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Hunting and the Evolution of Egalitarian Societies: Lessons from the Hadza

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Abstract: Political hierarchies are common in human societies but absent among many mobile hunter-gatherers. So egalitarian social organizations have been attributed to limits that foraging imposes on wealth accumulation. But male-dominance hierarchies characterize all the great apes. our nearest relatives. The absence of wealth is not enough to explain the absence of hierarchy. Recently this evolutionary problem has received renewed attention by anthropologists who argue that egalitarian arrangements indicate distinctly human capacities for cooperation. Here I review work that challenges this view. The challenges suggest that hunting has played an important role in human evolution but one different than is widely assumed: Hunting is an arena of male competition. When hunters target big game, the unpredictability of success undercuts hierarchy with implications for the evolution of egalitarian societies and also for the evolution of marriage. I outline these arguments and then discuss applications to paleoanthropology as well as to the nonegalitarian patterns that are so characteristic of ethnographically known huntergatherers in Aboriginal Australia.

In the hunting and gathering societies that anthropologists have long described as egalitarian, "differences among members, apart from sex and age, tend to be ephemeral" (Fried 1967:34). Substantial differences of wealth and power emerge in larger, denser, more settled populations usually associated with farming and herding; so the lack of political hierarchy among mobile foragers is seen to be more like the societies in which humans evolved. Recently some scholars (for example, Boehm 1993, 1996, 1997; Knauft 1991) have revived attention to the question posed by considering the human patterns in a broader comparative context. Marked male dominance hierarchies

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are found among all the great apes. Like other nonhuman social organizations, those of our closest congeners show that power differences among individuals of similar age and sex can persist in the absence of wealth differences. Since male dominance hierarchies characterize all the pongids, some of whom are more closely related to us than they are to each other, male dominance hierarchies probably characterized our common ancestors. The disappearance of steep male hierarchies with the evolution of egalitarian societies requires explanation.

An earlier generation of scholars attributed the difference between human and nonhuman primates to sharing, "the paramount invention that led to human society . . . because it underlay the division of labor that probably increased early human productivity" and provided the "solution to maintenance problems as the human species radiated over the globe" (Fried 1967: 106). Boehm and Knauft also highlight food sharing and an associated array of "leveling mechanisms," which they see as indicative of distinctly human capacities for cooperation that enable humans to solve collective action problems that defeat other apes.

Here I dispute one part of that argument and then take advantage of the other. I begin with a contrarian view of hunting and meat sharing, reviewing data and argument largely from one ethnographic case, the Hadza of northern Tanzania who display the elements common to egalitarian foragers: men hunt large animals and meat is widely shared; women gather; and monogamy is the common pattern. I summarize work that calls into question three fundamental propositions about cases like the Hadza: (1) that meat sharing is a practice to ensure against the riskiness of hunting for a living, (2) that hunters provision their families, and (3) that hunters are usually monogamous because they can only afford to support one wife. If the case against conventional explanations for human hunting and sharing is correct, longstanding explanations for egalitarian societies must also be revised. I turn to the hunting and meat-sharing patterns now widely documented for chimpanzees, then use the comparison to speculate on some effects that the much larger prey size taken by humans could have on behavioral capacities and social organization. A final section considers implications of this argument for hypotheses about the paleoanthropological record as well as for the nonegalitarian societies of some modern hunter-gatherers.

The "Hunting Hypothesis"

Human evolution is widely assumed to depend on a few key behavioral innovations propelling other changes that distinguish (at least some) hominids from other apes. Hunting has long been highlighted as the keystone innovation. According to the classic argument, males hunt to provide food to share with their mates and offspring. Females can then afford to bear and rear more expensive children. Not only the sexual division of labor but other distinctively human patterns of cooperation arise because game animals are large enough to allow sharing; and hunting is risky enough to require it. Challenges

to this scenario have continued to mount in paleoanthropology, primatology, and hunter-gatherer behavioral ecology, but it remains a persistent foundation for ideas about human evolution.

Influential syntheses in the fifties and sixties linked hunting to the use of stone tools, expanded brains, and the appearance of bipedal locomotion (Laughlin 1968; Steward 1968; Washburn and Lancaster 1968). Subsequent fossil discoveries showed that bipedalism antedated both the appearance of stone tools and marked cranial expansion by millions of years (Johanson and White 1979). Reappraisal of early archaeological sites led to skepticism that they clearly indicated hunting (Binford 1981, 1985). There is no current consensus about which or even whether archaeological sites associated with any hominid fossil taxon clearly indicate big-game hunting (Binford 1985; Mellars 1996), but syntheses for popular consumption (Johanson 1992; Leakey and Lewin 1992) continue to imply it, and arguments about the evolution of other human capacities, to depend on it (Deacon 1997).

Several decades ago, striking differences between the foraging strategies of humans and apes provided part of the warrant for the influential hypothesis that hunting was the key to human evolution. Since then, an expanding record of observations on an increasing number of populations shows that the differences were overdrawn. Among chimpanzees, one of our sister species, males hunt much more frequently and more successfully than previously supposed (Boesch and Boesch 1989; Stanford 1996; Wrangham and Bergmann-Riss 1990), falsifying notions that hunting separates hominids from the other apes. Not only can hunting be an important activity among chimpanzees, but it is a male specialty, refuting the proposition that sex differences in foraging strategies are distinctively human (Galdikas and Teleki 1981). Moreover, among chimpanzees meat is almost always shared (Goodall 1986), but not with offspring, disproving both the old claim that "food is never shared" (Service 1962:38) among nonhuman primates and the associated assumption that food sharing would imply family provisioning. The chimpanzee patterns show that even unequivocal evidence of hominid hunting would not be enough by itself to imply that nuclear families are elementary economic units.

Ethnographic challenges to the conventional scenario have also mounted. Both new data sets and reappraisal of old reports have been used to argue that among people who hunt and gather for a living in low latitude environments, men are not usually working to provision their families. Results of research among the Hadza of northern Tanzania provide a specific illustration.

The Hadza

The Hadza are a small population, numbering about 750, defined as a group by the fact that they speak a common language and largely marry among themselves (Blurton Jones et al. 1992). They live in the rugged hill country of the Eastern Rift Valley, just south and east of Lake Eyasi, northern Tanzania. The climate of this region is warm and dry. Annual rainfall averages 300-600 mm, most of it falling in the six-to-seven-month wet season

(November to May). Local plant communities are dominated by mixed savanna woodland, and large-game animals are abundant.

At the time of first European contact, around the beginning of this century, the Hadza reportedly had this area largely to themselves and lived entirely by hunting and gathering (Blurton Jones et al. 1996; Obst 1912). Local incursions by non-Hadza pastoral and agricultural groups were recorded as early as the 1920s and continue, particularly in the northern part of Hadza country, right to the present (Woodburn 1988). Archaeological evidence suggests that hunters, herders, and farmers have all occupied this area, at least intermittently, for several millennia. Hunter-gatherers alone have been present far longer (Mehlman 1988).

During the past 60 years (and especially since the mid-1960s), various segments of the Hadza population have been subjected to a series of government-and church-sponsored settlement schemes designed to encourage them to abandon the foraging life in favor of full-time farming (Ndagala 1988). None of the projects has been successful, and in every case, most of the Hadza involved have returned to the bush, usually within a few months. In each instance, some Hadza have managed to avoid settlement and continued to live as hunter-gatherers.

Hadza Hunting

Hadza hunters kill or scavenge large animals at an overall mean rate of 4.89 kg (live weight) of prey per hunter-day (Hawkes et al. 1991). During one field period of about a year (1985–1986), the large prey taken by hunters gave an average of about 1 kg (live weight) per consumer per day. This is more than twice Lee's (1979) estimate for !Kung foragers living in the Dobe area of Botswana in the 1960s. Hadza underline the importance meat has for them by describing themselves as meat eaters (in contrast to their pastoralist and farming neighbors). Big game provides a large and highly valued component of the Hadza diet.

The high average, however, comes with substantial variation. Not only does the success of individual hunters vary, but there are also differences in the amount of meat all acquire by hunting method (intercept or encounter), and from week to week, season to season, and year to year. Intercept hunting was unusually successful in the late dry season of 1985, hunters earning a rate more than three times higher than their rate with this method in the late dry of 1986 (7.56 kg per hunter-day as compared with 2.44 kg per hunter-day; Hawkes et al. 1991). During the 1985 late dry, their take by all methods amounted to an average of almost 2 kg per consumer-day. But they averaged less than one-third as much over all other seasons. Variation around these averages is of course compounded by variation from day to day and week to week, as well as among consumers on any given day. The lower the camp mean, the more likely some residents get none.

The Payoff to the Hunter Himself for His Effort

The average acquisition rates are an obvious way to measure the hunter's "income" for his effort. The high average seems to provide an obvi-

ous answer to the question: why do Hadza men hunt? But counting the nutritional value of the entire prey animal as the payoff to the hunter is justified only if he and his family consumed it all, or if he (or his family) exchange the portions that they don't eat for something else. The first of these is clearly not the case. Large prey are widely shared, a process that begins as soon as people arrive at the carcass. Parties of men, women, and children usually converge on the site, both to eat and to transport meat home (O'Connell et al. 1988, 1990). About 13 kg (bone weights excluded) is the average size of meat shares transported to households with a resident man (Hawkes et al. 1998).1

In the sample used for that estimate, the household of the responsible hunter held a significantly larger share than other households for carcasses that contained more than 100 kg of meat, about 10% for the hunter and 7% to others. When the carcass contained less than 100 kg of meat, the share to the hunter's household was not statistically different from the share to other households (in this sample it was actually smaller), and the shares average about 10% of the total. These data are the basis for estimating that a Hadza hunter's household generally keeps 10% or less of the meat from his kill

(Hawkes et al. 1998).

It could be that the rest of the carcass is the hunter's property as well; but instead of eating it all, he exchanges shares for shares each recipient has given him in the past or will owe him in the future. If so, his kill earns him the hunter's share plus the "exchange value" of the rest. Qualitative observations suggest that the meat others take is not the property of the hunter. Neither the hunter nor others behave as though he has a right to exclude them. The larger the carcass, the bigger the magnet it is to potential claimants. The style of claims conforms to descriptions from many ethnographers of egalitarian societies (for example, see the summary in Erdal and Whiten 1994). Classic characterizations note that claimants do not say please and thank you (Sahlins 1972) and that, in fact, there is sometimes an edge of threat. Peterson (1993) has labeled this pattern "demand sharing." That style is generally evident among the Hadza and especially salient at kill sites. Arguments sometimes break out about shares and their size. Claims, not just by men but by women as well, often take the general form of "where's mine?" The hunter who made the kill (or appropriated the carcass from other primary predators) plays no evident proprietary role.

This appearance could of course be deceptive. While ownership is classically defined as the right to exclude other users, it also classically includes the right to transfer ownership to someone else. Perhaps the shares that claimants take are tallied as exchanges in subtle ways that our observations miss. Ethnologists have long assumed that hunters share meat because, by giving up portions when they can, they obligate recipients to repay them when fortunes are reversed. If shares cancel past debts and create future obligations, then the spread of shares would trace the hunter's lines of credit. If the hunter were the proprietor of the carcass, those who were successful more often would owe less to others, have more others in (deeper) debt, and be more promising investments for the future. Better hunters should therefore give up less of their own kills, receive more from others, and spend less time hunting.

Quantitative data show the first of these only under certain conditions, and the absence of the other two. Better hunters do not keep larger shares of kills that contain less than 100 kg of meat, but they do keep bigger fractions when carcasses exceed this size. There is wide variation in overall success rates among Hadza hunters. A man's relative success rate has an effect on the size of his household share only when (a) he acquired the carcass and (b) it is more than 100 kg of meat. Better hunters do not get larger shares from the kills of others; and they do not spend less time hunting. They spend *more* (Hawkes et al. 1998). The quantitative patterns are mostly consistent with the qualitative appearance of things: no debts and obligations accumulate because the carcass is not the hunter's property in the first place. One pattern, the larger shares that better hunters keep of their own kills when the carcass is very large, stands out as anomalous. It is a pattern that remains to be explained.²

The Hadza observations are largely consistent with the hypothesis that meat is shared because it is a valuable resource that attracts many consumers who harvest from the carcass much as they would when exploiting any other valuable food resource. Hungry contestants demand "their" share and complain if it appears too small. The result is widespread sharing of large carcasses. This pattern conforms to one formally modeled by Blurton Jones (1984, 1987) as "tolerated theft." While the label suggests to some that "thieves" are stealing from "owners," acquisition confers no special ownership rights in Blurton Jones's model. The shares are the property of successful claimants. To the extent this model fits the Hadza pattern, the hunter's contribution to pro-

visioning his household is no more than the share he claims for it.

Big-Game Hunting as Family Provisioning

The patterns reviewed so far do not show hunters "paying" for shares they receive at another time with the shares that go to other households. The only meat the hunter gets for his effort is his household's share of the prey. On cursory appraisal the size of shares might look like effective provisioning. But quantitative comparisons of the opportunity cost show otherwise. The time men spend targeting one set of resources is time not spent taking others. The take-home rates for available alternatives can be calculated and compared.

The household share is a rough estimate of the hunter's contribution to family consumption when he hunts big game. The overall average acquisition rate for hunters is 4.89 kg/day (live weight; Hawkes et al. 1991). If we assume that the hunter's household keeps 10%, then his "take-home" rate is .49 kg/day. Hadza men spend 4.13 hrs/day hunting on average, making their average that he was taken here.

age take-home rate .12 kg/hr.

Assuming that the hunter's household keeps all small prey, the hunter's take-home rate for small game is 100% of his acquisition rate. Measured rates for pursuing small prey on encounter were derived from the participation of Hadza hunters in an experiment (Hawkes et al. 1991). All those recorded were higher than .12 kg/hr, and those recorded for setting snares are higher still. Men would bring home more *on average* to their households if they included small animals in the suite of prey they regularly pursue.

The rates for large game can also be compared with gathering plant foods by converting kilograms of meat to calories. If large animals are estimated at 1500 Cal/kg live weight (following Lee 1979), a rate of .12 kg/hr (live weight) gives 180 Cal/hr. This rate is lower than all but the very youngest children earn gathering (Blurton Jones et al 1989; Hawkes, O'Connell, and Blurton Jones 1995). In the long run, big-game hunting is inferior to available alternative strategies for provisioning families.

Moreover, this comparison of average rates actually ignores the biggest problem, the immensely greater variance, and so enormous risk of failure for big-game hunting. Perhaps one day or two without food is survivable, but weeks are not. Days without food push people, especially children, below a threshold from which they cannot recover. If women and children depended on food supplied by their husband or father, then a run of unsuccessful days would be devastating. The high average daily acquisition rates of Hadza hunters are due to the very large size of the prey. The average daily success rate, on the other hand, is .034 prey per hunter. An average hunter can expect a full month of failures for every day he scores. The geometric mean of arithmetic means of weeklong runs of days would be the more appropriate evaluation of real nutritional payoffs for consumers depending on this food source. Based on products rather than sums, geometric means fall to zero whenever zeros are encountered. With this measure, the expected provisioning payoff for big-game hunting is nothing at all.

Sharing has been widely touted as a good solution to this variance problem (Smith 1988; Winterhalder 1986). Longstanding arguments about sharing as the distinctly human behavioral innovation that allows ancestral human groups to overcome the otherwise fatal risks of depending on the hunt are based on qualitative versions of the same insight (Boehm 1993, 1997; Fried 1967; Service 1962). This assumes that the shares supplied to others are the price required for shares to be received from them. But Hadza men successfully claim equivalent shares of the kills of others no matter whether or how much meat they have captured in the past. A household with the hunter's share of 20 kg of meat may seem to pay little cost in sharing the remainder: How much more could its members use? But if sharing out does not affect the shares claimed in the future, then sharing cannot be counted as "banking" the "extra."

Food in general, and certainly meat, has limited life as a valuable resource. If it must be eaten immediately, then any more than the hunter and his family can eat at once has no nutritional value for them; as a consequence, its appropriation by others poses no cost. But in this environment, the meat not eaten immediately does not become valueless. Cut into sheets or strips, it quickly acquires a protective rind that extends its edibility. People dry meat regularly, planning trade with non-Hadza neighbors. They succeed at carrying off a bundle of dried meat to trade only when the glut of meat in camp stays ahead of consumption. The barrier to storing meat is not a technological one. Instead, there is a "social barrier" to the use of surplus meat—usually too many people, visitors as well as residents, are ready to eat it.

Hunters' Children and Hunters' Wives

The pattern of results reported so far is inconsistent with the proposition that Hadza men hunt in order to provide for their families. Other well-studied tropical foragers display this pattern as well (Hawkes 1993). But even if men are not making the foraging choice that would best serve the nutritional interest of their households, the households are visible social units. There is a persistent relationship between particular men and particular women and children. Perhaps the hunter's household benefits enough that women improve the nutrition of their children by marrying hunters. In the Hadza case, the hunter's share of carcasses with more than 100 kg of meat is more than twice the size of others. This benefit is also relatively larger for better hunters (who already get the hunter's share more often).

Larger household shares for very large prey would not explain why men hunt. But given the hunting, larger shares to hunter's households could provide an economic reason for women to marry and to prefer marrying a better hunter than a worse one. If the advantage were small enough to disappear when divided with a second wife, monogamous marriage to the best unmarried hunter would be a better choice than not marrying or being a second wife. Patterns like this could preserve elements of the hunting hypothesis to explain both the continuous pairing (marriage) that distinguishes humans and the frequent monogamy of hunters.

To see whether a father's hunting success had a measurable effect on the relative nutritional status of children in his household, we analyzed a sample of Hadza children's weight changes over several seasons in 1985–1986. In some seasons the weight gains of children in households of better hunters were more positive, indicating that they were better nourished. The most obvious interpretation of this pattern is that better hunters feed their children more meat. If so, differential weight changes would have to be associated with the timing of father's actual kills. But they are not. Instead, the correlation is with father's overall success rate—which we interpret to be an index of his reputation as a hunter (Hawkes et al. 1998). It is not household meat shares that predict children's weight gains, but some other pathway links father's hunting reputation to the nutritional welfare of his children.

The link in this case is through wives and mothers. The foraging efforts of Hadza women have a measurable effect on the nutritional welfare of their children and grandchildren (Hawkes et al. 1997). When Hadza mothers are not nursing, variation in the time they spend foraging predicts variation in the weight changes of their weaned children. With the arrival of a new baby, mothers sharply reduce their foraging, while grandmothers increase their effort, providing the nutrient stream to support their weaned grandchildren (Hawkes et al. 1997). If men were family providers, we might expect that the wives of those who provided more could afford to work less; this expectation is the usual argument made about the evolutionary role of hunting in allowing husband-fathers to reduce the burden on their mates. But the Hadza pattern is just opposite to what might be expected from the standard scenario.

The wives of better hunters spend significantly *more* time foraging (Hawkes et al. 1998).

The children of better hunters do better nutritionally, not because they are supported by their fathers but because of the foraging efforts of their mothers and grandmothers. Better hunters are married to harder-working wives. This leaves no elements of the standard scenario unchallenged. If men do not hunt to provision their families and women do not gain economic benefits from their husbands, then the usual explanations both for men's devotion to hunting and for marriage itself are called into question.

So Why Do Men Hunt?

Why do men devote substantial effort every day to foraging choices that provide less to their own wives and children than to neighbors? In the Hadza case, people learn the story of a carcass acquisition. But the hunter is not the owner of the carcass. Most of the meat goes to others; and the size of those shares is unaffected by past (and likely future) carcass acquisition by the recipients. Nevertheless, adult Hadza men spend an average of more than four hours a day hunting, and younger, unmarried males spend even more (Hawkes et al. 1997, 1998). This has large consequences for the average diets of everyone in the community, women and children as well as men. But any man who took shares from the big game acquired by others while spending his foraging time gathering and taking small prey would supply more food to his own family. This would mean less meat all around. But the largemeat fraction in the "community diet" comes at a short-term cost to the diet of a hunter and his family. If the hunters earn some other benefit, then that might account for the widespread tendency of men to pay this cost.

A previous generation of anthropologists assumed that hunting and food sharing distinguished human from nonhuman primates. Chimpanzee hunting, known since Goodall's first report in the early sixties, was assumed to be aberrant or rare (Reynolds 1967). The substantial fractions of meat in the diets of human foragers show that hunting is an important human activity, while the trivial amount of meat in chimpanzee diets implied that hunting was not of much importance in that species (Hill 1982). Data now available show that, in contrast to early assessments, hunting is a frequent activity of male chimpanzees at several long-term study sites (Boesch and Boesch 1989; Uehara et al. 1992; Wrangham and Bergmann-Riss 1990). Since male chimpanzees do not hunt to provision families, explanations for their hunting might illuminate the human patterns as well.

Chimpanzee Hunting

Both the frequency of hunts and the time spent at it are more difficult to assess for chimpanzees than for human subjects because only active pursuits are clearly evident to observers. At Tai, Boesch and Boesch (1989) recorded 100 active pursuits over 299 observation days. Wrangham and

Bergmann-Riss (1990) tallied the Gombe record to adjust for various sampling biases and estimated an average success rate per adult male of .037 prey/day—a number arrestingly close to the Hadza big-game success average of .034 prey/day.

The maximum benefit a chimpanzee hunter is likely to get for his effort depends on what happens after a successful capture. The following general sequence has been described by many observers at different study sites. Adult males near the prey rush to seize the carcass. Using threats and sometimes attacks, they rip the carcass apart. After this "initial division" in which possession is established, aggression is rare, but clusters of beggars surround those holding portions. The clusters persist sometimes for the hours required for full consumption of the prey. During this time possessors may refuse or ignore supplicants. They may allow mutual feeding on the same piece or actively proffer pieces. Sometimes possessors, having fed for a while themselves, relinquish the remaining carcass. In general, the larger the carcass, the more individuals engage in attempts at consumption over longer periods of time. Goodall (1986:373) describes "occasions when the solicitations of begging chimpanzees made it all but impossible for the possessor to feed; at the very least they are a source of irritation." The descriptions show that meat is a desirable food, and the acquisition of a carcass is initially a time of great excitement. Even after excitement peaks, sociality is heightened through the protracted period of consumption.

Adult males gain possession of portions in the initial division, and they are also most successful at begging shares from possessors. Females get less but are actively involved. Within this pattern additional biases have been detected. In Teleki's (1973) data set from Gombe, females were both more likely to beg meat from male possessors and more likely to get some when in estrus. Stanford (1996) also reports meat for sex exchanges. But this pattern does not prevail generally (Goodall 1986; Boesch and Boesch 1989; Nishida et al. 1992). Nishida and colleagues (1992) found "favoritism of coalition partners," mostly other adult males, in their long record of the sharing patterns of one alpha male at Mahale. This male was among the most successful hunters, and even more successful at obtaining control of carcasses from other hunters. He shared with males who were allies, his probable mother, and a few other females, but not his most threatening competitors, the beta male and the young males rising in the dominance hierarchy.

Nishida and colleagues (1992:160) propose the hypothesis that meat sharing is a "political strategy, used to establish and reinforce alliances." They report two occasions in which the alpha male himself "scarcely ate" from a large carcass he had secured but held it "only to let other chimpanzees nibble meat from it until it was all consumed" (Nishida et al. 1992:172). The Mahale researchers' observations recall de Waal's (1982) interpretation of the behavior of a male in the captive Arnhem colony. When the subordinate male beta challenged the alpha status of another male, the challenger distributed fresh leaves "to become popular in the colony and perhaps to gain female support" (de Waal 1982). In light of this interpretation it is noteworthy that at Mahale the beta males and the rising young males who got no shares from the alpha

male were not excluded by his refusals to allow them shares. The young males "usually watched from a distance, and never approached"; furthermore, a beta male, described as the alpha's "major rival," "has never been seen to beg for meat from" the alpha male (Nishida et al. 1992:168-169).

The descriptions and hypotheses focus attention on the opportunities that hunting affords to display competitive standing and to reinforce alliances. It is a very social activity. Individuals can rarely monopolize a carcass unless they escape the social group, because of the demands of other claimants. First, other males try to grab pieces to control, and then both males and females deferentially press to be allowed a taste. Dominance relationships can be tested both in the struggle for possession of pieces of the carcass and in the subsequent interactions during the lengthy period of consumption.

The burden of evidence suggests that hunting is much more than a feeding activity. Male chimpanzees hunt and share meat, at least in part, to ensure or perhaps improve their competitive standing in relation to other males. Sharing is inevitable partly because contests over a carcass make the cost of not sharing too high to pay. These costs include both physical defense and the "irritation" that Goodall describes from the intense attention of beggars. Meat is also shared to reward deference to the possessor's social standing. Those allied

with him can benefit from his generosity.

According to these working hypotheses, the benefits for hunting and meat sharing are clearly greater for males than for females. The smaller size of females limits their likely success at defending carcasses from attempts at aggressive appropriation by larger, stronger males. And alliances play a larger role in establishing and maintaining high status for males than females (Goodall 1986). Even though females can hunt as effectively as males (Boesch and Boesch 1989; Wrangham and Bergmann-Riss 1990), males have more to gain from it.

In addition to explaining why hunting is a male specialty, the associations between meat sharing and male competition for dominance rank can also explain why males are more likely to hunt under some circumstances than others. Stanford and colleagues (1994) show that over a ten-year observation record at Gombe, chimpanzee pursuits of red colobus increased with (1) the number of males in the party, (2) the overall party size, and (3) the number of females in the party with estrous swellings. If meat sharing tests dominance rank and strengthens alliances, then males should be more likely to hunt when these things matter most. It is consistent with this hypothesis that the strongest predictor of hunting in the Gombe data set was the third of these variables: the number of estrus females in the party (Stanford et al. 1994).

Big-Game Hunting and Dominance Hierarchies

The Effects of Prey Size

Scholars have previously emphasized that chimpanzees only take small animals, whereas humans routinely hunt prey larger than themselves (Isaac 1978). If males in ancestral populations hunted to maintain or improve their competitive standing among other males, then a marked increase in prey size would have large effects on the relative success of alternative behavioral strategies.

The Hadza case is an instructive human example for examining prey size effects. While the success rates of Hadza hunters (.034 prey per hunter-day) are almost identical to the success rates of chimpanzee hunters at Gombe (.037 prey/hunter/day; Wrangham and Bergmann-Riss 1990),⁴ Gombe chimpanzees eat very little meat while the Hadza consume large amounts. The extreme difference is entirely due to the difference in prey size. Colobus monkeys are the favored prey of chimpanzees (at Gombe and elsewhere). The mean weight of these prey at Gombe is 4.4 kg (with a mode of 1 kg; Stanford 1996). For a Hadza sample of 71 carcasses taken by encounter, intercept, and competitive scavenging over 256 days of observation (2,072 hunter-days), the mean carcass weight (adjusted when scavenged carcasses were not intact) was 143 kg (Hawkes et al. 1991, 1998).⁵ Because of the difference in prey size, Hadza hunters with success rates essentially identical to those of chimpanzees make about thirty times the amount of meat available for consumption that chimpanzees do.

Even though meat is a small fraction of chimpanzee diets, with negligible amounts eaten by all but the adult males (Wrangham and Bergmann-Riss 1990), everyone gets very excited at a kill. An increase in prey size increases the number and size of shares and so increases the prospects of eating more meat for all. Even when tools rather than teeth are used to dismember the carcass, big animals take so long to dismember that potential consumers at some distance from the site where the carcass is butchered easily arrive in time to participate in the sharing. Among the Hadza, men, women, and children leave other tasks when they learn of a meat-eating opportunity and converge on the carcass site. The potential for conflict over the meat scales up accordingly. Not only do many individuals of mixed sexes and ages meet over a resource much too large to sequester, but many of the contestants are armed.

Simple conflict models designed to explain contest behavior in any species (Maynard Smith and Price 1973; Maynard Smith 1982) confirm intuition that contestants do better over a series of encounters if they adjust their tendency to engage in contests with other claimants in the following way: readiness to fight for a resource goes up the greater the value of the prize. When costly injuries are likely, however, the gains go up if the general readiness to fight goes down (for a review, see Pusey and Packer 1997).

The variation in chimpanzee sharing patterns described above conforms to these cost/benefit regularities. Juvenile prey are sometimes too small for division (Boesch and Boesch 1989); a small carcass is not worth contesting. Females do not participate in the initial aggressive contest for a carcass. They would likely pay a greater cost in fighting with larger males and would benefit less from being the center of a beggars' cluster and controlling subsequent sharing.

The Use of Conventions

The simple models of resource contest also show that when fights are costly to all, those who use an arbitrary asymmetry as a convention to settle a contest, like order of arrival, do better over a series of encounters than those who do not (Maynard Smith and Price 1973; Maynard Smith 1982). In chimpanzee carcass distributions, the initial contest for possession of pieces usually involves a physical struggle, but after that aggressive behavior is rare. This difference could be entirely a function of package size; once divided, the pieces are too small to be worth a fight. But the persistence of the begging clusters with subsequent transfers under the tacit approval of the possessor (Boesch and Boesch 1989; Goodall 1986; Teleki 1973) suggests the possibility that chimpanzees are using an "ownership" convention.

The ubiquitous use of conventions is widely recognized as a human speciality (Schelling 1960; Sugden 1986). Reliance on salient but arbitrary asymmetries to determine strategies of conflict would be especially favored with frequent encounters among more claimants over much larger carcasses. In the case of the Hadza, more people show up to claim shares, and they come further to do so, the larger the carcass (O'Connell et al. 1990). In addition to the number of claimants escalating the cost of any attempt to monopolize meat, there is also the matter of weapons. Like all ethnographically known hunters, Hadza men and boys always travel armed. More claimants, plus bows, arrows, and knives, inflate the potential cost of emotional display, favoring selfcontrol and increased emphasis on conventional settlements. In the Hadza example, people often raise their voices over shares of meat, but we have never observed a physical fight.

Egalitarian Consequences of Attention to Hunters

With larger prey size there is much more meat for all. Meat is a substantial component of the diets of Hadza of both sexes and all ages, so everyone has good reason to be concerned about hunting success. Successful hunters are themselves valuable resources. Hunting prowess may be among a man's most important characteristics. Among Hadza hunters, as in other ethnographic cases, mean success rates differ, showing the marked effects of skill. Among the Hadza, interview data confirm both that hunters' rankings are of interest to others and that they are quite consistent from year to year. Boys are especially good at ranking those in their own and just older cohorts (thougha matter of some initial surprise—this is not something closely monitored by young women; Blurton Jones et al. 1997). Some men are, and are known to be, much better hunters than others. They should be more desirable neighbors as a consequence.

The Hadza case is similar to several other ethnographically known examples in which hunting is awarded high importance. Prey size is the variable that propels the widespread consumption that makes the success of any hunter of interest to all. The contrast with chimpanzee hunting is instructive. Even though chimpanzees clearly value meat and are excited at the prospects of meat eating, individuals gain so little meat from any male's hunting success that many other factors affect his standing in the dominance hierarchy. The elevated importance that hunting has for humans makes its unpredictability more important as well, and both go up with prey size. When success and failure have a large impact on everyone's consumption but no one can sustain a string of successes, dominance hierarchies are undercut.

Using the Hadza rates as the example, even the best hunter usually fails to score, and the least skilled and experienced sometimes succeeds. The two-sided consequence, that good hunters cannot be relied on to succeed and that even boys can sometimes provide a bonanza for all, regularly undercuts hierarchical rankings. Any hunter's success on one day will always be followed by failures, limiting the extent to which anyone can maintain superiority over others. The absence of flamboyant self-aggrandizement among hunters has been remarked by many ethnographers (for example, Lee 1969). Anyone who brags about his superiority will have his claims soon countered by the success of another (Hawkes 1992).

What About Marriage?

If hunting is important because everyone has a stake in the success of any hunter, then households are not units of production among huntergatherers, and marriage is not an economic partnership. Women and children get shares from the kills of all men, so the meat fraction of their diet can be large whether or not they have a resident husband/father and whatever his own hunting success. The observation stimulates another question: If hunters are not paternal provisioners, why do women form persistent pairing relationships with them? Among the Hadza, a surprisingly large fraction of women of childbearing ages, about one-fourth, are not married at any given time (Blurton Jones et al. 1996). Still, as in most egalitarian societies, most women between the ages of 20 and 45 are married. The hunter's household does get a larger share of the very largest carcasses, but as noted above, this benefit has no detectable effect on the nutritional status of household members (and the wives of better hunters actually work more). If hunters are not provisioning their wives and children, then what explains the pairing of spouses that distinguishes people from all the great apes?

Comparison with chimpanzee mating systems underlines some of the distinctive features of human marriage. Dominance ranking is a key variable in the mating strategies of chimpanzee males. Alpha males can successfully displace other males seeking to mate with females in peak estrus, but they cannot monopolize more than one female at a time, and even one can be a problem when there are many insistent rivals (McGinnis 1979). A lower-ranking male can also gain paternity if he can successfully separate a female in estrus from the social group and lead her away in consortship (Tutin 1979). This strategy can be so successful that Goodall has suggested selection may not currently favor "the huge expenditure of energy and the high degree of risk in a male's attempts to rise to the top of the hierarchy" (1986:478).

Consortships, usually lasting no more than a few days, have been charac-

terized as "incipient pair bonds" (Stanford 1996). But there is a very important difference between a human marriage and a chimpanzee consortship: the latter persists only so long as the pair remains separated from other community males. Whenever other males are present, those of higher rank can inhibit copulation attempts by lower-ranking males and solicit copulations with any female. The alpha can (almost) monopolize matings with any female in peak estrus, and females in that state are more likely to be in parties with multiple males. While the variance in male reproductive success is limited by the length of any male's tenure in alpha status and by the success of consortships, there is a general association between high rank and reproductive advantage (Ellis 1995).

If dominance hierarchies were undercut by an increase in prey size as described above, and that change also favored a tendency to settle contests by convention rather than conflict, there would be consequent changes in mating patterns as well. One possibility is that those changes would favor increased allocation to mate guarding. Modeling suggests that when males cannot gain a substantial edge in other forms of mating competition, they do best to devote their effort to mate guarding (Hawkes, Rogers, and Charnov 1995). Surprisingly, even when paternal investment has large effects on the number or survival of the offspring of mates, pure mate guarding spreads against paternal investment in the models. Marriage is, among other things, a public acknowledgment of a husband-wife relationship. In that sense it is a convention for mate guarding, a convention by which one man's claims are recognized by other men.

Implications for the Wider Variation

The arguments here dispute the role that hunting is usually assumed to play in human evolution. If hunters don't support their mates and offspring, then hunting does not usher in the nuclear family as the fundamental economic unit. The basis for rejecting that "hunting hypothesis" has given rise to another. The "politics" of big-game hunting and meat sharing suggest that when divisible resources are large enough to be of interest to many, their recurrent acquisition favors emotional control and the use of conventions in strategies for conflict that avoid costly fights. Since average capture frequency generally goes down for encounter hunting as prey size goes up, the carcasses large enough to interest many consumers are also unpredictably acquired. A big-game hunter cannot sustain claims of superiority.

Comparisons and contrasts between one particular case of modern human foragers and a general chimpanzee composite with special emphasis on Gombe have been used to make this evolutionary argument. While chimpanzees are the closest living relatives of modern humans, the character and diversity of ancestral and collateral hominids, much more closely related to us, remain to be considered. While the Hadza are similar in many ways to other modern human populations foraging for a living in low-latitude environments, not all mobile hunter-gatherers are egalitarian. The hunting hypothesis developed here has implications for both paleoanthropology and variation among ethnographically known modern human foragers.

Some Paleoanthropological Implications

In the past few years, advances in primatology and paleoanthropology have led in contradictory directions. On one hand, the exploration of chimpanzee behavior both in captive populations and in the wild has shown animals with unexpectedly sophisticated cognitive and strategic capacities. The more we know about chimpanzees, the more human they seem. On the other hand, the accumulating record of paleoanthropology includes an increasingly diverse array of hominids, modern humans representing only one, very recent variant. Hominids that must have differed not only from living species but from each other crowd in the shrinking space between chimpanzees and modern humans.

How did the behavior of members of these fossil taxa differ from moderns? If big-game hunting could undercut male dominance hierarchies and favor a general use of conventions to settle contests, which hominids were big-game hunters? The earliest archaeology is about 2.5 million years old. It consists of stone tools in association with the bones of large animals and was initially read to indicate both large-animal hunting and other social arrangements very like those of (some) modern hunter-gatherers (Isaac 1978). Challenges to these inferences stimulated work to establish primary context and behavioral associations between the tools and the animal bones at several early sites (Isaac 1984). With those things established, archaeologists focused on whether the sites indicate hunting or scavenging, whether the assemblages were transported, and if so, how far (Binford 1981, 1985; Blumenschine and Marean 1993; Bunn et al. 1988; O'Connell et al. 1990; Rose and Marshall 1996).

The Hadza example (O'Connell et al. 1988) shows that competitive scavenging and hunting can be coordinate strategies of carcass acquisition for modern humans, as they are for other large-bodied terrestrial predator-scavengers (Houston 1979). This case also shows that women and children, as well as men other than the hunter, can be involved in consumption whether or not a carcass is transported. For the arguments about male strategies made here, questions of scavenging versus hunting and of transport distance are tangential at best. The primary question is how often the hominids whose behavior contributed to the formation of Pleistocene sites had access to large carcasses. Certain kinds of rare events, like beached whales, have high archaeological visibility (Binford 1981; Stern 1993). But it is average frequency in the day-to-day lives of the hominids, not archaeological salience, that determines the payoffs for alternative behavioral strategies.

Note that prey acquisition rates are generally inversely related to prey size. Modern humans can take small animals at surprisingly high rates even without projectile weapons (Hill and Hawkes 1983). Ache foragers in the forests of eastern Paraguay regularly take mammals in the size range of the colobus monkeys hunted by chimps. In that size range (under 10 kg), Ache hunters capture an average of .66 prey/hunter-day—a rate eighteen times higher than

the chimpanzee rate. Even if Plio-Pleistocene hominids were not as adept at hunting small prey as modern humans, they might well have been more efficient at it than chimpanzees are. But as long as prey are small, the number of consumers who can benefit from a carcass is limited. Increased efficiency at taking small animals would not have the effects on strategies of conflict and on dominance hierarchies associated with success at large-prey acquisition.

Two variables seem especially likely to affect big-game hunting and scavenging success rates. First is the encounter rate with prey, a function of the population density of large herbivores and of carnivores who provide the richest scavenging opportunities. These densities are related to each other and to annual rainfall. Using estimates of annual rainfall in the locale of the early hominid archaeological sites, O'Connell and colleagues (1988) speculate that in some settings and at some times large-animal densities may have been even higher than in modern Hadza territory. On these grounds Plio-Pleistocene hominids might have encountered large prey at least as frequently as do the modern Hadza.

A second variable affecting the success of Hadza men as both hunters and competitive scavengers is their hunting technology: bows and poisoned arrows. The absence of comparably efficient weapons, perhaps until the last half of the upper Pleistocene (Klein 1989), suggests that success rates for hunting large prey may have been low until then (Binford 1985). Patterns in faunal assemblages also indicate a change in this time period (Stiner 1993). If success rates were low enough that large carcasses represented only rare windfalls, then other domains for male competition would overshadow hunting and competitive scavenging, and the benefits for emotional control and conventional solutions to contests would also be fewer.

If big-game hunting appears only with behaviorally modern sapiens, the associated emotional control and regular use of conventions could have allowed moderns to spread into environments previously unoccupied by hominids. The colonization of Sahul, for example, the landmass that includes Australia and the continental islands of New Guinea and Tasmania, was only achieved by substantial water crossings through Wallacea. The construction of serviceable watercraft was a prerequisite, but also the patience to sail in small boats for tens of kilometers even if visible cues provided navigational targets (Irwin 1993). Levels of emotional control that permitted modern humans to make that crossing when other hominids did not (O'Connell and Allen 1998) could be the lasting legacy of big-game hunting.

Ethnographic Variation and the Puzzle of Australia

If big-game hunting shaped the political style of modern humans and the unpredictability of capturing large prey undercut hierarchies, they could help explain variation in social arrangements among ethnographically known moderns. When big-game hunting opportunities decline, it is a less important arena for male competition. Young men cannot escape subordinate status by taking large animals to demonstrate their value as desirable neighbors and associates.

Aboriginal Australia has always presented difficulties for ethnological generalizations about egalitarian societies. For example, in the center of the continent ethnographers found hunter-gatherers in ecological settings much like the habitat of the Hadza in the dry tropics of Africa. Yet instead of the lack of male hierarchies reported elsewhere, ethnographers working in Australia described "gerontocracies" in which old men, no richer than hunters elsewhere, wielded power over young; and polygyny was common (Strehlow 1970). If the traditional view were correct, the view that men support their families and are monogamous when they can only support one wife, then Australian men like hunters elsewhere would have had monogamy ecologically imposed upon them (Alexander et al. 1979; Wilson 1975).

One response to the failure of Australia to fit the standard expectations was the suggestion that the greater "power" of some men allowed "socially imposed polygyny" (Flinn and Low 1987). That suggestion, anomalous if nuclear families are assumed to be economic units and men are assumed to provide for their wives, is exactly the one to pursue in light of the contrarian hypothesis offered here.

When people first arrived in Australia, social arrangements might have been much like those seen ethnographically among hunters elsewhere. But in Australia, unlike all other continents occupied by humans, the terrestrial vertebrate populations persisting into the Holocene included no very large-bodied species. Archaeologists dispute the timing of the last extinctions of Pleistocene megafauna in Australia, but most agree that they antedate the Holocene (Allen and O'Connell 1995). Unlike the Americas, which also suffered massive extinctions when people arrived, in Australia the species remaining after initial extinctions included no animals with average adult body weights greater than 40 kg. And kangaroos, the only animals that large, experience periodic population crashes that sharply reduce the chance that hunters will encounter them in the arid center of the continent (Gould 1980).

With the disappearance of almost all big game, the opportunity for young men to undercut the superiority of their elders by procuring large meat bonanzas would have disappeared as well. Male competition could then take forms that allow steeper, more persistent hierarchies, even in the absence of wealth differences. Resulting social organization would still be stamped by the modern human reliance on emotional control and the use of conventions to settle contests, including contests over mates. But without big-game hunting to eclipse the prominence of senior men, the fact that they would always have prior claims and previously established allies could allow the older men to successfully hold wives against more weakly competitive younger men. The distinctive complexity of Australian marriage arrangements could arise when mate-guarding conventions are generally in use but male hierarchies are no longer undercut by the constantly anticipated but always unpredictable capture of large prey.

Conclusion

I began this essay by reviewing reasons why longstanding assumptions about the role of hunting in human evolution are unsustainable. If hunting is an arena for mating competition among males, then it may play an important role in human evolution quite different than usually supposed. Competition in the form of big-game hunting and competitive scavenging would result in repeated captures of large carcasses. The size of the bonanzas would allow many more than the hunter to claim shares. Hunting success would be of great interest to all. At the same time, captures would be unpredictable. A hunter's success on one day would be outshone by the subsequent success of another. The value of meat to all, combined with the unpredictability, could undercut male hierarchies and so result in the egalitarian patterns widely observed among mobile hunter-gatherers. In addition, potentially dangerous contests over large prey could have favored the use of conventional solutions to settle conflict. Strategies of conflict over food that use conventions could be extended to strategies of conflict over mates, with implications for the evolution of marriage. These particular ideas may prove incorrect, but they stem from theory and data that are compelling enough to justify further work.

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Notes

- 1. Household share weights are not equivalent to the amount consumed by household members because cooking occurs where other camp residents may join the eating, sometimes in front of houses, sometimes in public activity areas. Residents of other camps are especially likely to visit and "help eat" when they know there is meat in camp. "Visiting so-and-so to eat meat" is not an uncommon description of how someone spent the day. Sometimes visitors not only eat but depart with uncooked portions. Household share provides only a rough index of consumption.
- 2. The larger the carcass, the larger the party that assembles to transport meat from the acquisition site (O'Connell et al. 1990). It is likely that the number of visitors who arrive to "help eat the meat" is also a function of carcass size. Perhaps the hunter's larger share of the biggest carcasses is dictated partly by that expectation. Those known to have taken less may be more successful at parrying visitors' demands.
- 3. The sample of household shares measured meat—edible tissue only. In this comparison I assume that the inedible fraction was distributed in the same way.
- 4. The larger the prey, the rarer the captures (for encounter hunting), a pattern due to the systematic relationship between body size and population density. Human hunters achieve much higher rates than chimpanzees do for prey in the same size range. As noted above, Hadza rates for small animals are much higher (Hawkes et al. 1991).

- 5. The sharing sample discussed earlier is biased toward the largest prey; the mean estimated carcass weight for that sharing sample is 261 kg, an average of 152 kg of edible tissue.
- 6. For prey from 20 kg to 40 kg, the Ache rate falls to .06 captures/hunter-day. Two larger prey species sometimes taken by Ache hunters, capybara (avg. 60 kg) and tapir (avg. 150), are taken so rarely that no captures were observed over one observation period of 674 hunter-days (Hawkes et al. 1982).

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