

## CHAPTER TEN

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# FORAGING DIFFERENCES BETWEEN MEN AND WOMEN

### *Behavioural ecology of the sexual division of labour*

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Non-human primates forage mostly to feed themselves. Since this is not true of human foragers, a sexual division of labour and regular food-sharing have been nominated as the evolutionary keys to a distinctively human way of life (e.g. Washburn and Lancaster 1968). The evident economic co-operation among men and women is used to justify the view that families or larger social groups are units of common interest with members deployed to meet group needs. Here I provide theoretical and empirical justification for the contrary view that the interests of individuals, and the way these vary with sex, age and ecology, can better explain human foraging patterns and the social strategies of which they are part.

To set the problem, I begin with a summary of the influential scenario that makes a sexual division of labour the key transition in human evolution. This is followed by a brief sketch of the general orientation of behavioural ecology and some of its primary conceptual and modelling tools, especially those that apply to understanding behavioural differences between the sexes. After this I review some sex-biased foraging and social strategies among other primates as a means of illustrating these tools in use and providing a background for their application to human patterns. I then consider some examples of recent work on foraging practices among hunter-gatherers that focus on fitness-related trade-offs and the way they differ with sex, age and ecology. This work shows that differences between the sexes are as important among people as they are among other primates. Females trade off alternatives that give different benefits to their children; males trade off parenting benefits for benefits in mating competition. This view of the sexual division of labour locates

it more clearly within the general primate variation. It also underlines similarities in the conflicts of interest arising among men and women who forage for a living and the sexual conflicts among people who make a living in other ways.

## HUMAN EVOLUTION

The substantial contribution men make to feeding children distinguishes human social arrangements from those of other primates. Washburn saw this as a consequence of the switch made by ancestral males to hunting, creating 'a wholly new set of interpersonal bonds. When males hunt and females gather, the results are shared and given to the young, and the habitual sharing between a male, a female, and their offspring becomes the basis for the human family' (Washburn and Lancaster 1968: 301). Lancaster and Lancaster put it this way: 'The division of labor between human males and females and the regular sharing of food represents the true watershed for differentiating ape from human life ways' (1983: 36). They noted that male care of young is more frequent in primates than other mammals, but the one thing they do not do is regularly bring food to their mates and offspring – 'the evolution of the role husband/father is unique to the human species and represents major ecological and social specializations' (1983: 42).

... the fundamental platform of behavior for the genus *Homo* was the division of labour between male hunting and female gathering, which focused on a unique human pattern of parental investment – the feeding of juveniles. The importance of contributions by both the male and female parent toward juvenile survival reduced the significance of sexual selection in human reproductive strategies and emphasized parental investment and parental partnerships for the rearing of children.

(1983: 51)

This scenario compellingly ties an array of salient features into a coherent package, linking ecological changes to shifts in resource exploitation and consequent social strategies, all through appeal to adaptive advantages. Possible conflicts of interest among family members seem overshadowed by longer-term common interests. But the problem with the argument is that explanatory appeals to natural selection require careful attention to distinctions between individual and group benefits. Despite extensive discussion of the importance of this distinction (e.g. Williams 1966a), and influential demonstrations of pervasive conflicts of interest between mates and among closest kin (Trivers 1972, 1974), anthropologists continue to think of small kin-based communities, especially the families composing them, as units of common interest. Reasons to revise this widely accepted view of the economic and social basis of the sexual division of labour continue to accumulate.

## BEHAVIOURAL ECOLOGY

Two sets of ideas are fundamental to behavioural ecology. First is the assumption that, as the products of evolution, living things have been designed by natural selection (Williams 1966a). This warrants the expectation that individuals will tend to do things likely to enhance their own fitness. (For extended discussion of applications to human behaviour see, e.g., Alexander 1979, Betzig, *et al.* 1988, Borgerhoff Mulder 1991, Chagnon and Irons 1979, Cronk 1991, Daly and Wilson 1983, Smith and Winterhalder 1992, Symons 1979). This has an important entailment: the fitness interests of individuals are rarely perfectly coincident, hence conflicts of interest among family or group members can result in outcomes that do not maximize group benefits or average benefits among members.

The second distinctive feature of behavioural ecology is its explicitly economic perspective (Maynard Smith 1978a, Parker and Maynard Smith 1990). Because time and energy are limited, individuals always face allocation problems. More to one thing means less to something else. Every action exacts the opportunity cost of missed benefits from alternatives foregone. Using the working assumption that individuals have been designed to choose options likely to give them higher net fitness, investigators seek to explain a pattern by discovering how it serves the fitness of those displaying it better than available alternatives. This involves posing hypotheses about (1) the particular (fitness-related) effects it has, the 'goal', (2) the constraints on achieving that goal and (3) the currency in which the options are evaluated. Simple optimality models are used when the pay-offs for a strategy do not depend on how many others adopt it. When the pay-offs vary as others use the same strategy, frequency-dependent optimality models that take mutual adjustments into account are appropriate. Evolutionary game theory (Maynard Smith 1982) has proven especially useful.

The tools of optimality modelling require investigators to be quite explicit about their construal of any pattern of interest. This is both a peculiar strength of the approach and the source of what some see as its irritating inflexibility. Investigators make biologically informed guesses about the fitness-related problem the subject is trying to solve. This requires hypotheses about the effects or goals of the behaviour, and about the costs and benefits of alternative means to achieve that goal. Formal models serve to show what individuals would necessarily do to achieve a particular goal under specified constraints. If subjects don't behave as modelled they are not meeting that goal, and/or they face other constraints. Models that have proven most useful have focused on very simple trade-offs, use readily measured currencies to assess alternatives and incorporate few constraints. For example, the prey model of foraging theory (Stephens and Krebs 1986) shows which resources a forager will

pursue to maximize its mean rate of energy capture if it can only spend time either searching for or handling resources (so this is the only trade-off), and if resources with known average handling rates are encountered sequentially at a known rate (these are the only constraints). Lack's (1947) model of optimal clutch size is another example, where the trade-off is between clutch size and survivorship per offspring (because daylight constrains parents in the total amount of food they can deliver to the nest) and the hypothesized goal is maximum number of surviving offspring per clutch. The utility of the models is not just a matter of whether or how often subjects seek these goals under these constraints. The simplicity of the models, and the relative ease with which key variables can be measured, makes patterns in falsification themselves informative (e.g., Lessells 1991, Stephens and Krebs 1976). For example, bird and insect clutches are often smaller than the size that would maximize the number of survivors per clutch, leading to hypotheses about different goals and trade-offs (Charnov and Krebs 1974, Williams 1966b).

### SEX DIFFERENCES

Understanding the fundamentally different ways in which males and females gain reproductive success supplies a foundation for expecting differences in a wide array of phenotypic strategies. In all sexually reproducing populations, including humans, each individual has both a mother and a father. Although each contributes half the genetic material, males and females can differ enormously in the other investments they must make to produce offspring. Trivers (1972) recognized that the extent of this difference determines the power of sexual selection, the aspect of selection that spreads characters according to their effects on competition for mates (Darwin 1871). The measure best capturing the key sex difference is the relative rate of offspring production (Clutton-Brock 1991). The slower reproducing sex necessarily limits the rate of offspring production. In humans for example, only the number of women determines the possible rate of baby production. A population including exactly 100 women can produce a maximum of about 100 babies a year, whether it includes 10 men or 10,000. One man could potentially monopolize all the paternity. Since all babies have a mother and a father, imbalanced sex ratios make average reproductive success higher for the rare sex. If, for example, females are rare, so that mothers get more grandchildren on average through daughters than through sons, then selection favors biasing toward daughters. As a consequence, equilibrium sex ratios are usually even, making the mean reproductive success of males and females equal (Charnov 1982, Fisher 1930). Then when any male gains higher reproductive success than the average female, other males must have reproductive success lower than the female mean. Because male fitness can be so much more strongly affected by differential success at getting

mates, it is selection on males that often favours allocating reproductive expenditure to mating effort. So Darwin noted widespread patterns of male-male combat, in which males compete to displace each other from mating opportunities, and female choice, in which males have been selected to display characteristics that females prefer in mates.

Maynard Smith's model of the evolution of parental care illustrates mating and parenting trade-offs that could be important in shaping reproductive strategies among animals generally (Maynard Smith 1977). He showed that each of the four possible patterns: female and male care (common among birds), female only care (common among mammals), male only care (not uncommon among fish) and no care (also frequent among fish) could be evolutionarily stable depending only on the values of three variables: offspring survivorship as a function of the number of 'parents' caring; number of offspring a female can produce depending on whether or not she devotes effort to care; and probability that a male will successfully mate again if he does not stay to care.

A particularly interesting feature of the model is that certainty of paternity plays no role (Maynard Smith 1978b, cf. 1982); i.e. male care can be an evolutionarily stable strategy (ESS) even if paternity certainty is very low, and no care or female only care can be an ESS even if certainty of paternity is very high. Recently new techniques to assess paternity have uncovered astonishingly high rates of 'extra pair paternity' in birds (Birkhead and Møller 1992), even though 'monogamy' with 'biparental' care is common. Relationships between care and probable paternity have been observed in some species (e.g. Davies 1992), but cross-species comparisons show paternal probability to be a poor predictor of male care (Møller and Birkhead 1993).

Maynard Smith's model highlights key differences between the sexes in the trade-offs they may face in committing a unit of reproductive effort. For males, parental care may cost the missed opportunity of additional matings, while females trade off increases in quality for quantity of offspring. The model's great virtue is in deriving so much from so little, and flagging what may be key differences between the sexes. But some of the empirical patterns we wish to explain add complications. Direct offspring care may not be the only way females expend parental effort and males may sometimes gain mating advantages by providing care.

### OTHER PRIMATES

The distinction between parental and mating effort seems quite straightforward: expenditure aimed to increase the number and/or fitness of offspring vs. that aimed to increase success at gaining mates. Much work over the past fifteen years focused on primate reproductive strategies has revised prior expectations about the character of these two kinds of expenditure. Primate females, like other mammals, reproduce at a slower

rate than males can, so males are expected to compete for matings and females to be choosy. Yet some primate females are extremely libidinous, actively seeking copulations with many males. While extra copulations might increase the number of offspring produced by a male they cannot have that effect for females. Hrdy (1979) suggested that multiple copulations by females are actually parenting effort. Males are often a source of danger or aid to infants and juveniles and differentially so depending on their possibility of paternity. Thus a female may increase the survivorship of her offspring by spreading the possibility of paternity widely (Hrdy and Whitten 1987).

The key link in this argument between male behaviour toward infants and juveniles and their probability of paternity has been challenged. While the relative frequency with which primate males care for infants has been generally assumed to be a function of the possibility of paternity and labelled paternal investment, males often contribute to the welfare of infants unlikely to be their own. Smuts (1985) noted that baboon males who made such contributions had greater chances of being chosen to mate by the infant's mother. Reviewing the patterns of male care across primate species Smuts and Gubernick (1992) found that probability of paternity was not clearly linked to the probability of care and concluded that their evidence 'calls into question the hypotheses that male-infant caregiving in non-human primates is primarily a form of paternal investment and suggests, instead, that male-infant care is sometimes a form of mating effort' (1992: 20). Male care of infants and juveniles may be mating effort even among monogamous primates (Price 1991, Whitten 1987).

The kind of care males provide rarely involves food delivery. But males of some species hunt. This is more frequent among chimpanzees than previously supposed and may earn mating pay-offs. Goodall (1968) early reported hunting at Gombe, and Teleki noted that males preferentially shared meat with oestrous females (1973). Boesch and Boesch (1989) reported more frequent hunting among chimpanzees at Tai. Females hunt much less often than males although they can be as successful at it as males are. Re-analysis of the frequency of hunting at Gombe (Wrangham and Bergmann-Riss 1990) showed overall rates to be about as high as those at Tai. Additional data and analysis provided by Stanford *et al.* (1994) shows marked short-term and seasonal variation in hunting frequency at Gombe and some similar patterning in this variation between Gombe and Tai as well as between Gombe and Mahale (Takahata *et al.* 1984). In addition to individual differences in hunting frequency, Stanford *et al.* show that there is a marked association between the number of males in a group, the number of oestrous females in the group and the frequency of hunts. They suggest that it is not variation in prey profitability or encounter rates but 'social' factors that account for hunting 'binges'. Social benefits could be either direct preferential treatment by females

or preferential alliances with hunters by other males, the latter in turn advantageous in mating competition. A related supposition comes from Nishida *et al.*'s report of the long-term pattern of meat-sharing by one male at Mahale, suggesting that 'it may be a political strategy, used to establish and reinforce alliances' (1992: 160).

In addition to the fact that male chimpanzees hunt and share their prey, other sex differences in foraging patterns (e.g. Boesch and Boesch 1984, 1989, Galdikas and Teleki 1981, Goodall 1986, McGrew 1992, Strum 1981) and food-sharing (Feistner and McGrew 1989, Silk 1978, Strum 1981) occur among chimpanzees and other primates. Altman (1980) showed how much nursing infants interfere with the foraging of baboon mothers and how dramatically mortality risks shift from mother to offspring at weaning. Fifteen years ago Wrangham (1979) pointed out that the key determinants of reproductive success for male and female primates are so different that explanations for varying 'social systems' should begin with those determinants. For females the main problem is access to food and so the characteristics of food resources should largely determine how they are distributed. The distribution of females determines the main problem for males: how much paternity they can gain (or lose) in competition with other males.

The work on other primates shows that for females parental trade-offs shape behaviour generally, including foraging activities. Males, by contrast, may hunt, share meat and care for infants not to invest in offspring but rather to gain mating advantages. This work highlights the potential for mistaking the benefits individuals gain from their behaviour. Recent work on hunter-gatherers corroborates the importance of the problem and shows how sex-specific trade-offs affect foraging strategies.

### HUNTER-GATHERERS

From the perspective of behavioural ecology people are expected to adjust their activity patterns as the pay-offs for alternative allocations of time and effort vary. If so, ethnographic patterns should differ accordingly. Differences in the character, distribution, and abundance of local plants and animals affect the rates of nutrient acquisition for different foraging strategies. Differences in the ways men and women can enhance their own fitness affect the trade-offs they face in choosing foraging tasks.

The accumulating quantitative picture of foraging activities among people who depend on wild foods shows that there can be substantial overlap in the resources taken by men and women (e.g. Dwyer and Minnegal 1991, Goodman *et al.* 1985) and that under some circumstances spouses spend large fractions of their foraging time working together (Bailey and Aunger 1989, Hart and Hart 1986, Hewlett 1992, Stearmen 1987). Sometimes men and women both hunt and gather. Satisfactory

explanations will need to account for the variation in the extent of the overlap between the foraging practices of women and men.

To illustrate how the exploration of sex-specific trade-offs can help explain ethnographic variation, I summarize two sets of ethnographic comparisons that employ this perspective. Women's foraging patterns and the way these are affected by child welfare goals and trade-offs between components of parenting are reviewed first. I then consider men's trade-offs.

### Women's foraging

#### *Trade-offs between foraging and child care: the example of the Hiwi and the Ache*

Acquisition (and/or processing) of some resources but not others may be effectively carried out in combination with child care. Resource choice often requires women to trade-off higher nutrient acquisition rates for child care benefits (Brown 1970, Hurtado *et al.* 1985, Murdock and Provost 1973). The extent of these trade-offs could be represented as one variable, the potential nutrient acquisition rates as another. Imagine the first variable as a continuum. At one extreme the two activities are mutually exclusive, at the other they are so perfectly compatible that a unit of time spent on one can also be spent on the other, with no loss of efficiency in either. Between these extremes tasks differ across the range of mutual interference.

The benefits expected for child care will also vary. Hurtado *et al.* (1992) report some of the ways trade-offs between foraging and child care benefits vary among Ache and Hiwi women. Differences in the environments of the two populations affect foraging opportunities, and also the prevalence of health threats to children that can be reduced by close supervision. The Ache inhabit the subtropical forests of eastern Paraguay in which resources are relatively abundant and evenly distributed throughout the year (Hill *et al.* 1984). Insect pests are also ubiquitous and cleared spaces minimal at daytime rest spots in the forest and in temporary foraging camps usually occupied for only a single night. These features 'make the forest a very unsafe area for unsupervised infants and children the year round' (Hurtado *et al.* 1992: 191). The Hiwi live in the savannahs of western Venezuela where resource distribution varies markedly in both space and time (Hurtado and Hill 1990). Main camps are occupied continuously for many years while temporary seasonal camps are used during the 'almost entirely pest-free' dry season, 'making camps an extremely safe area for infants and children' (Hurtado *et al.* 1992: 190). Hiwi women have less to gain from child care than Ache women do. On the other hand the acquisition rates they can earn are much lower than those available to Ache women.



*Individual vs. team foraging rates: the example  
of the Hadza and the !Kung*

In addition to the trade-offs with child care that may adjust the resources women choose to exploit and the time they devote to food acquisition, there is a third way in which child welfare may guide women's strategies. Women may promote larger collective daily totals of food for their family's consumption by enlisting their children in nutrient acquisition and/or processing. Under some circumstances this could entail high costs in child welfare, but sometimes that trade-off might be slight and women might best serve their own fitness by adjusting their foraging to maximize the 'team rate' they jointly earn with the participation of their children. The importance of this 'team rate' is illustrated in the food acquisition patterns of Hadza foragers in northern Tanzania and in the quite different patterns of !Kung speakers foraging in the Dobe area of northwestern Botswana in the 1960s.

The Hadza inhabit the East African savannah, the Dobe !Kung the northern edge of the Kalahari. Annual rainfall patterns are similar and both regions are home to the plant and animal species of the arid African tropics. In broad terms their environments are alike. However the rocky hill country of the Hadza with many visible landmarks and long vistas differs from the much flatter sandy terrain of the Dobe area. The Hadza have many more surface water sources, large ungulates are more abundant, more baobabs dot the hills, and patches of berries and nutrient-dense tubers are more extensive. There are no mongongo groves.

When foraging was the main subsistence activity !Kung children acquired little food themselves until their teenage years (Draper 1976, Draper and Cashdan 1988, Lee 1968). In contrast, Hadza children are energetic foragers providing substantial amounts of their nutritional requirements by their own efforts while very young (Blurton Jones *et al.* 1989, Hawkes *et al.*, in prep.).

Models based on measurement of the rates of nutrient acquisition that women and children can earn for alternative foraging strategies in these two settings show that the differences in the distribution and character of local resources account for the behavioural differences. Experimental foraging excursions around Dobe (Blurton Jones *et al.* 1994, forthcoming) and measurements of Hadza children's return rates near base camps (Blurton Jones *et al.* 1989, Hawkes *et al.*, in prep.) showed that near-camp foraging is profitable for Hadza but not !Kung children, explaining why Hadza but not !Kung youngsters forage unaccompanied by adults.

Hadza children also join adults in long forays to distant resource patches, travelling as far as !Kung women do when they visit the mongongo groves. The rates of caloric acquisition that children and adults earn both near camp and in the berry patch explain why Hadza women take their children older than 5 or 6 years on these long trips (of nearly ten hours,

duration including about an hour and a half of travel each way). Children can earn a rate much closer to the adult rate when picking berries. Since a child consumes food it acquires itself as well as that provided by its mother, the amount of food a woman makes available to her children depends not just on her own rate but on her 'team rate', the rate she and her children earn collectively. The choice that maximizes the team rate of a woman and a child on long foraging excursions is to travel to the berries.

The 'team rates' to be earned by a woman and her children foraging around Dobe also explain why !Kung youngsters didn't go to the mongongo groves. The main dry season resource here is the mongongo nut. While experimental foraging trips showed that the nut groves provided foraging return rates substantially higher than any closer patches, mongongo nuts, unlike either berries or tubers, require substantial processing (Hawkes and O'Connell 1981, 1985). Lee reports that 'children over eight and all adults of both sexes do most of their own cracking. Children 4 to 7 eat smaller quantities of nuts and these are cracked for them by their parents or older siblings' (Lee 1979: 277-278, original emphasis). Blurton Jones *et al.* (forthcoming) show that if a child were to travel with mother to the nut grove and carry (and then crack) enough nuts to cover its own nutritional requirements, the mother-child team rate would be *lower* than it is when the child devotes that amount of food related work time just to cracking nuts. By refusing to take children to the groves, leaving them at home to crack nuts for themselves and younger siblings, !Kung mothers maximize the rate at which their 'team' compiles edible nutrients.

*Trade-offs between childbearing and feeding and caring for grandchildren:  
the issue of menopause*

Women's foraging practices vary with ecological differences in the costs and benefits of various contributions they can make to the welfare of children. This has implications for understanding menopause and age-specific differences in women's foraging practices. A woman's childbearing years end sharply at about the middle of maximum life span (Pavelka and Fedigan 1991). From the perspective of life-history theory this is a striking puzzle. Williams (1957) addressed it when he elaborated a theory to explain how natural selection could account for senescence and its wide variation across the living world. Among the predictions of life-history theory Williams noted that there should be no 'post-reproductive' life and suggested that when there was a long period of juvenile dependency, mothers who stopped bearing offspring as their pregnancies got riskier with age might gain the benefit of increased survival for their last born. However menopause is absent among other primates (Pavelka and Fedigan 1991) even though late pregnancies can cost the survival of older and

still dependent offspring (e.g. chimpanzees; Goodall 1986, 1989). Long juvenile dependence is common among primates; menopause is not.

Post-menopausal Hadza women spend more time digging tubers, the most energetically expensive resource women take, than do women of childbearing age. To explain this as a consequence of fitness trade-offs we suggested an amendment to Williams' 'grandmother hypothesis' that focuses on a way in which women but not other female primates can earn substantial fitness benefits from helping their daughters (Hawkes *et al.* 1989).<sup>1</sup> When juveniles depend on their mothers for food, this changes the fitness trade-offs not only for the mothers of small children but for the mothers of those mothers. The more a female forages to feed her children the more help in either child care or food acquisition can affect the limits these place on her reproductive success. The more valuable this help, the more fitness a woman can gain by helping her adult daughter. By this argument the important fitness benefits for post-menopausal women come from the increases they promote in reproductive success of adult daughters.

Such a verbal argument about the direction in which important parameters might vary is one thing, constructing models with reasonable values that actually give the expected outcome is another. One evolutionary model shows that reduced childbirth mortality cannot account for menopause, although increases in children's reproductive success might (Rogers 1993). Another, using values for variables derived from the Ache, shows it possible but unlikely that the benefits of grandmothing in that case are higher than the benefits of continuing to bear children (Hill and Hurtado 1991). Alternative models and estimators remain to be tried.<sup>2</sup>

These examples show that many aspects of women's foraging practices, the resources they choose, the time they spend foraging, and the ways these vary by age and among ethnographic cases, can be explained by considering how women can best contribute to the welfare of their children. Trade-offs between different components of parenting differ by age and among ethnographic settings; the character and amount of women's labour differs accordingly.

### Men's foraging

Resources that men preferentially acquire often come in large packages, with high day-to-day variance in foraging success (Hawkes 1990, Hawkes *et al.* 1991, Kaplan and Hill 1985a). When men target these resources they bring home little or nothing on many, sometimes most, days, and when they are successful their capture is widely shared. Thus many of the daily nutrients consumed by women and children in foraging communities are acquired by men who are not their husbands or fathers, while husbands and fathers are contributing little, and that undependably, to their own families. Since men could adopt the same foraging practices

that women do, which would often mean bringing home a larger, steadier contribution to family consumption (Hawkes 1990, 1991, 1993), an obvious hypothesis is that instead of maximizing child welfare, they are, at least sometimes, serving a different goal. As noted above for males generally, men may have something to gain (or lose) depending on the effort they devote to mating competition.

Mating benefits that men might earn for their foraging practices remain largely unmeasured. It is easier to show that they are not choosing foraging targets that would give higher family earnings (Hawkes 1991, 1993, Hill *et al.* 1987), than to show mating pay-offs. Empirical support for the hypothesis that men earn mating benefits for their foraging is strongest for the Ache where better hunters are more often reported as sexual partners by women (Kaplan and Hill 1985b). Modelling can clarify the possibilities. Since the benefits a man can earn from trying to gain additional mates depend on what other men do, the pay-offs for alternative strategies are frequency dependent. Game theory models can accommodate both the zero-sum competition with other men for paternity and also the non-zero-sum pay-offs for increasing the number of offspring women can raise. One such model (Hawkes 1990) shows the relative success of the alternative male strategies of family provisioner (who brings in a steady amount of food varying little from day to day so that it reliably supports a family but never much extra) and show-off (who brings in wildly varying amounts, no reliable minimum to support a family, but occasional bonanzas much greater than a family can consume making a feast for the neighbours as well). When values estimated from Ache data are assigned to the variables in that model, 'showing off' is a robustly stable strategy.

Hadza men are primarily big game specialists. Hunting and scavenging large carcasses (O'Connell *et al.* 1988), they capture an extremely high average rate of 4.9 kg of prey per day (Hawkes *et al.* 1991). But hunters also commonly fail to kill or scavenge anything for weeks, sustaining an average 0.97 probability of failure each day (Hawkes *et al.* 1991). When they are successful, the carcass is shared throughout the camp and with neighbouring camps as well, only a small fraction going to the hunter's own family. If a man sought to feed his offspring, other available strategies, including hunting and trapping small animals (Hawkes *et al.* 1991) or gathering fruits and tubers as women do (Hawkes 1993) would be better choices.

!Kung men around Dobe in the 1960s hunted large animals, also with high failure rates (Lee 1979, Yellen 1977: Appendix B). In Lee's month-long quantitative record only one hunter succeeded in taking any large animal. These men also hunted and trapped small animals and gathered vegetable food (Hawkes 1987, Lee 1979, Yellen 1977: Appendix B). To the extent the smaller and more reliable packages of the latter were less widely shared, they contributed more directly to family provisioning. !Kung men

may have had relatively more to gain from parental investment (and less from mating effort), and so, in terms of the 'provisioner/show-off' model, pursued a mixed strategy, allocating some effort to each (Hawkes 1990: 163–165). The wide variation in foraging activity among the men in Lee's group of subjects (Hawkes 1993, Lee 1979) might be due to individual differences in the benefits a man expects from each kind of effort.

In the case of the Hiwi, men spend little time in foraging and 'share most of the meat and other foods they acquire with their spouse and offspring only' (Hurtado and Hill 1992: 40). This may be a case in which a man has very limited mating opportunities beyond his current spouse. It is important to note that it need not imply little mating effort. Women can be unavailable as potential mates because they are absent, because they refuse or because they are effectively guarded or defended by other men. A general pattern of monogamy could be the result of intense mating competition, with men unable to attract more than one mate or defend more than one.

Comparison of these four ethnographic cases suggests that where men have more mating opportunities they allocate more time to foraging practices that garner widely shared foods. They do this instead of maximizing the amount of food they supply to their own families. Hurtado and Hill (1992) have described the marked contrast in mating opportunities available to Ache and Hiwi men. Among the Ache amicable inter-band relations facilitate frequent visiting and so increase the pool of possible mates. The Ache have high female fertility, a growing population with relatively large young age cohorts, and a nearly even adult sex ratio through middle age, all of which increase the number of reproductive opportunities an Ache man can have. In addition, sexual joking and intimate interactions are common among Ache men and women who are not spouses. By contrast, among the Hiwi visiting is little tolerated, female fertility is lower and the sex ratio is strongly male biased through middle age (Hurtado and Hill 1992: 39). Interaction among Hiwi men and women not married to each other is very restricted. 'While serial monogamy and extramarital promiscuity is very common among the Ache, stable lifetime monogamous unions with almost no extramarital copulation is the normative mating pattern among the Hiwi' (Hurtado and Hill 1992: 40). Associated with these differences are marked differences in foraging effort. Ache men spend long hours foraging (Hill *et al.* 1985), nearly seven hours a day every day, for resources that are widely shared (Hawkes 1991, Kaplan and Hill 1985a). Hiwi men, by contrast, do not forage every day – about two days a week in the dry season (Hurtado and Hill 1987), and an average of less than three hours a day in any season (Hurtado and Hill 1990). The food they acquire goes mostly to their wives and children (Hurtado and Hill 1992).

Contrasts between the Hadza and the !Kung are not as extreme but they are notable. Hadza work effort is yet to be reported although a

provisional tabulation (Hawkes *et al.* 1987) shows men to spend about thirty-four hours a week foraging compared to the twenty-two hours reported by Lee (1979: 278) for the !Kung. In the 1960s the !Kung hunted large animals only a few days a week in some seasons (Hawkes 1987, Lee 1979, Yellen 1977) and spent substantial fractions of their foraging time gathering vegetable food and hunting and trapping small animals. Hadza men hunt almost every day for big game. They usually forgo small animals and rarely bring home vegetable food. These differences could follow a higher pay-off for mating effort among Hadza men. Three other differences suggest that Hadza men do have more mating opportunities. First, Hadza women have higher fertility (Blurton Jones *et al.* 1992). Second, 10 per cent of !Kung women in Howell's record were married to Bantu (Howell 1979) whereas only 4 per cent of Hadza women are married to villagers (Blurton Jones *et al.* in prep.) implying that the !Kung face stiffer mating competition from outsiders. Third, while only 8 per cent of !Kung women between 20 and 45 were unmarried, the proportion of unmarried Hadza women in that age range is 24.5 per cent (Blurton Jones *et al.*, in prep.).

### THE BROAD PATTERN OF VARIATION

In the ethnographic cases here, as among most hunter-gatherers, monogamy is the usual pattern. The explanation commonly given for its prevalence among foragers is that a husband and wife form 'a generalized economic group constituted to produce the local conception of livelihood' (Sahlins 1972: 79). That view of the sexual division of labour is challenged here. Cultural anthropologists have also recognized that marriage assigns mating rights in a particular woman to a particular man (Goodenough 1970). If marriage is often about mating competition among males (Wilson and Daly 1992), the common monogamy of the Ache, Hadza, Hiwi and !Kung should not obscure differences among these cases in the extent to which males can successfully monopolize access to mates. The role sperm competition has played in shaping aspects of human physiology and behaviour is only just emerging (Baker and Bellis 1993, Smith 1984), but it shows that 'extra pair' copulations and defence against them have long been important options.

Men sometimes do expend substantial effort in parenting, and differential risks of physical harm to children from step- and genetic fathers (Daly and Wilson 1988) provide clear evidence of the important role that confidence of paternity may play in men's behaviour toward children. Concern about probable paternity seems to be widespread (Daly and Wilson 1982), perhaps especially where economic property rights are important. Scholars have noted that men take less responsibility for their wives' children when confidence of paternity is low (Alexander 1974, Hartung 1985, Kurland 1979). The array of sometimes extreme practices to ensure paternity

certainty (Wilson and Daly 1992), especially elaborated when differential wealth and power can be transferred (Dickemann 1979a), seems aimed to prevent paternal effort from going astray. But sometimes the clear effect is to prevent other men from gaining mating access, whether or not any paternal effort follows (e.g. Dickemann 1979b: 175–176). Large differences can exist in both the parenting and mating options open to men of different classes (Lancaster and Kaplan 1992). The two kinds of effort need not always interfere. For example, men may be much more likely to care for a child they have fathered when they expect future matings with its mother. The extent of the interference and the extent to which the probable pay-offs differ may vary especially widely with the large wealth differences in stratified societies.

Some aspects of male behaviour that have generally been assumed to be paternal investment among both people and other primates may be mating effort instead. The assumption that men forage largely to provide for their families obscures similarities in two directions, those between some foraging practices and activities of other primates that earn social benefits, as well as similarities between foraging for widely shared resources and other 'status-seeking' activities associated with different subsistence patterns. Men may sometimes have more to gain from mating than parenting and they may trade off parenting benefits when the two interfere with each other.

The trade-offs for women are quite different. Modelling and measuring the many ways females can affect the welfare of their offspring continues to generate promising hypotheses to explain diverse aspects of female behaviour, from multiple copulations (Hrdy 1988) to styles of parenting (Blurton Jones 1993). An appreciation of the role that children's abilities can play in women's foraging practices may have large implications for understanding the constraints on other primates. As with humans, juveniles are not as competent in food acquisition as adults (Janson and van Schaik 1993). To the extent that youngsters' competence varies with resource type, primate mothers might sometimes increase their own fitness by foregoing resources that maximize their own rate of nutrient acquisition to exploit resources that offspring can acquire more efficiently. This highlights one of the consequences that human nutrient acquisition efficiency has for feasible foraging opportunities. When women can acquire food at a rate high enough to feed their weaned children, they can afford to make greater use of resources that juveniles cannot competently exploit.

The general analytical framework here directs attention to the trade-offs women face when different components of parenting interfere with each other and the trade-offs men face when parenting and mating interfere with each other. From this perspective the sexual division of labour is the outcome of males and females each pursuing their own fitness interests. The small sample of cases was chosen to illustrate the use

of those conceptual tools. For each case the patterns observed provoke questions about the available alternatives and their probable pay-offs to individual actors. The analytical framework can, in principle, guide investigation to ever finer precision in description and explanation, a potential especially useful to ethnographers seeking to account for particular cases. When the larger goal is to construct hypotheses about the past, however, more precision increases the difficulty and inflates the likelihood of failure. The more variables that must be estimated, the more chances to be wrong. The work discussed here converges on some important differences between the sexes and their patterned interaction with features of ecology. From this perspective the sexual division of labour, its character and variation, is the outcome of men and women facing different fitness trade-offs. To the extent that observed patterns can be explained in these terms, received views of families, or larger social groups, as units of common interest will be revised. Robust archaeological implications remain to be elaborated but the challenge to common assumptions about hunting and nuclear families is clear. Large effects on the activity patterns of women and children appear to follow from differences in the acquisition and processing requirements of broad categories of plant resources. Continuing work will show whether we can develop models with a few key variables that can give us testable hypotheses about the past.

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### NOTES

- 1 This is in marked contrast to the reduced foraging among older !Kung women in the 1960s reported by Lee (1985), a difference that may turn on the high processing requirements of mongongo nuts. Older women foraging in the Dobe area may increase the food production rates of their adult daughter's team more by staying in camp to crack nuts. Among the Hiwi, senior women are, like the Hadza, more active tuber diggers (Hurtado and Hill 1987). The Ache population has few senior women due to the heavy death toll on elders in the 1970s.
- 2 Arguments that the fitness pay-offs through increased reproductive success of daughters account for menopause (whether the mismatch between the end of childbearing and general senescence is seen as 'stopping early' or living longer) imply a particular pattern of sex-biased dispersal. Adult daughters would have to stay with their mothers, a pattern opposite to the male philopatry/female dispersal surmised to be characteristic of hunter-gatherers on ethnographic grounds (Ember 1978), general among hominids on phylogenetic grounds (Foley and Lee 1989, Ghiglieri 1987, Wrangham 1987), and increasingly taken



as an established fact (e.g. Manson and Wrangham 1991, Rodseth *et al.* 1991). By the argument here, menopause is a piece of evolutionary evidence inconsistent with a phylogenetic history of male philopatry. There is also some relevant evidence from molecular studies. Melnick and Hoelzer (1993) provide a provocative summary of work on mitochondrial DNA in which they note that the pattern of variation in 'small aboriginal human populations' is similar to that seen in the highly female philopatric macaques, and differs notably from the genetic structure consistent with female dispersal found in human groups with a long history of property-holding.

## REFERENCES

- Alexander, R.D. (1974) 'The evolution of social behaviour.' *Annual Review of Ecology and Systematics* 5: 325–383.
- Alexander, R.D. (1979) *Darwinism and Human Affairs*. Seattle: University of Washington Press.
- Altman, J. (1980) *Baboon Mothers and Infants*. Cambridge, MA: Harvard University Press.
- Bailey, R. and Aunger, R. (1989) 'Net hunters vs. archers: variation in women's subsistence strategies in the Ituri Forest.' *Human Ecology* 17: 273–297.
- Baker, R. and Bellis, R. (1993) 'Human sperm competition: ejaculate adjustment by males and the function of masturbation.' *Animal Behavior* 37: 861–885.
- Betzig, L., Borgerhoff Mulder, M. and Turke, P. (1988) *Human Reproductive Behavior: A Darwinian Perspective*. New York: Cambridge University Press.
- Birkhead, T. and Møller, A. (1992) *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.
- Blurton Jones, N. (1993) 'The lives of hunter-gatherer children: effects of parental behavior and parental reproductive strategy.' In M. Pereira and L. Fairbanks (eds) *Juvenile Primates: Life History, Development, and Behavior*, pp. 309–326. Oxford: Oxford University Press.
- Blurton Jones, N., Hawkes, K. and Draper, P. (1994) 'Difference between Hadza and !Kung children's work: original affluence or practical reason?' In E.S. Burch (ed.) *Key Issues in Hunter-gatherer Research*, pp. 189–215. Oxford: Berg.
- Blurton Jones, N., Hawkes, K. and Draper, P. (forthcoming) 'Foraging returns of !Kung adults and children: why didn't !Kung children forage?' *Journal of Anthropological Research*.
- Blurton Jones, N., Hawkes, K. and O'Connell, J.F. (1989) 'Modelling and measuring costs of children in two foraging societies.' In V. Standen and R. Foley (eds) *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, pp. 367–390. Oxford: Basil Blackwell.
- Blurton Jones, N., Hawkes, K. and O'Connell, J.F. (in preparation) 'The global process and local ecology: how should we explain differences between the Hadza and the !Kung?' In S. Kent (ed.) *Cultural Diversity among Twentieth Century Foragers: An African Perspective*.
- Blurton Jones, N., Smith, L., O'Connell, J., Hawkes, K. and Kamuzora, C. (1992) 'Demography of the Hadza, an increasing and high density population of savannah foragers.' *American Journal of Physical Anthropology* 89: 159–181.

- Boesch, C. and Boesch, H. (1984) 'Possible causes of sex differences in the use of natural hammers by wild chimpanzees.' *Journal of Human Evolution* 13: 415-440.
- Boesch, C. and Boesch, H. (1989) 'Hunting behavior of wild chimpanzees in the Tai National Park.' *American Journal of Physical Anthropology* 78: 547-573.
- Borgerhoff Mulder, M. (1991) 'Human behavioural ecology.' In J. Krebs and N. Davies (eds) *Behavioural Ecology: An Evolutionary Approach*, 3rd edn, pp. 69-98. Oxford: Blackwell Scientific Publications.
- Brown, J. (1970) 'A note on sexual division of labor.' *American Anthropologist* 72: 1073-1078.
- Chagnon, N. and Irons, W. (eds) (1979) *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. North Scituate, MA: Duxbury Press.
- Charnov, E. (1982) *The Theory of Sex Allocation*. Princeton: Princeton University Press.
- Charnov, E. and Krebs, J. (1974) 'On clutch size and fitness.' *Ibis* 116: 217-219.
- Clutton-Brock, T. (1991) *The Evolution of Parental Care*. Princeton: Princeton University Press.
- Cronk, L. (1991) 'Human behavioral ecology.' *Annual Review of Anthropology* 20: 25-53.
- Daly, M. and Wilson, M. (1982) 'Whom are new-borns said to resemble?' *Ethology and Sociobiology* 3: 69-78.
- Daly, M. and Wilson, M. (1983) *Sex, Evolution and Behavior*. Boston: Willard Grant Press.
- Daly, M. and Wilson, M. (1988) *Homicide*. New York: Aldine de Gruyter.
- Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- Davies, N. (1992) *Dunnoch Behaviour and Social Evolution*. Oxford: Oxford University Press.
- Dickemann, M. (1979a) 'Female infanticide, reproductive strategies and social stratification: a preliminary model.' In N. Chagnon and W. Irons (eds) *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, pp. 321-367. North Scituate, MA: Duxbury Press.
- Dickemann, M. (1979b) 'The ecology of mating systems in hypergynous dowry systems.' *Social Science Information* 18: 163-195.
- Draper, P. (1976) 'Social and economic constraints on child life among the !Kung.' In R. Lee and I. DeVore (eds) *Kalahari Hunter Gatherers*, pp. 199-217. Cambridge, MA: Harvard University Press.
- Draper, P. and Cashdan, E. (1988) 'Technological change and child behavior among the !Kung.' *Ethnology* 27: 339-365.
- Dwyer, P. and Minnegal, M. (1991) 'Hunting in a lowland tropical rainforest: towards a model of non-agricultural subsistence.' *Human Ecology* 19: 187-211.
- Ember, C. (1978) 'Myths about hunter-gatherers.' *Ethnology* 17: 439-448.
- Feistner, A. and McGrew, W. (1989) 'Food sharing in primates: a critical review.' In P. Seth and S. Seth (eds) *Perspectives in Primate Biology*. New Delhi: Today and Tomorrow's Press.
- Fisher, R. (1930) *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Foley, R. and Lee, P. (1989) 'Finite social space, evolutionary pathways, and reconstructing hominid behavior.' *Science* 243: 901-906.

- Galdikas, B. and Teleki, G. (1981) 'Variations in subsistence activities of male and female pongids: new perspectives on the origins of human labor division.' *Current Anthropology* 22: 241-256.
- Ghiglieri, M. (1987) 'Sociobiology of the great apes and the hominid ancestor.' *Journal of Human Evolution* 16: 319-358.
- Goodall, J. (1968) 'Behavior of free-living chimpanzees of the Gombe stream area.' *Animal Behavior Monographs* 1: 163-311.
- Goodall, J. (1986) *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, MA: Harvard University Press.
- Goodall, J. (1989) 'Gombe: highlights and current research.' In P. Heltne and L. Marquardt (eds) *Understanding Chimpanzees*, pp. 2-21. Cambridge, MA: Harvard University Press.
- Goodenough, W. (1970) *Description and Comparison in Cultural Anthropology*. Chicago: Aldine.
- Goodman, M., Estioko-Griffin, A., Bion-Griffin, P. and Grove, J. (1985) 'Compatibility of hunting and mothering among the Agta hunter-gatherers of the Philippines.' *Sex Roles* 12: 1199-1209.
- Hart, T. and Hart, J. (1986) 'The ecological basis of hunter-gatherer subsistence in African rain forests: the Mbuti of Zaire.' *Human Ecology* 14: 29-55.
- Hartung, J. (1985) 'Matrilineal inheritance: new theory and analysis.' *Behavioral and Brain Sciences* 8: 661-688.
- Hawkes, K. (1987) 'How much food do foragers need?' In M. Harris and E. Ross (eds) *Food and Evolution: Toward a Theory of Human Food Habits*. Philadelphia: Temple University Press.
- Hawkes, K. (1990) 'Why do men hunt? Some benefits for risky strategies.' In E. Cashdan (ed.) *Risk and Uncertainty*, pp. 145-166. Boulder: Westview Press.
- Hawkes, K. (1991) 'Showing off: tests of another hypothesis about men's foraging goals.' *Ethology and Sociobiology* 11: 29-54.
- Hawkes, K. (1993) 'Why hunter-gatherers work: an ancient version of the problem of public goods.' *Current Anthropology* 34: 341-361.
- Hawkes, K. and O'Connell, J. (1981) 'Affluent hunters? Some comments in light of the Alyawara case.' *American Anthropologist* 83: 622-626.
- Hawkes, K. and O'Connell, J. (1985) 'Optimal foraging models and the case of the !Kung.' *American Anthropologist* 87: 401-405.
- Hawkes, K., O'Connell, J.F. and Blurton Jones, N. (1987) 'Hadza foraging time.' Paper delivered at the 86th Annual Meeting of the AAA, Chicago.
- Hawkes, K., O'Connell, J.F. and Blurton Jones, N. (1989) 'Hardworking Hadza grandmothers.' In V. Standen and R.A. Foley (eds) *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, pp. 341-366. Oxford: Basil Blackwell.
- Hawkes, K., O'Connell, J.F. and Blurton Jones, N. (1991) 'Hunting income patterns among the Hadza: big game, common goods, foraging goals, and the evolution of the human diet.' *Philosophical Transactions of the Royal Society London, Series B* 334: 243-251.
- Hawkes, K., O'Connell, J.F. and Blurton Jones, N. (in preparation) 'Hadza children's foraging.'
- Hewlett, B. (1992) 'Husband-wife reciprocity and the father-infant relationship among Aka Pygmies.' In B. Hewlett (ed.) *Father-Child Relations: Cultural and Biosocial Contexts*, pp. 153-176. New York: Aldine de Gruyter.

- Hill, K., Hawkes, K., Hurtado, A.M. and Kaplan, H. (1984) 'Seasonal variance in the diet of Ache hunter-gatherers in Eastern Paraguay.' *Human Ecology* 12: 145-180.
- Hill, K. and Hurtado, A.M. (1991) 'The evolution of premature reproductive senescence and menopause in human females: an evaluation of the "Grandmother Hypothesis".' *Human Nature* 2: 313-350.
- Hill, K., Kaplan, H., Hawkes, K. and Hurtado, A.M. (1985) 'Men's time allocation to subsistence work among the Ache of Eastern Paraguay.' *Human Ecology* 13: 29-47.
- Hill, K., Kaplan, H., Hawkes, K. and Hurtado, A.M. (1987) 'Foraging decisions among Ache hunter-gatherers: new data and implications for optimal foraging models.' *Ethology and Sociobiology* 8: 1-36.
- Howell, N. (1979) *Demography of the Dobe !Kung*. New York: Academic Press.
- Hrdy, S. (1979) 'Infanticide among mammals: a review, classification, and examination of the implications for the reproductive strategies of females.' *Ethology and Sociobiology* 1: 13-40.
- Hrdy, S. (1988) 'The primate origins of human sexuality.' In R. Bellig and G. Stevens (eds) *The Evolution of Sex*. Nobel Conference XXIII: 101-136. San Francisco: Harper and Row.
- Hrdy, S. and Whitten, P. (1987) 'Patterning of sexual activity.' In B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham and T. Struhsaker (eds) *Primate Societies*, pp. 370-384. Chicago: University of Chicago Press.
- Hurtado, A. and Hill, K. (1987) 'Early dry season subsistence ecology of Cuiva (Hiwi) foragers of Venezuela.' *Human Ecology* 15: 163-187.
- Hurtado, A. and Hill, K. (1990) 'Seasonality in a foraging society: variation in diet, work effort, fertility, and the sexual division of labor among the Hiwi of Venezuela.' *Journal of Anthropological Research* 46: 293-346.
- Hurtado, A. and Hill, K. (1992) 'Paternal effect on offspring survivorship among Ache and Hiwi hunter-gatherers: implications for modelling pair-bond stability.' In B. Hewlett (ed.) *Father-Child Relations*, pp. 31-76. New York: Aldine de Gruyter.
- Hurtado, A., Hill, K., Kaplan, H. and Hurtado, I. (1992) 'Trade-offs between female food acquisition and childcare among Hiwi and Ache foragers.' *Human Nature* 3: 185-216.
- Hurtado, A., Hawkes, K., Hill, K. and Kaplan, H. (1985) 'Female subsistence strategies among the Ache of Eastern Paraguay.' *Human Ecology* 13: 1-28.
- Janson, C. and van Schaik, C. (1993) 'Ecological risk aversion in juvenile primates: slow and steady wins the race.' In M. Perreira and L. Fairbanks (eds) *Juvenile Primates: Life History, Development, and Behavior*, pp. 57-76. Oxford: Oxford University Press.
- Kaplan, H. and Hill, K. (1985a) 'Food-sharing among Ache foragers: tests of explanatory hypotheses.' *Current Anthropology* 26: 223-245.
- Kaplan, H. and Hill, K. (1985b) 'Hunting ability and reproductive success among male Ache foragers.' *Current Anthropology* 26: 131-133.
- Kurland, J. (1979) 'Paternity, mother's brother, and human sociality.' In N. Chagnon and W. Irons (eds) *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, pp. 145-180. North Scituate, MA: Duxbury Press.
- Lack, D. (1947) 'The significance of clutch size.' *Ibis* 89: 302-352.

- Lancaster, J. and Kaplan, H. (1992) 'Human mating and family formation strategies: the effects of variability among males in quality and the allocation of mating effort and parental investment.' In T. Nishida, W. McGrew, P. Marler, M. Pickford and F. de Waal (eds) *Topics in Primatology, Vol. 1*, pp. 21–33. Tokyo: University of Tokyo Press.
- Lancaster, J. and Lancaster, C. (1983) 'Parental investment: the hominid adaptation.' In D. Ortner (ed.) *How Humans Adapt: A Biocultural Odyssey*. Washington, DC: Smithsonian Institution Press.
- Lee, R. (1968) 'What hunters do for a living, or, how to make out on scarce resources.' In R. Lee and I. DeVore (eds) *Man the Hunter*, pp. 30–48. Chicago: Aldine.
- Lee, R. (1979) *The !Kung San: Men, Women, and Work in a Foraging Society*. Cambridge: Cambridge University Press.
- Lee, R. (1985) 'Work, sexuality and aging among Kung women.' In J. Brown and V. Kerns (eds) *In Her Prime: A View of Middle-Aged Women*, pp. 23–36. South Hadley, MA: Bergen and Garvey Publishers.
- Lessells, C. (1991) 'The evolution of life histories.' In J. Krebs and N. Davies (eds) *Behavioural Ecology: An Evolutionary Approach*, pp. 32–68. Oxford: Blackwell Scientific Publications.
- McGrew, W. (1992) *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press.
- Manson, J. and Wrangham, R. (1992) 'Intergroup aggression in chimpanzees and humans.' *Current Anthropology* 32: 369–390.
- Maynard Smith, J. (1977) 'Parental investment: a prospective analysis.' *Animal Behaviour* 25: 1–9.
- Maynard Smith, J. (1978a) 'Optimization theory in evolution.' *Annual Review of Ecology and Systematics* 9: 31–56.
- Maynard Smith, J. (1978b) *The Evolution of Sex*. Cambridge: Cambridge University Press.
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Melnick, D. and Hoelzer, G. (1993) 'What is mtDNA good for in the study of primate evolution?' *Evolutionary Anthropology* 2: 2–10.
- Møller, A. and Birkhead, T. (1993) 'Certainty of paternity covaries with paternal care in birds.' *Behavioral Ecology and Sociobiology* 33: 261–268.
- Murdock, G. and Provost, C. (1973) 'Factors in the division of labor by sex.' *Ethnology* 12: 203–225.
- Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y. and Uehara, S. (1992) 'Meat-sharing as a coalition strategy by an alpha male chimpanzee.' In T. Nishida, W. McGrew, P. Marler, M. Pickford and F. de Waal (eds) *Topics in Primatology, Vol. 1*, pp. 159–174. Tokyo: University of Tokyo Press.
- O'Connell, J.F., Hawkes, K. and Blurton Jones, N. (1988) 'Hadza scavenging: implications for Plio-Pleistocene hominid subsistence.' *Current Anthropology* 29: 356–363.
- Parker, G. and Maynard Smith, J. (1990) 'Optimality theory in evolutionary biology.' *Nature* 348: 27–33.
- Pavelka, M. and Fedigan, L. (1991) 'Menopause: a comparative life-history perspective.' *Yearbook of Physical Anthropology* 34: 13–38.

- Price, E. (1991) 'Infant carrying as a courtship strategy of breeding cotton-top tamarins.' *Animal Behaviour* 40: 784-786.
- Rodseth, L., Wrangham, R., Harrigan, A. and Smuts, B. (1991) 'The human community as a primate society.' *Current Anthropology* 32: 221-254.
- Rogers, A. (1993) 'Why menopause?' *Evolutionary Ecology* 7: 406-420.
- Sahlins, M. (1972) *Stone Age Economics*. Chicago: Aldine.
- Silk, J. (1978) 'Patterns of food sharing among mother and infant chimpanzees in Gombe National Park.' *Folia Primatologica* 31: 12-42.
- Smith, E. and Winterhalder, B. (eds) (1992) *Evolutionary Ecology and Human Behavior*. New York: Aldine de Gruyter.
- Smith, R. L. (1984) 'Human sperm competition.' In R. L. Smith (ed.) *Sperm Competition and the Evolution of Animal Mating Systems*, pp. 601-659. Orlando: Academic Press.
- Smuts, B. (1985) *Sex and Friendship in Baboons*. New York: Aldine.
- Smuts, B. and Gubernick, D. (1992) 'Male-infant relationships in non-human primates: paternal investment or mating effort?' In B. Hewlett (ed.) *Father-Child Relations: Cultural and Biosocial Contexts*, pp. 1-29. New York: Aldine de Gruyter.
- Stanford, C., Wallis, J., Mpongo, E. and Goodall, J. (1994) 'Hunting decisions in wild chimpanzees.' *Behaviour* 131: 1-18.
- Stearns, A. (1987) 'Making a living in the tropical forest: Yuqui foragers in the Bolivian Amazon.' *Human Ecology* 19: 245-259.
- Stephens, D. and Krebs, J. (1986) *Foraging Theory*. Princeton: Princeton University Press.
- Strum, S. (1981) 'Processes and products of change: baboon predatory behavior at Gilgil, Kenya.' In R. Harding and G. Teleki (eds) *Omnivorous Primates: Gathering and Hunting in Human Evolution*. New York: Columbia University Press.
- Symons, D. (1979) *The Evolution of Human Sexuality*. New York: Oxford University Press.
- Takahata, Y., Hasegawa, T. and Nishida, T. (1984) 'Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982.' *International Journal of Primatology* 5: 213-233.
- Teleki, G. (1973) *The Predatory Behavior of Wild Chimpanzees*. Lewisburg, PA: Bucknell University Press.
- Trivers, R. (1972) 'Parental investment and sexual selection.' In B. Campbell (ed.) *Sexual Selection and the Descent of Man 1871-1971*, pp. 136-179. Chicago: Aldine.
- Trivers, R. (1974) 'Parent-offspring conflict.' *American Zoologist* 14: 249-262.
- Washburn, S. and Lancaster, C. (1968) 'The evolution of hunting.' In R. Lee and I. DeVore (eds) *Man the Hunter*, pp. 293-303. Chicago: Aldine.
- Whitten, P. (1987) 'Infants and adult males.' In B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham and T. Struhsaker (eds) *Primate Societies*, pp. 343-357. Chicago: University of Chicago Press.
- Williams, G. (1957) 'Pleiotropy, natural selection, and the evolution of senescence.' *Evolution* 11: 398-411.
- Williams, G. (1966a) *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton: Princeton University Press.
- Williams, G. (1966b) 'Natural selection, the costs of reproduction and a refinement of Lack's Principle.' *American Naturalist* 100: 687-690.

- Wilson, M. and Daly, M. (1992) 'The man who confused his wife with a chattel.' In J. Barkow, L. Cosmides and J. Tooby (eds) *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, pp. 289–322. New York: Oxford University Press.
- Wrangham, R. (1979) 'On the evolution of ape social systems.' *Social Science Information* 18: 334–368.
- Wrangham, R. (1987) 'The significance of African apes for reconstructing human social evolution.' In W. Kinzey (ed.) *The Evolution of Human Behavior: Primate Models*, pp. 51–71. Albany: State University of New York Press.
- Wrangham, R. and Bergmann-Riss, E. (1990) 'Rates of predation on mammals by Gombe chimpanzees, 1972–1975.' *Primates* 31: 157–170.
- Yellen, J. (1977) *Archaeological Approaches to the Present: Models for Reconstructing the Past*. New York: Academic Press.

# THE ARCHAEOLOGY OF HUMAN ANCESTRY

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