarding may be a more common, longer-standing reason for marriage. Minnegal claims that the Ache provide a counterexample, but she is mistaken. One of the four cases examined in Blurton Jones et al. (2000), the Ache have a very high divorce rate associated with an unusually high operational sex ratio, exemplifying the increased instability of pairing where the number of paternity chances per male is high.

Hames and Wenzel mention the likely importance of paternal provisioning at least in some seasons among Arctic hunter-gatherers. The fancy technological requirements for colonizing these latitudes kept people from doing so until very recently. Siberia was occupied less than 40,000 years ago (Goebel 1999); people behaving in ways similar to the modern Inuit mentioned by Hames and Wenzel have only been in place since the Holocene (e.g., Dumond 1987). This takes us back to the question of generality. The stringent requirements for successful high-latitude occupation make these cases especially interesting for some questions, perhaps for the question of when (and why) paternal investing ever becomes the common pattern in human communities. Evidence continues to accumulate that the circumstances making it the priority strategy for most men are less common in the present than previously thought and even more unlikely among early humans in the Africa of long ago.

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