Dimorphic foraging behaviors and the evolution of hominid hunting

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ABSTRACT

In contemporary foraging societies men typically hunt more than women. This observation has played an important role in many reconstructions of hominid evolution. The gender difference in human hunting, likely a product of both ecological and cultural factors, is mirrored by a similar sex difference among nonhuman primates. Existing explanations of such primate behavioral dimorphism are augmented by the recognition of an additional factor that may contribute to differences between males and females in the value of meat. Episodic female immunosuppression is a normal part of reproduction. Because meat is a source of pathogens, females can be expected to exhibit less constant attraction to meat. Sexual dimorphism in the attraction to meat may then contribute to dimorphic foraging specializations, a divergence that is likely augmented by the differential value of insectivory across the sexes. With the rise of cultural transmission of foraging knowledge, dimorphic foraging behaviors would have been reinforced, creating a more comprehensive gender-based division of labor.

SUMMARY FOR TRANSLATION INTO ITALIAN

In contemporary foraging societies men typically hunt more than women, a fact that has played an important role in many reconstructions of hominid evolution. The gender difference in human hunting appears to be a product of both ecological and cultural factors: On the one hand, women favor low variance foraging strategies and, on the other hand, cultural constructions of the meaning of hunting behaviors, weapons, etc. shape women's opportunities to hunt. Importantly, the cultural determinants of the gendered nature of hunting, while affected by factors such as patriarchy, likely also stem from a precedent that predates human culture since, among nonhuman primates that hunt, males hunt considerably more frequently than females.

Although a variety of explanations have been developed to explain the sexual dimorphism characteristic of nonhuman primate hunting behavior, such explanations are incomplete. Existing explanations of are augmented by the recognition of an additional factor that may contribute to differences between males and females in the value of meat. Because pregnancy involves harboring foreign genetic material, mammalian reproduction involves immunosuppression, a phenomenon which first manifests during the luteal/metestrus phase. Because meat is a source of pathogens, females can be expected to exhibit less constant attraction to meat, as natural selection should have reduced the subjective value of meat during periods of immunosuppression. In extant nonhuman primates sexual dimorphism in the attraction to meat may contribute to dimorphic foraging specializations. This divergence is likely augmented by the differential value of insectivory across the sexes as, in addition to being a low risk, low variance food source, eusocial insects may also constitute a relatively pathogen-free source of animal protein. As hominids increasingly relied upon socially transmitted information, existing dimorphic foraging strategies would have been further reinforced due to sex differences in the opportunities for learning and modeling the two behavioral types. At the same time, sex-based foraging strategies would have offered the advantage of complementary strengths in cooperative breeding pairs. In turn, cultural processes, including exploitation by patriarchal males, would likely have normalized and moralized such sex differences, creating a truly gender-based division of labor.

1. INTRODUCTION

All known societies exhibit a gender-based division of labor (Brown [1991]). Among extant foragers, although the distinctions are relative rather than absolute, men hunt and women gather (see Murdock [1965]; McGrew [1979], [1992]; Kaplan *et al.* [2000]; Noss and Hewlett [2001]). This elementary pattern has played a central role in a variety of reconstructions of hominid evolution (Lee *et al.* [1969]; Campbell [1976]; McGrew [1979], [1992]; Hawkes [1996]; Stanford [1999]), and has likewise been employed in attempts to explain a variety of psychological attributes of modern humans (cf. Binnie-Dawson [1984]; Silverman and Eals [1992]; McBurney *et al.* [1997]; Joseph [2000]). A wide range of endeavors can thus be informed by a more complete understanding of the factors which, over the course of hominid evolution, may have generated, perpetuated, and enhanced sexual dimorphism in foraging behavior.

Despite the overarching nature of the gendered division of labor in foraging societies, a number of well-documented ethnographic cases (see Noss and Hewlett [2001]) indicate that, given the right circumstances, women hunt extensively. Similarly, the archeological record suggests that women in disparate foraging societies engaged in some hunting (cf. Wadley [1998]; Jarvenpa and Brumbach [1995]). Consistent with these observations, although initial theoretical efforts at explaining the gendered nature of human hunting relied upon factors such as the constraints posed by pregnancy and nursing, available ethnographic examples reveal that such considerations do not in fact prevent women from hunting (Brightman [1996]). More recently, in a detailed examination of the Aka of Central Africa, Noss and Hewlett [2001] found that women's decisions as to when and how to hunt were best explained as a combination of behavioral ecological and cultural factors. Viewed from an ecological perspective, women's hunting was characterized by attractively low variance and high average rates of return. Viewed from a cultural perspective, women's hunting demonstrated how culturally constructed concepts of gender determined which techniques, game, and weapons were considered appropriate for women. Noss and Hewlett therefore conclude that the division of labor in foraging societies must be viewed as a product of the dynamic interaction of economically rational decisions made by women and cultural precedents, where the latter may partially reflect the former, but are also subject to factors such as patriarchal attempts to monopolize production of a valued resource. Without questioning these conclusions, I propose that such cultural precedents may have ancient roots indeed, for they may stem in part from panprimate sex differences in the constancy of the attraction to meat. While I will return to the question of culture at the conclusion of this paper, my central purpose here is to demonstrate that a hitherto-neglected aspect of physiological sexual dimorphism may contribute to the behavioral dimorphism characteristic not only of human hunting, but also of hunting among our extant primate relatives.

2. THE DANGERS OF MEAT-EATING

In disparate human societies, meat is the most valued food type (see Wilson [1973]; Speth [1991]; Simoons [1994]; Stanford [1999]; Mann [2000]). Reflecting this emic perspective, investigators have often assumed that meat is of equal intrinsic (rather than social) value to males and females, and hence that sex differences in hunting behavior in part reflect differences in the costs of obtaining and retaining prey. However, meat is a mixed blessing, with intrinsic costs that may differ across actors.

While it is extremely nutritious, meat is also dangerous. Animals harbor a diverse array of microbes and protozoans, either as hosts or as endosymbionts (cf. Schantz and McAuley

[1991]). Because the composition of animal tissues is fundamentally similar across species, organisms that exploit one species' tissues are often able to do likewise with the tissues of another species. Furthermore, when an animal dies, most of its immune defenses cease functioning, allowing for the proliferation of pathogens, whether they are present in the animal at death or simply ubiquitous in the environment. Meat consumption thus carries the intrinsic risk of pathogen ingestion.

Animals adjust their consumption of plants in light of the hazards posed by secondary compounds (cf. Freeland and Janzen [1974]). Although some of the relevant cues are postingestive, many hazardous plants have highly detectable properties, as secondary compounds are often bitter and pungent (see Hladik and Simmen [1996]). In contrast, although bacteria produce detectable odors when proliferating on meat, detection may generally not be possible with regard to pathogens (particularly endosymbiotic organisms) present at death, and the same may hold true for many protozoa.

Evidence supporting the assertion that, because of the potential for disease transmission, meat is not an unqualified good comes from the special status of meat as a stimulus for primates and other animals. Consistent with the threat of disease (Hamilton and Busse [1978]), among the three highly predatory nonhuman primates (chimpanzees, capuchins, and baboons), with few exceptions, individuals do not scavenge, apparently viewing found carcasses as largely inedible (Muller et al. [1995]; Stanford [1999]:121; S. Perry, personal communication; Strum [1983]). Olive baboons readily consume novel vegetable foods, yet meat consumption, particularly of novel prey species, is highly dependent on social cues (Strum [1983]). Even the domestic cat, a carnivore, may display neophobia towards raw meat (Bradshaw, Healey et al. [2000]). Rhesus macaques do not normally eat meat. However, experimental lesions of the amygdala in this species lead to increased exploration, coprophagia, and meat-eating, a result that can be interpreted as indicating that all three behaviors are normally restricted by a single inhibiting mechanism (Aggleton and Passingham [1981]). Likewise, electrical stimulation of the amygdala in the domestic cat results in strong aversions to meat (in contrast to lesser reductions in milk and cereal consumption) (Lewinska [1968]). Extended protein deprivation in rhesus macaques leads to increased consumption of many normally avoided foods, yet, despite the value of meat as a source of protein, meat consumption remains depressed relative to most foods (Hill and Riopelle [1975]). Lastly, consistent with the dual status of meat as a concentrated source of protein and a potential vector for disease, rats develop conditioned aversions to high-protein foods more easily than to high-carbohydrate foods (Bernstein, Goehler et al. [1984]).

Among Westerners, animal products are prototypical elicitors of disgust (see Angyal [1941]; Rozin and Fallon [1980]; Fallon and Rozin [1983]), and the same is true among the Bengkulu of Sumatra (author's fieldnotes). Western subjects are quicker to reject novel foods of animal origin than other novel foods (Pliner and Pelchat [1991]), and Simoons ([1994]:305-307) cites descriptions of similar neophobia towards foods of animal origin among the Guiana Indians, ancient Assyrians, and Carib Indians. Although persuasion can overcome neophobia with regard to other food types, it has no effect with regard to foods of animal origin (Martins, Pelchat et al. [1997]). Meat is the central target of conditioned food aversions -- if even habitually consumed meals are followed by nausea, meat is the constituent most likely to be singled out, with desire being replaced by disgust (Mattes [1991]; Rodin and Radke-Sharpe [1991]; Midkiff and Bernstein [1985]; de Silva and Rachman [1987]; Fessler and Arguello [n.d.]).

3. REPRODUCTIVE IMMUNOSUPPRESSION

The potential for infection as a result of meat consumption suggests that the value of meat for a given individual should in part be a function of the individual’s immunological status. In particular, the hazards of meat eating will loom larger for immunocompromised individuals. Although females are generally more immunologically robust than males as a consequence of the immunosuppressive effects of testosterone (cf. Angele *et al.* [1998]), reproduction involves a dramatic and episodic reversal of this difference.

Pregnancy entails the presence of foreign tissue within the mother’s body, a condition normally provoking an immune response. Implantation and gestation therefore necessitate suppression of the maternal immune response (see Loke and King [1997]). The down-regulation of cell-mediated immunity that follows conception carries the unavoidable cost of increased maternal vulnerability to pathogens. Moreover, this condition is not restricted to pregnancy. For most of its’ duration, the luteal phase of the menstrual cycle constitutes a preparatory period in anticipation of the invasive implantation of a blastocyst in the uterus. This suggests that the luteal phase should be characterized by a degree of immunosuppression, a prediction supported by both direct (e.g., Schwarz *et al.* [2000]) and indirect (see Fessler [2001]) measures.

The above results indicate that reproductive females are likely to be at increased risk of infection both during pregnancy and, to a lesser degree, at punctuated points during nonconceptive cycles. In keeping with the risk that meat poses as a vector for pathogen ingestion, meat is the principal target of food aversions that develop during pregnancy (Flaxman and Sherman [2000]), and the focus of the overwhelming majority of gestational food taboos (Fessler [2001]). Meat consumption is also reduced during the luteal phase (Alberti-Fidanza *et al.* [1998]; see Fessler [2001] for review). Disgust is prominent in subjects’ explanations of meat avoidance (Santos and Booth [1996]; Rozin *et al.* [1997]). Nausea and vomiting, the bodily counterparts to disgust, are markedly more common during both pregnancy and the luteal phase; although researchers have yet to examine eliciting stimuli for luteal phase distress, it is clear that meat and meat odors are primary elicitors of nausea and vomiting during pregnancy (see reviews in Flaxman and Sherman [2000]; Fessler [2001]; [2002]).

4. SEX DIFFERENCES IN MEAT CONSUMPTION

In light of the nutritional value of meat, one might suppose that episodic decreases in meat consumption would be compensated for through increases during other periods. However, with the exception of lactation, fewer calories are consumed during other phases, and this limits the amount of meat ingested. Compared to other food types, meat is energetically costly to digest and absorb (cf. Westerterp *et al.* [1999]), and hence available energy reserves may constrain meat consumption. In addition, the demands that protein places on the liver and the kidneys limit protein intake as a percentage of calories consumed (see Speth [1991]).

Consistent with the existence of episodic reductions in the utility of meat that are not matched by equivalent increases in utility during other periods, ethnographic (see Wilson [1973]; Spielmann [1989]) and archaeological (see Cohen and Bennett [1993]) accounts reveal that, in many traditional societies, women consume(d) less meat than men. However, because men are generally more powerful than women, and because men often institute proscriptions which constrain women in order to benefit men, it is possible to explain gender differences in meat consumption as a consequence of differential access to, rather than desire for, meat (O'Laughlin [1974]; Simoons [1994]; Brightman [1996]; Noss and Hewlett [2001]). However, in contrast to such ambiguous cases, a number of findings suggest that, independent of any patriarchal constraints, women are less attracted to meat than men. Meat is culturally devalued in Tamil Hindu households, yet, despite being socially dominant, men often eat more meat than women (Ferro-Luzzi [1985]). In present-day Western societies women are generally able to select food free of direct constraints imposed by men, yet Western women eat less meat as a proportion of their diet (Hess *et al.* [1993]; Galan *et al.* [1998]; Perl *et al.* [1998]; Beardsworth and Bryman [1999]; Fraser *et al.* [2000]), find meat more disgusting (Kubberod *et al.* [2002]), and are more likely to become vegetarians (Worsley and Skrzypiec [1998]; Neumark-Sztainer *et al.* [1997]; Beardsworth and Bryman [1999]). Among the inhabitants of the Ituri forest, women possess a greater number of idiosyncratic meat avoidances resulting from revulsion at animal products (Aunger [2000]), while Western women are more likely than men to possess conditioned aversions to meat (Mattes [1991]), and less likely to crave meat (Weingarten and Elston [1991]; Schoberberger *et al.* [1997]). These findings suggest that, averaged over periods of months or years, women experience less attraction to meat than do men.

Nonhuman primates are often used as a source of insight into the behaviors, social structure, and selection pressures that may have characterized early hominids. Paralleling the divergent foraging behaviors of men and women in extant hunter-gatherer societies, among highly predatory nonhuman primates, marked sex differences exist in the frequency and intensity of hunting behavior. A wide variety of factors have been adduced to explain this sex difference. Although many, or even all, of the postulated causes may apply, examination of the data suggests that existing explanations are incomplete.

5. HUNTING BEHAVIOR OF NONHUMAN PRIMATES

Predation in Pan troglodytes

At Gombe, the most exhaustively studied of chimpanzee communities, the diet, while varying considerably across time and individuals, consists of approximately 60% fruit, 25% leaves, 5% flowers, 5% seeds, 3% msc., and 2% meat (however, the energy and excitement invested in hunting apparently far outweighs meat's dietary significance) (Goodall [1986]). The mean kill rate per male per 100 hours of observation is 0.31, while for females the figure is only 0.01 hunting (see Rose [1997]). McGrew [1979], [1992] suggests that a number of factors contribute to a pattern wherein males hunt more than females, while females engage in more insect gathering. He notes that, as a consequence of intrasexual selection (and, possibly, the fitness benefits of predator defense), males are larger and better armed than females. This reduces the dangers posed by resistant prey, and increases the male's ability to defend his kill from potential usurpers, a factor which is augmented by male dominance in the social structure. In addition, unencumbered by dependent offspring or pregnancy, males are able to roam farther, thereby increasing the likelihood of encountering prey. These same factors make it easier for males to engage in acrobatic chases. Conversely, pursuit, attack, and defense of the kill are potentially more costly for females given the likelihood that offspring will be injured or killed in these processes. Lastly, hunting is both energetically costly and of highly uncertain outcome, and pregnant or lactating females, having high energy demands, may be less able to afford such gambles.

Although much of the available data is congruent with McGrew's perspective, some evidence suggests that male armaments and size advantages alone cannot explain sexually divergent chimpanzee behavior. 75% of the colobus monkeys killed at Gombe are immature (see Rose [1997]), suggesting that great size and strength are unnecessary, and the same applies in the case of the piglets and antelope fawns which constitute secondary targets (Stanford [1999]). Stanford notes that “at Gombe there was one elderly male . . . who was an accomplished hunter even though in his last years he had lost the muscle tone needed for treetop agility as well as nearly all of his teeth,” ([1999]:36). At the same location, one female, apparently infertile and hence unburdened by offspring, was an active and successful hunter (Stanford [1996]) (note that, given her infertility, her heightened interest in meat is also congruent with the immunosuppression hypothesis – J. Moore, personal communication).

Predation in Cebus capucinus

White-faced capuchins rely primarily on fruit (50-80% of diet, varying by region) and insects (20-40% of diet), but nevertheless consume a significant amount of meat in some areas (Chapman [1987]; Chapman and Fedigan [1990]; Fedigan [1990]). Males attempt predation approximately 50% more often than females, and are twice as successful; mean kill rates per 100 hours of observation are 0.37 versus 0.13, respectively (Rose [1997]). Adult females are 70% of adult male weight, and have canines only 77% the size of male canines (Fedigan [1990]). This dimorphism may explain the markedly greater male participation in the hunting of larger prey, such as adult squirrels (Rose [1997]). However, dimorphism is unlikely to explain all aspects of hunting behavior, as some juvenile and subadult males hunt extensively even though they are no larger than adult females (Fedigan [1990]). Many prey do not pose much of a threat to the hunter -- nearly 40% of prey taken in Rose’s sample were nestling birds and eggs. Coati young, a raccoon-like mammal, though typically taken while only a few weeks old, are sometimes defended by adults, which are twice the size of capuchins (Perry and Rose [1994]).

Nevertheless, this possibility does not necessarily deter capuchin females, as capuchin mothers sometimes raid coati nests with their infants clinging to them (S. Perry, personal communication). Despite the innocuous nature of birds and eggs, and the manageable threat of coatis, in each category, males catch more than females (Rose [1997]). Hence, although smaller body size and dependent offspring may limit females' participation in the more explosive chases, these factors do not fully explain females' lesser hunting of smaller animals.

Females capuchins suffer greater prey theft than males, apparently as a result of both sexual dimorphism and sex-based dominance patterns, but the overall rates of theft are low -- Rose reports four incidents involving the theft of coati pups or squirrels, of which three of the victims were females, but this is out of a total of 78 kills of these prey. These low rates may reflect the deterrent effects of theft, i.e., those individuals who are most likely to lose prey to thieves do not hunt. However, this is unlikely to be a universal explanation, since Fedigan reports that "[t]wo of the most frequent meat eaters [in her study group] are old, postprime, subordinate males that often obtain and hold onto prey, even when they are threatened by younger, more dominant males" ([1990]:203).

Fedigan suggests that, as McGrew proposed for chimpanzees, the pattern of sex differences in hunting may reflect a female capuchin preference for a "low-expense, low-but-predictable return strategy" ([1990]:203). However, this again is likely to be more applicable to pursuit hunting than to the consumption of nestlings and eggs, yet males still engage in the latter behavior more frequently than females. Rose suggests that, in both capuchins and chimpanzees, hunting may be an exaptation from a pattern of aggressive defense against predators. While Rose does not link this idea to the sex difference in hunting, the patterns are congruent, as male capuchins are more aggressive in predator defense (S. Perry personal communication) and the same appears to be true of chimpanzees (Boesch [1991]). Ardrey [1961] proposed that primate hunting derives from social aggression, and sexual dimorphism suggests greater male aggressivity in all predatory primates. R. Wrangham (discussant at HBES 2000, Amherst, MA U.S.A.) hypothesizes that chimpanzee hunting is an exaptation from intergroup aggression; such aggression primarily involves males, and the same is true in capuchins (Perry [1996]). In support of these exaptation arguments, both chimpanzees and capuchins lack the stereotypical killing behavior seen in carnivores, and the high level of arousal surrounding chases resembles aggressive behavior. However, both exaptation arguments apply principally to the pursuit of larger prey -- aggressivity is unneeded in raiding birds' nests, for example.

Although opportunity costs may play a role in sex differences in chimpanzee hunting, this is unlikely to be the case for capuchins. First, males and females range as a single group (S. Perry personal communication). Second, males spend 17% of their foraging time on the ground, while females spend only 1%, yet most of the prey species and their nests are arboreal (Fedigan [1990]). In sum, while existing explanations of sex differences in chimpanzee hunting apply to capuchins as well, they are most compelling with regard to the largest class of prey, leaving sex differences in other predatory behavior incompletely explained.

Predation in Papio anubis

Baboons practice selective omnivory (Altmann [1998]) with considerable variation across time and location. Broadly, the baboon diet is 30% fruit, 20% roots and storage organs, 20% leaves, 10% flowers, and 4% meat and insects (Whiten *et al.* [1991]). Extremely high predation rates were recorded in one group (Strum [1981]; Harding and Strum [1976]). Strum reports substantial interindividual variation with regard to both active hunting and interest in prey killed by others, with some females showing greater interest in meat than some males. However, males as a class are more likely to display such interest than females, and this despite the fact that, while females are undistracted by their own sexual receptivity or the possession of infants, males consistently choose to forsake hunting opportunities and kill attendance in favor of sexual or same-sex social behaviors.

Over four years both rates of predation and per capita involvement steadily increased. Initially, hunting was an almost exclusively male activity; those few females who hunted often had their prey stolen by males (see also Harding [1973]). However, female hunting increased and, along with it, females more frequently maintained control over prey despite male threats, the frequency of which also declined. Yet, despite a substantial reduction in the costs of defending a carcass, even at the peak of female hunting, females constituted only 24% of captors despite making up 28% of the troop, in contrast to male figures of 31% and 20%. Hence, while sex differences in dominance/threat capacity may have contributed to differences in hunting, they are unlikely to be a principal explanatory factor.

The principal prey were very young gazelle fawns and hares, neither of which pose a threat to the hunter -- during some periods, hunting by juveniles nearly matched that of adult males. Hence, neither sexual dimorphism nor sex differences in the costs of injury adequately explain differing hunting rates; sex differences occur even in predation on relatively defenseless birds. Gazelle pursuit places dependent offspring at risk, and hence this may contribute to the sex difference, but it cannot explain the low rates of female predation on hares and birds. Males are larger and more aggressive than females, and baboons lack stereotyped killing behavior, and hence any of the exaptation arguments may apply, but a sex difference in aggressivity seems most applicable to differing rates of predation on large prey. Harding and Strum suggest that the greater ability and willingness of males to venture far from the troop in pursuit of target prey serves to preserve the sex difference, but this applies principally to the hunting of ungulates. Moreover, male pursuit behavior only developed several years after extensive hunting was first observed. Hence, as in the case of capuchins, the sex differences in hunting observed among olive baboons are not fully accounted for by existing explanations.

Primate behavior and reproductive immunosuppression

Because the basic physiology of both pregnancy (cf. Slukvin *et al.* [1999]) and menstrual cycling (Bentley [1999]) is similar across primates, it is likely that, if the account of endogenous contributions to sex differences in human meat consumption is correct, similar factors will also apply among nonhuman primates. Pan-primate patterns of sex-specific foraging motivations may thus contribute to the sex differences in hunting behavior evident in chimpanzees, capuchins, and baboons. Skeptics may note that estrus chimpanzee females beg meat from males (Mitani and Watts [2001]), suggesting that the low frequency of female hunting does not reflect a low level of female interest in meat. However, this pattern neither confirms nor disconfirms the immunosuppression hypothesis. Progesterone, the proximate trigger of reproductive immunosuppression, is low during the periovulatory period and postpartum, and females are unlikely to be immunosuppressed during these periods. Accordingly, estrus or lactating females should not exhibit the temporally limited aversion to meat predicted to characterize the luteal phase/metestrus and early gestation (Strum [1981] claimed no influence of sexual state on female hunting; however, because only one of eleven individuals described remained in the same state throughout the period examined, and no breakdown of behavior per state is provided, the data are ambiguous on this point).

Parallels in luteal phase changes in behavior between humans, yellow baboons (Hausfater and Skoblick [1985]), and vervets (Rapkin *et al.* [1995]) suggest that other primates share the social concomitants of subjective changes which, in humans, are associated with highly patterned ingestive behavior (Dye and Blundell [1997]). Laboratory and field studies of a variety of rodents, primates, and other mammals reveal menstrual cycle periodicity in caloric intake and/or time spent feeding that greatly resembles the periodicity evident in humans (cf. Czaja [1975]; Rosenblatt *et al.* [1980]; Bielert and Busse [1983]; Fessler [in press]). However, methodological limitations (uniform lab diet, poor data resolution, and/or lack of dietary variety in field studies) preclude drawing any firm conclusions regarding periodicity in dietary preferences and selectivity.

7. INSECTIVORY AS AN ALTERNATIVE TO HUNTING

Insectivory in the common chimpanzee

In chimpanzees, the sex difference in carnivory is inverted in insectivory (the same is true, but to a lesser extent, in capuchins (Fedigan [1990]; insectivory is more important in capuchins than in chimpanzees, a fact in keeping with their smaller body size -- because all known ancestral hominid species were the size of chimpanzees or larger, the latter provide a better model of hominid insectivory than do capuchins). As McGrew [1979], [1992] notes, in comparison with hunting, insect gathering is a low-risk, sedentary, and interruptible activity, and does not lead to extensive social conflict over prey. Insect gathering is thus highly compatible with caretaking. The energetic demands of insect gathering are lower than those of hunting, and the return is more certain, factors that probably make it attractive for pregnant or nursing females with high caloric needs. Termite fishing, the most common form of intensive insect gathering, takes place at permanent termite mounds, and knowledge of these locations allows females to plot efficient paths to the mounds, further reducing energetic costs. Finally, specialization by sex reduces the number of competitors for a given resource, a factor that is likely to be especially attractive to females given their heightened vulnerability to the costs of conflict. To McGrew’s list can be added one more factor: Compared to meat, termites may constitute a relatively pathogen-free source of animal protein.

Insects as a relatively pathogen-free source of animal protein

Dampwood termites (Zootermopsis angusticollis) develop immunity to bacteria following limited exposure (Rosengaus *et al.* [1999]), and possess specialized excretory adaptations that create a hygienic environment within the nest (Rosengaus *et al.* [1998]). Infected individuals do not transmit fungal diseases to nestmates, apparently because of the hygienic effects of allogrooming, which increases in frequency following disease exposure. Allogrooming also increases survivorship, apparently by reducing the disease load of infected individuals (Rosengaus *et al.* [1998]), and there is evidence of the social transfer of immunity to naïve individuals (Traniello *et al.* [2002]). Similarly, the pattern common in social insects of so-called undertaking behavior, the heaping of dead nest members, may serve a hygienic function. Hence, via a variety of avenues, the nest is protected from pathogen invasion. While chimpanzees feed primarily on other types of termites (Uehara [1982]; McGrew [1979]), all of these species share the adaptive challenge that their sociality greatly increases exposure to pathogens. All social termites may thus possess adaptations that reduce the likelihood that a nest will harbor disease, and this may also be true of other social insects gathered by chimpanzees, such as the driver ant (McGrew [1979], [1992]).

In evaluating the relationship between social insect hygiene and chimpanzee insectivory, several caveats are in order. First, it is possible that many microbes which are innocuous to insects, and hence less likely to be filtered out by their hygienic and immunological adaptations, are harmful to chimpanzees. Second, it is possible that bacteria which are symbiotically harbored by insects are pathogenic in chimpanzees. These considerations point to the need for research on the specifics of particular chimpanzee-insect-microbe triads. While awaiting such results, I suggest that, although it is likely that social insects are the favored target of chimpanzee insectivory because they constitute a dense resource patch, their relative freedom from pathogens increases their adaptive utility for immunocompromised individuals. This feature may compound the advantages listed by McGrew that insect gathering holds for females, thereby further increasing sexual specialization in chimpanzee foraging behaviors.

Insectivory and gathering

Discussions of the role of sexually dimorphic foraging strategies in hominid evolution frequently include the utility of reciprocity among individuals pursuing different economic strategies (cf. Kaplan *et al.* [2000]). Although many scenarios focus primarily on hunting, McGrew [1979], [1992] and Tanner and Zihlman [1976] draw attention to the need to explore the phylogeny of gathering, particularly in light of the many extractive techniques typical of human gatherers. McGrew suggests that chimpanzees evince several preadaptations for the hunter-gatherer lifestyle, for not only do males specialize in hunting, but females also specialize in extractive gathering, with insect collection being prototypical of such techniques (see also Fedigan [1990]).

Insects constitute an important food in many human societies, and likely did so for much of human history (McGrew [1979]; Kelly [1995]:87; Southgate [1991]; O’Dea [1991]; Defoliart [1995]). Three categories of insects are principally targeted by humans as a consequence of their spatial density: a) those, such as grasshoppers, in which large numbers appear simultaneously; b) larvae that are localized due to egg deposition or similar factors; and c) social insects such as termites, ants, and bees (see Defoliart [1995]). Little systematic information is available on the distribution of either the gathering or the consumption of insects by women and men. However, following McGrew’s reasoning, it seems plausible that, in the ancestral past, insect-gathering was primarily a female occupation, particularly with regard to categories (b) and (c), the localized insects. Likewise, if lower risks of disease transmission contribute to preferential female chimpanzee insectivory, the same would likely be true of ancestral humans, particularly with regard to the social insects.

8. REPRODUCTIVE IMMUNOSUPPRESSION AND THE EVOLUTION OF HOMINID SOCIAL STRUCTURES

Reproductive immunosuppression may have affected the evolution of hominid foraging behavior, and resulting social structure, in a number of ways. Females are likely to have been pregnant for much of their adult lives (Strassmann [1997]), resulting in a reduction of interest in, or an outright aversion to, meat, and this will have contributed to decreases in their efforts, both direct and indirect, to obtain it. Because the luteal phase involves immunosuppression akin to that of pregnancy, menstrual cycling before and between pregnancies is likely to have entailed periodicity in the attraction to meat. Together with the factors discussed by McGrew and others, periodic reductions in female attraction to meat are likely to have produced dimorphic patterns of hunting and meat consumption akin to those evident in common chimpanzees, white-faced capuchins, and olive baboons.

Human hunting is an extremely skill-intensive activity, one that takes approximately 20 years to master (Ohtsuka [1989]; Kaplan *et al.* [2000]). Although this reflects the complexity of the cultural knowledge that must be acquired, given that all hominids lack(ed) specialized morphological adaptations such as large teeth or claws, a similar, albeit proportionately reduced, consideration will have applied throughout hominid evolution (cf. Stanford [1999]:36-7). Hence, with the rise in importance of cultural information, sex differences in the overarching attraction to meat are likely to have resulted in even greater divergence of foraging practices, as females would have been less motivated to acquire the requisite knowledge (cf. Strum [1981]). In contrast, insectivory may have been attractive to female hominids for many of the reasons that pertain among female chimpanzees, possibly including the opportunity for efficient protein acquisition with a reduced risk of pathogen transmission. The extractive skills employed in exploiting social insects may have both enhanced, and developed in conjunction with, the ability to utilize a wide variety of non-animal resources (McGrew [1992]:119). Because insect nests and similar resource patches can be exploited by a number of individuals at once, female allies, whether kin selected or otherwise, could harvest simultaneously, facilitating social transfer of gathering expertise. The multiple factors affecting both motivation and opportunity to participate in hunting or gathering may ultimately have resulted in parallel, gender-specific cultural foraging traditions in most populations.

Ultimately, while insectivory has retained a place in women's foraging repertoires, its significance likely declined in proportion with increases in male provisioning. In contemporary hunter-gatherer societies, reproductive females consume more food than they produce, while males generate a huge surplus, allowing for a shorter interbirth interval and increased lifetime reproductive success relative to chimpanzees (Kaplan *et al.* [2000]). Particularly during lactation, a prolonged period of high energy demands and no reproductive immunosuppression, female fitness can be greatly enhanced through male provisioning of meat, a pattern that may ultimately have led to meat's overshadowing of insects in the human female diet without perturbing the basic gender differences in foraging strategies, i.e., men hunt and women gather.

In the above model, differing payoffs for different foraging strategies provides the initial impetus for sexually dimorphic behavior; this dimorphism is then reinforced through differential access to social models for imitation, learning, and other forms of social information transfer. Importantly, because humans tend to moralize prevailing patterns of behavior (Fessler and Navarrete [n.d.]), cultural beliefs are likely to have arisen that validated and underlined a gendered division of labor. Lastly, because men are often able to monopolize power, self-serving male arbiters of cultural values may frequently have further rigidified this division as a way of maintaining control over access to a valued resource.

In sum, subjective changes selected for by the conflict between a female's reproductive and immunological systems may have contributed to divergent female and male foraging strategies, a difference which would have both set the stage for, and coevolved with, social patterns involving intersexual reciprocity and cooperation. In turn, with the rise of hominid carnivory, selection may have refined prophylactic adaptations in a manner that enhanced feedback loops, the net result being that humans are the only primates who both vomit in response to meat odors during pregnancy and rely on a sexual division of labor, reciprocity, biparental care, and an elaborate cultural repertoire.

While many of the factors postulated in the above account are unlikely to be preserved in the archeological record of hominid evolution, key features of the hypothesis can be tested using these extant primate species, as the following predictions can be derived:

- Among hunting species, female primates should exhibit cyclic variation in their attraction to meat (testable experimentally) and in their engagement in hunting behavior (testable observationally) as a function of position in the estrus cycle and/or stage of pregnancy.
- Species of primates that hunt should exhibit sex-based information transfer, i.e., imitation, stimulus enhancement, and similar phenomena (cf. Whiten *et al.* [1996]) should flow along sex lines, particularly between adults and juveniles.
- The species of insects exploited by female chimpanzees should present a lower risk of pathogen ingestion on a per-gram-of-protein basis than the mammals exploited by male chimpanzees.

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