The Evolutionary Basis of Sex Variations in the Use of Natural Resources: Human Examples

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People, unlike other primates, regularly consume foods acquired by others. When people forage for a living, women and men customarily acquire different foods and consume the products of each other's work. This distinctively human "sexual division of labor" has seemed the hallmark of human resource use. If men and women have different economic specialties, marriage creates a social unit that deploys their different capacities to serve family needs. Other distinctively human patterns then seem to arise from this fundamental economic cooperation between the sexes. In recent decades, the use of evolutionary theory to investigate and explain social behavior across the living world has revealed pervasive conflicts of interest between (as well as within) the sexes. Application of these tools to human examples shows the "sexual division of labor" to be the economic aspect of different and conflicting reproductive agendas for women and men. A review of some examples from communities where people hunt and gather for a living illustrates that families are not units of common economic interest. As with other primates, males and females have different reproductive goals and these differences shape sex differences in patterns of resource use.

Sex differences among mammals are obvious to even the most casual observer. Evolutionary theory provides tools for exploring and explaining the variable character and extent of those differences by distinguishing mating and parenting effort and exposing the reasons why males usually gain more from competing with each other for mates, females from competing for resources that contribute to offspring welfare (Low, this volume).

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But standard scenarios of human evolution postulate a key departure from general mammalian patterns, one that would have made the sexes much more alike. In these scenarios, ancestral males hunt to supply food for their mates and offspring so that nuclear families become basic economic units. This sharp increase in men's parental effort reduces the remainder available for mating competition.

The ethnography of contemporary hunter-gatherers has provided one of the main lines of evidence for this argument. Men usually hunt and women gather. Since women and children eat meat procured by men, the "sexual division of labor" is assumed to indicate husbands and fathers supporting their households, making nuclear families the basic economic units of human societies. But closer study of food sharing patterns shows that hunters often supply more food to people outside their households than to their own families. The interests of nuclear family members diverge in fundamental ways. I review reasons to consider the hypothesis that men hunt not for parental payoffs, but for mating advantages instead.

After a brief description of sexual selection theory, I summarize common assumptions about hunting and human evolution, and then report the patterns emerging from studies of the Ache of Eastern Paraguay and the Hadza of Northern Tanzania. In both cases hunting provides a substantial fraction of the diet. But a hunter's kill is widely shared, distributing nutritional benefits to women other than his wife and children other than his offspring—as well as to other men. Women allocate most effort to supporting their children while men choose resources that supply less for their families than alternatives would. Meat is more widely shared than plant food. This is a reason for people to favor hunters as neighbors. The favorable attention from many who expect meat shares can give alliance and mating advantages to hunters. If so, the basic sex differences in resource use among other mammals may have been more important in human evolution and in ethnographic variation than generally supposed.

SEXUAL SELECTION

Darwin developed his theory of sexual selection (1871) to explain striking features of behavior and morphology that, unlike other adaptations, seemed to reduce rather than enhance chances of survival; and that occurred in only one sex, usually males. Observing that these features played a role in mating, either in contests between males, or in attracting females, he theorized that they were shaped by selection through effects on mating success.

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Evolutionary biologists have since elaborated the underlying reasons for such sexual asymmetries (Low, this volume). The variable that distinguishes females from males across the living world is a difference in the size and number of gametes they produce, few relatively large rich eggs, many small resource-poor sperm. Consequently, potential rates of reproduction (Clutton-Brock & Vincent, 1991; Clutton-Brock & Parker, 1992) are usually lower for females than for males. But each offspring has both a mother and a father, so actual rates are always limited by the slower sex. In primates, females can usually reproduce at a potential maximum rate of about one offspring a year. Males, on the other hand, can potentially reproduce at a rate of (more than) an offspring a day. In a population with 100 members of each sex, 100 babies could be born in a year, one to each female, and they could all be fathered by a single male.

This thought experiment shows why mating competition is an inevitable problem for males in a way that it is not for females. The number of babies born is limited by the number of females. Any male who increases the number of babies he fathers decreases the number fathered by others. Paternity competition is a zero-sum game. If one of the males in the population imagined above fathered all the babies, the 99 other males would be cut out entirely. When sex ratios are near even (where selection usually sets them), any male with higher reproductive success than the female average leaves less than that for other males. This fundamental asymmetry between the sexes explains why selection favors different capacities and tendencies among males and females. Among females, fitness is most strongly affected by the number of successful offspring raised, favoring capacities and tendencies to acquire and control resources that contribute to the welfare of offspring. Among males, fitness is most strongly affected by success in competing with other males over sexual access to females.

HUMAN FAMILIES

The economic role of men has been assumed to indicate substantial reductions in these sex differences in human evolution. In the 1950s and 60s Sherwood Washburn synthesized three lines of evidence: comparative primatology, paleolithic archaeology, and ethnology to construct a powerfully influential scenario of human evolution.

Nonhuman primates rarely hunt or share food. Juveniles and adults of both sexes feed themselves, adult males playing no "economic" role in the lives of their mates and offspring. The archaeological record suggested an important difference in the patterns of our hominid ancestors. That record

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begins at the Plio-Pleistocene boundary, about 2 million years ago, with stone tools and the bones of large animals, a combination Washburn and others read to indicate that males were hunting and transporting meat home to share. Ethnographic descriptions of contemporary hunter-gatherers seemed to fill out this picture. People who forage for a living regularly acquire food they carry home and share. Men generally hunt and women and children consume the meat they acquire, so men seem to be family providers. These elements supported Washburn's persuasive inference that the initial evolutionary innovation that gave rise to other distinctively human attributes was hunting by males to provision their families (Washburn & Lancaster, 1968).

Since these arguments were developed, new fossil evidence has shown unexpected variation in the hominid lineage and the long persistence of taxa that antedate the archaeological record (Foley, 1995; Klein, 1989). Reappraisal of the archaeology has challenged the inferences of hunting and home bases from the early record (Binford, 1981). Nevertheless, absent a satisfactory alternative, essential elements of the scenario remain influential (e.g., Diamond, 1992, pp. 68–71). In particular it is widely assumed that men are distinctive among the primates in making substantial allocations to parental effort, therefore less to mating competition—thus blunting the effects of sexual selection (Lancaster & Lancaster, 1983). Among contemporary foragers men hunt, and it is assumed that they do so to support their wives and children.

The two ethnographic cases to be described challenge these assumptions. While radical in light of conventional wisdom about hunter-gatherers, this is a challenge easily anticipated in light of general sex differences, and the reasons for them. The possibility is not just that ethnographic variation is wider than commonly appreciated, but that the patterns illustrated in these examples are themselves likely to be quite common but overlooked because the proposition that men are providing for their families has come to be one of those "known facts" that need no test.

TWO ETHNOGRAPHIC CASES

Modern people and modern environments differ from those of the past, but contemporary behavior can shed light on ancestral patterns in the same way that any particular (and therefore unique) experience or set of observations can adjust expectations about others. Particular instances exemplify general processes. Where people hunt and gather for a living, they

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face daily problems that have deep antiquity in human experience: these provide an ethnographic opportunity to view such problems, see what solutions people choose, and evaluate whether and how features of local ecology shape both. Any particular example represents only a small fraction of some larger possible range of variation. But each case offers a chance to see whether variables are related in expected ways. If so, the systematic relationships provide the basis for hypotheses about likely patterns elsewhere, under different circumstances, including those of the past.

The Ache

The Ache (Hill, 1983; Hill & Hurtado, 1996) occupy the forests of eastern Paraguay, an area just outside the Amazon Basin. As is typical of foragers, Ache men hunt, targeting a wide variety of mammals, birds, and reptiles. Tapirs are the largest animals they hunt, weighing up to 150 kg. But tapir encounters are extremely rare and the largest of the animals regularly taken, brocket deer and white lipped peccary, have adult body sizes less than 40 kg. Men spend most of their hunting day away from women and children, sometimes coordinating their activities with other men (Hill & Hawkes, 1983; Kaplan et al., 1990). Women spend their days in company with other women and children (Hurtado, 1985; Hurtado et al., 1985). The Ache are unusual among ethnographically known foragers for their frequent residential moves. On most days women, carrying household goods and children, walk through the forest following the hunting men. The women stop often to rest and sometimes to gather plant foods, honey or insects. In the afternoon, when camp is set, nuclear families become visible. Each woman sets a fire for the night, and while there is daylight she may leave to gather food nearby. Women spend little time in food acquisition (Hurtado, 1985; Hurtado et al., 1985) and contribute a relatively small fraction of the calories consumed by Ache foragers (Hill et al., 1984), less when they are nursing infants, more when they are not nursing and have other children to feed (Hurtado, 1985; Hurtado et al., 1985). Men arriving from a day of hunting settle at the fires of their wives, although they may also leave again to collect plant foods nearby.

The association of nuclear families with hearths suggests these might be economic units, with members pooling the food they have acquired for joint consumption. Sharing among hearths is frequent, so systematically collected quantitative data are required to determine whether nuclear families are consuming more of the food acquired by their members (Kaplan, 1983; Kaplan et al., 1984; Kaplan & Hill, 1985a). Two salient points emerge from the record of observations. First the overall amount of sharing

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beyond the nuclear family is very high. About three quarters of the food anyone eats was acquired by someone outside their own nuclear family. Second there are systematic differences in the amount of sharing by resource type. The resources that only men take, game animals, are so widely distributed that family members get no more than anyone else. The resources that women most often take are less widely distributed, nuclear family members getting more than others. So families are economic units for some resources but not for others—specifically not for honey or game animals.

Since Ache men not only hunt but also take (collect) all the resources women do, it is possible to test whether the resource itself or the sex of the acquirer determines the extent of the sharing. Partial correlations show that sharing is robustly patterned by resource type. Each resource has its own sharing signature—no matter who acquired it. Men take more of the ones less likely to go to their own family members (Hawkes, 1991).

Men have widely varying hunting success rates (Hill & Hawkes, 1983). The differences persist from one year to the next (Kaplan, 1983), reflecting skill, not just luck. The men who are more skillful hunters, and therefore bring more meat for all, also spend more time hunting than do less successful hunters. This pattern suggests they have more to gain from additional time spent hunting than do less successful hunters. But the sharing patterns spread the *consumption* gains for their extra work across the foraging group.

By choosing the narrowly shared collected foods, women serve the goal of feeding their children. Men, by choosing game animals and the widely shared collected foods, are serving a different goal. They are targeting resources that many will consume. This makes them valuable neighbors, increasingly so the better hunters they are. If other things are equal, they should find more ready allies when disputes arise. Other men might be more tolerant of their sexual overtures to other women. Women for the same reasons might be more interested in traveling with these men than with those whose foraging efforts brought them little.

The Ache sharing patterns and sex biases in resource choice challenge the view that hunting is largely a kind of parental effort. Meat is so widely shared that the wife and children of a hunter consume no more than others. By hunting, a man is choosing to acquire resources that mostly go to those outside his own family. The benefits he gets for doing so could be favorable attention from those outside his family, which increase his chances of enlisting allies and succeeding in mating competition. Men who are more successful hunters *do* have more mating opportunities and higher reproductive success (Kaplan & Hill, 1985b).

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The Hadza

The savannahs of East Africa present different foraging constraints and opportunities to hunter-gatherers. The Hadza (Blurton Jones et al., 1992) in northern Tanzania occupy residential bases for weeks, sometimes months at a time. Dome shaped brush structures provide spatial distinction for nuclear families. But during the day, when adults are in camp, they spend little time in or near their houses, women joining other women and men joining men to sit in public activity areas. In all seasons most Hadza women and children forage together. Parties leave home early in the morning, usually accompanied by a man or older boy armed with bow and arrows to guard against meetings with strangers, most likely pastoralists tending their herds in the neighborhood. The foraging parties usually target a particular resource, tubers at any time of the year, berries or baobab in seasons when they are ripe (Hawkes et al., 1989). Nursing infants and children about 5 years of age and older often accompany their mothers even on trips of long distance and duration (Hawkes et al., 1995). Although Hadza youngsters are active foragers, and increasingly so as they get older, their acquisition rates fall below those of adults (Blurton Jones et al., 1989; Hawkes et al., 1995). Relative juvenile effectiveness varies among resources, and women adjust their resource choices not to maximize their own personal acquisition rates but those of the "team" that includes their children (Hawkes et al., 1995). Data as yet unpublished show that women make adjustments in their foraging patterns, attending less to their older children when they have a nursing infant. Older women, "grandmothers," spend more time foraging for tubers—the most energetically expensive of the plant resources—than do women of child bearing age (Hawkes et al., 1989). Unpublished data show that "grandmothers" are especially important in maintaining the nutritional status of children whose mothers are nursing a younger infant. Women share resources with foraging companions while away from home, and with those who assemble to claim shares on their return, but manage to retain a substantial fraction for later household consumption. The correlations between the nutritional status of women and their children and grandchildren (unpublished data) show this differential consumption by family members, confirming that women are providing for their children and grandchildren.

Mothers and children with the addition of grandmothers may be seen as consumption units for an array of resources they gather. There are also times when husbands and wives and their children regularly forage together. In the honey season family parties form, women and girls carrying the containers, boys and men pegging and climbing the trees, smoking the

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bees, and extracting the honey. When these trips are successful large amounts of honey are eaten by all before returning to camp. On arrival others assemble quickly to claim shares. If the take has been large enough, successful honey collectors will retain some for household consumption later. Sometimes and especially in a good honey year, a husband and wife may accumulate enough to carry off to trade with neighboring villagers who use it to make a fermented drink.

Most of the time Hadza men are hunters specializing in big game. Warthogs and impala mark the smaller end of the range they usually target. The larger ungulates in this habitat ranging up to giraffe are all included, leaving only elephants, who they say are too dangerous to hunt. They also compete successfully with local carnivores for the carcasses of all these animals (O'Connell et al., 1988). Whenever men leave camp they are armed with poison arrows and vigilant for any hunting opportunity. On most days they devote time specifically to hunting, usually by themselves, although tracking parties of men and boys form when a hunter reports a solid strike. In addition to the time boys spend with foraging parties of women and other children, they also hunt with age-mates. In the late dry season, when game animals are tied to the restricted points of surface water, men and older boys hunt at night from blinds set over water or along game trails.

The character of the hunting opportunities here sharpens a pattern that is much less marked among the Ache. Daily acquisition averages for Hadza hunters are higher than those of Ache hunters (hourly averages twice as high) but instead of the Ache failure rate of every fourth day or so (Hill & Hawkes, 1983; Hawkes, 1990), the average Hadza hunter is successful only one day in *thirty* (Hawkes et al., 1991). It is the enormous size of Hadza prey that turns rare successes into a high daily average. And this prey size increases the sharing radius. Not only other members of the hunter's camp, but residents of neighboring camps come to claim shares. Other men, as well as women and children come to the kill site both to eat and also to carry portions home.

The differences in hunting success among Hadza hunters are even greater than among Ache hunters, but all men, even those who have not been successful in a long time, take part in consumption. Men, women and children assemble at a carcass to claim shares. The claims often have an edge of demand and are often couched in terms of the relative size of one's share compared to those of others (Blurton Jones, 1987). Attempts to refuse a hungry crowd would be costly—even though there would be clear benefits to those who could monopolize a large carcass. The technology for storing meat is readily available and widely used. People can and do dry

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meat, some at the kill site and more on return home, frequently trying to accumulate enough to take off to trade for tobacco, marijuana, corn, millet, or other goods. But substantial accumulation is rare because household members, neighbors, and visitors eat it as quickly as it is dried. Since individuals successfully claim shares whether or not they have provided them in the past, and since there is a ready technique to store meat, sharing cannot be explained as a way to "bank" resources that would otherwise lose their value.

By hunting big game the average Hadza hunter has a 97% chance of coming home empty handed everyday. When he is successful the meat goes mostly to others. An experiment (Hawkes et al., 1991) showed one way a man could contribute more, and more often, to his family's consumption. Men were paid to hunt and trap small animals to see what success they might have in this environment. Results showed that they earned a smaller but much more regular return than they earned specializing in big game. Since small animals are mostly eaten by family members, a man who hunted them (while continuing to take shares from any large carcasses) would provide more for his family than a man who did not. Men could also collect plant food, something they often do to feed themselves, although they rarely collect much to bring home. By specializing in big game men are forgoing alternatives that would provide more for their own families.

What benefits do they get instead? Data currently under analysis show that the wives and children of better hunters are better nourished, a pattern that seems initially to contradict the preceding claims. But the same data show that family members' weight changes do not track a man's hunting successes. Instead children's nutritional status is correlated with the foraging adjustments their mothers (and grandmothers) make according to the age, and nursing status of their coresident children. Women differ in how well they handle the day-to-day problems posed by the nutritional needs of their children. Children of better hunters are generally better nourished because of their *mothers* (and grandmothers).

FAMILIES AGAIN

Nuclear families are visible groups, and monogamy is the common pattern for both the Ache and the Hadza. Alexander et al. (1979), assuming that men hunt to provide for their families, argued that monogamy is frequent among foragers because, without farming or herding, men are rarely able to support more than one wife. Alexander and colleagues distin-

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guished this "ecologically imposed" from the "socially imposed" monogamy occurring in societies with marked wealth differences but legal sanctions against polygyny. Flinn and Low (1986) noted that hunter-gatherers in Aboriginal Australia, no wealthier than monogamous foragers elsewhere, were often polygynous. They suggested that the greater "power" of some men allowed "socially imposed polygyny." This exposed a problem in Alexander's typology that is compounded by the patterns reviewed here. If "social" and "ecological" factors are independent, ecological variables cannot explain social behavior. But the examples reviewed here, like the whole field of behavioral ecology, show that the fitness-related tradeoffs imposed by local ecological constraints have social components. The prevalence of monogamy among foragers like the Ache and Hadza depends as much on social variables as polygyny does among some Australian foragers, as much as monogamy—or polygyny—does among people depending on other subsistence strategies.

If hunting is the main arena for competition among men, a better hunter may displace another in contests for a particular wife, with day-to-day unpredictability preventing him from being enough "better" than other men to successfully defend more than one wife at a time. According to this hypothesis monogamy could result, independently of women's preferences, from very high levels of mating competition among men—not just, as is often assumed, from men investing little in mating effort. Alternatively women might prefer to marry better hunters if those men are more favorably treated by others (Hawkes, 1993) and the favors extend to their children (Hill & Kaplan, 1988; Hawkes, 1990). Since that should lead to polygyny for the best hunters, a more complicated pattern of female choice would be required to account for the data. Either way, it is not the number of dependents a man can support but the character of the mating competition, itself conditioned by local ecology (Hawkes, 1990, pp. 163–4), that emerges a more likely primary determinant of marriage patterns (see also Hurtado & Hill, 1992).

Studies of birds, other primates, and recent modeling converge with the patterns reviewed here in showing that mating competition plays a more prominent role in shaping male strategies than recently supposed. The work on birds is especially suggestive since classic explanations emphasizing the role of paternal care in promoting monogamy in humans parallel those long used to explain the prevalence of avian monogamy: males can help raise expensive offspring (Lack, 1968). Recent research shows strong mating competition in many bird species where previously large paternal effort and attendant weak mating competition have long been assumed (see review in Davies, 1991).

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Adult male primate contributions to the welfare of infants and juveniles have been assumed to depend on some possibility of parental payoff to the males. But recent work suggests that in many species caring males earn mating and not parenting benefits as females prefer to mate with carers (Smuts, 1985; Whitten, 1986; Smuts & Gubernick, 1992). Very general models built to investigate the way that a male's payoffs for mating competition vary with the frequency of competitive challenges from other males show that this frequency dependence has powerful effects. Selection favors large allocations to mating competition even when male help could make a big difference in the number of offspring raised by their mates (Hawkes et al., 1995). In light of the results from these other lines of inquiry the human patterns reviewed here are not surprising. Ethnographic attention to the choices open to individuals and the fitness related costs and benefits likely for each is relatively recent. Better understanding of how these vary with sex, age, and local ecology will improve the prospects for explaining not only sex differences in resource choice but variation in other aspects of social behavior within and among human societies.

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