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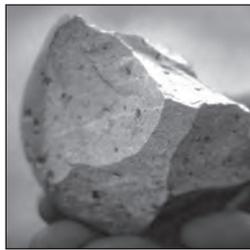
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NUMBER 1

THE OLDOWAN:

Case Studies Into the Earliest Stone Age

Edited by Nicholas Toth and Kathy Schick



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COVER PHOTOS

Front, clockwise from upper left:

- 1) *Excavation at Ain Hanech, Algeria (courtesy of Mohamed Sahnouni).*
- 2) *Kanzi, a bonobo ('pygmy chimpanzee') flakes a chopper-core by hard-hammer percussion (courtesy Great Ape Trust).*
- 3) *Experimental Oldowan flaking (Kathy Schick and Nicholas Toth).*
- 4) *Scanning electron micrograph of prehistoric cut-marks from a stone tool on a mammal limb shaft fragment (Kathy Schick and Nicholas Toth).*
- 5) *Kinesiological data from Oldowan flaking (courtesy of Jesus Dapena).*
- 6) *Positron emission tomography of brain activity during Oldowan flaking (courtesy of Dietrich Stout).*
- 7) *Experimental processing of elephant carcass with Oldowan flakes (the animal died of natural causes). (Kathy Schick and Nicholas Toth).*
- 8) *Reconstructed cranium of Australopithecus garhi. (A. garhi, BOU-VP-12/130, Bouri, cranial parts, cranium reconstruction; original housed in National Museum of Ethiopia, Addis Ababa. ©1999 David L. Brill).*
- 9) *A 2.6 million-year-old trachyte bifacial chopper from site EG 10, Gona, Ethiopia (courtesy of Sileshi Semaw).*

Back:

Photographs of the Stone Age Institute. Aerial photograph courtesy of Bill Oliver.

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CHAPTER 8

SEX DIFFERENCES IN CHIMPANZEE FORAGING BEHAVIOR AND TOOL USE: IMPLICATIONS FOR THE OLDOWAN

BY KEVIN D. HUNT

ABSTRACT

Chimpanzee positional behavior, diet, activity budget and canopy use differ between males and females. Contrary to expectations based on body size and the demands of pregnancy and lactation, females have a lower quality diet than males. Males ate more fruits, especially those harvested from large trees, ate at larger patches, ate terrestrial items more often, ate more piths, and ate more meat. Females ate more invertebrates, more small-patch fruit, more seeds, and more leaves. Items eaten by females were high in protein and high in calcium compared to males. Female-selected foods required greater handling times. Items selected by males contained high proportions of sugars or digestible hemicellulose, were found in large patches, or could be harvested from the ground. Most differences appear to be due to higher male social rank, since they parallel differences between high and low ranking males. Female selection of leaves does not follow rank-effect predictions, but is attributed the nutritional demands of pregnancy and lactation. This pattern suggests that low-ranking individuals — including females compared to males, and juveniles compared to adults — are under greater pressure to reduce handling times than are high-ranking individuals, since individuals with high-handling time diets would realize the highest return from “short cuts.” Such sex differences might have been found in early hominins, given their greater body-size dimorphism. If so, early hominin males may have concentrated on terrestrially gathered food items, nutrient-dense foods, large food items, and other easy-to-process resources. It follows that females were more arboreal, ate foods lower in nutrient density, ate smaller foods,

and selected foods that required greater processing times. Paralleling chimpanzee sex differences, female hominins likely used tools more often. Even among earliest toolkits we should expect to find female tools specialized for processing low-return food resources that require substantial handling times, and tools that can be used arboreally. Early hominin males likely utilized tools designed to harvest terrestrial items. A wooden digging stick/spear/club useful for harvesting underground storage items, utilizable in spearing prey, or in group defense against conspecifics, and heavy enough to serve as a club, seems a likely early hominin tool.

KEY WORDS:

Sex differences, Division of Labor, Early hominin diet, Chimpanzee, Arboreality, Food Processing

INTRODUCTION

Living humans are so profoundly dependent on technology, even in comparison to the most adept non-human tool users, that analogies between *Homo sapiens* and proto-tool-users may seem pointless. Fire is a complicating factor. Even the most technologically simple human toolkits, toolkits hardly different than those of chimpanzees (McGrew, 1992), are used in the context of fire (Wrangham *et al.*, 1999). Apes, by contrast, offer a technologically simple anchor point from which we might extrapolate toward modern humans to model selective pressures that acted on the first hominin stone toolmakers. Among the biological pressures that may have influenced the form of the earliest human toolkit is the timing of the origin of sex differences in foraging strategies.

ARE HUMANS UNIQUELY UNIQUE?

Our concept of ourselves as unique underwent a shift in perspective after World War II. The New Physical Anthropology increasingly drew on theory and data from biology (Cartmill *et al.*, 1986). Accordingly primatology, perhaps a more natural fit in biology, established itself within bioanthropology. As information about primate ecology and behavior mounted, humans seemed less unique. However unique living humans are, it began to seem likely that early hominins were not so special, and that while our early ancestors may have been quite unusual apes, they were not *uniquely* unique, but just *Another Unique Species* (Foley, 1987). As human capacities for tool use, language, self-concept, and complex social interactions blurred into ape capacities, human paleontologists shortened their lists of human traits considered unique to perhaps a score: relative brain size (including correlated traits such as increased cognitive capacity, and lengthened life-history variables such as age at maturation), bipedality, high heat tolerance (*sensu* Wheeler, 1991, including nakedness and sweating), high diet quality (and consequent small guts), social network size, use of composite tools, sexual division of labor (including mutualistic exchange between the sexes), and language capacity. Human uniqueness has led some to question the utility of *referential models* for the origin of tool use, i.e., models that draw on a single referent, and others may even argue that humans are unusual enough that even conceptual models — models that draw on rules linking selective pressures to adaptations (*sensu* Tooby and DeVore, 1987) — are questionable. I consider that parallels between humans and chimpanzee culture and ecology are profound (McGrew, 1992; Whiten *et al.*, 1999), but nevertheless I will approach my analysis with these cautions in mind.

Sex Differences in Diet and Foraging Strategy as Division of Labor in Human Societies

Students of human foraging noted that the pattern of *sexual division of labor* was rather consistent across cultures. That is, tasks that females took on in one culture tended to be female tasks in others as well. In a survey of 185 societies (Murdock and Provost, 1973), 23 activities were found to be performed mostly by males, and nine activities were seen to be predominantly female tasks. Many of these activities, such as net making or ore-smelting, can be dismissed as unimportant for early tool-users. They will be excluded from discussion here. Among tasks that early hominins might have performed, Murdock and Provost found that males more often engaged in hunting large fauna, woodworking, fowling, stoneworking, bone/horn/shell working, mining and quarrying, bonesetting and other surgery, butchering, and honey-collecting. Females were more likely to engage in gathering small aquatic fauna, gathering vegetal foods, and preparing vegetal foods.

The root-cause of these differences was debated. Perhaps, it was argued, tasks had sex-specific costs and benefits, and each sex allocated time and energy to tasks according to the net benefit to that sex. Emerging from the welter of factors that were proposed as influencing time- and energy-allocation strategies was the likelihood that nursing, and to a lesser extent other child-care duties (Brown, 1970; Sanday, 1973; Gough, 1975; Parker and Parker, 1979) shift female foraging strategies toward tasks that are compatible with infant care. Heavy physical labor was eventually dismissed as incompatible with nursing. As a further burden, proximity to a safe infant cache was seen as important (Brown, 1970). Damping sex differences is the capacity for humans, like other primates, to perform at least low-risk subsistence activities while carrying infants, and the fact that older offspring may be quite independent. While Mead (1949) was rightly dismissive of many of Malinowski's (1913) explanations of sex differences, she recognized that there is a reproductive basis for the capacity of males to better afford "sudden spurts of energy" compared to females (Mead, 1949: 164). Two selective pressures are profound: infant survival depends on mother having access to calories for lactation that are both *consistent* and *adequate*. To nourish infants mothers cannot suspend nutrient acquisition for long. Paternal physical condition is freer to vary without directly affecting the survival of their offspring. Males may be quite active for short bursts, and then inactive during recovery. Cross-sectional geometry of long bones suggest that a pattern of higher male activity existed at least as early as the Middle Paleolithic (Ruff, 1987).

In her review of research on sexual division of labor, Brown (1970) found that "repetitive, interruptible, non-dangerous tasks that do not require extensive excursions" are most compatible with child care. The net nutritional value of the resources acquired via these tasks, she contended, is greater than that contributed by males. Whereas some recent research questions the axiom that gathering is necessarily a more reliable strategy than hunting (Hurtado *et al.*, 1985; Hurtado and Hill, 1990), the vital status of gathering has been recognized consistently (Tanner and Zihlman, 1976; Zihlman, 1978, 1981), even if it has not been empirically demonstrated. Twenty-five years after Brown (1970), Hurtado *et al.* summarized their work on division of labor in the Hiwi and Ache as follows: "Women seem to have solved the problem of obtaining energy and allocating time to raising offspring by adopting strategies which increase male productivity, by relying on male provisioning and by spending time and effort in activity types that are readily compatible with childcare and expose the young to minimum risks."

Are Sex Differences in Diet and Foraging Strategy a Uniquely Human Feature?

Surprisingly quickly, data on chimpanzee foraging stripped away much of what was considered unique

about human sex differences in food-getting strategies. Although the null hypothesis that male and female apes might have *no* sex differences is a null hypothesis that is, in Eckhardt's (1981) words, "nuller than most," the extent of ape sex differences was unexpected. At first implicitly (Goodall, 1968) and then explicitly (McGrew, 1979) sex differences in chimpanzee diet, habitat use, tool use, and other foraging behavior was articulated. In particular, McGrew (1979) recognized a long list of sex differences that have been confirmed in subsequent work. There is a strong bias for females to harvest invertebrates (McGrew, 1979), and ants in particular are gathered arboreally almost exclusively by females (Nishida, 1973; Nishida and Uehara, 1980; Uehara, 1986, 1987). Males are hunters: in 48 of 49 cases at Gombe where sex was identified, it was a male that killed mammalian prey (McGrew, 1979). McGrew noted that more mobile and wide-ranging male chimpanzees hunted, and females engaged in activities that he characterized as gathering, a pattern he found similar to that of modern humans. A similar trend was observed at Tai, Ivory Coast where 281 of 331 identified hunters were male, and 31 of 38 successful hunters were male (Boesch and Boesch, 1989). In a review of chimpanzee sex differences in morphology, life-history variables and patterns of affiliation, Hiraiwa-Hasegawa (1987) pointed out the need for a rigorous, evolutionary approach.

McGrew (1979, 1981) considered the meaning of these differences for human tool-use origins. Noting that chimpanzee females use tools to capture prey, whereas males do so only rarely, he suggested that human tool use originated in "solitary female-foraging activities, [not] hunting" (McGrew, 1979: 461). Throwing among chimpanzees is rare, he noted; it is engaged in not for hunting, but for defense or aggression. Throwing is a male behavior (N=44; Goodall, 1968, reviewed in McGrew, 1981). In contrast to most scenarios for the evolution of hunting, McGrew (1981) argued that early hominins were poorly adapted for competing with large carnivores for carcasses, and therefore that scavenging was an insignificant part of their food-getting behavior. He concluded that females were more likely to have invented *facilities*, such as lures and traps, which are principally gathering devices, not hunting devices, and that carrying devices were likely invented by and used by females first.

The timing of the habitual use of carrying devices may be the most important unanswered question in the origin of hominin stone tool use. Efficient transport of stone tools and/or raw materials is a significant barrier to stone tool use. The issue of carriage is a more troublesome than it might appear at first glance. Without carrying devices, keeping track of stone tools while engaged in two-handed gathering activities, which I will argue below was a critical early hominin strategy, is difficult. Tools would have to be left on the ground during arboreal foraging, necessitating returning to the cache

site. This retrieval cost can be large, if in the course of unbroken gathering the forager is several trees and many meters away. If tools are carried in the hands during travel, they curtail the normal primate feed-as-you-go strategy, which involves frequent use of both hands for gathering, even when terrestrial. As each shrub, tree, herb, or clump of grass is encountered, tools must be deposited on the uneven, leaf-littered ground, and must be rediscovered and retrieved later — or the resource must be ignored. Tool carriage, in other words, must push the early hominin food-collection strategy toward larger, more compact food patches. One solution to this problem, assuming early hominins had no carrying devices, might be long-term stone tools caches. This strategy implies a proto-home base, and such a central place foraging is widely rejected for early hominins (Sept, 1992).

The lack of containers or carrying devices among wild chimpanzees suggests that carrying devices are not readily conceived by a chimpanzee-like mind, in which category I would include early hominins, though like many composite devices, they are utilized readily enough when provided by humans (e.g., the bonobo Kanzi makes frequent use of a backpack). Materials from which to construct a carrier are not as available as one might expect. Woven devices for early hominins can be dismissed immediately. Animal products look promising, but absent tanning or other quite complicated processing they decay quickly. In drier habitats where decomposition might be slowed, when hides and other animal tissues are not immediately eaten they dry to the consistency of plywood. The conception of carrying devices seems outside early hominin intellectual capacities. Such speculation, however, is incomplete and unsatisfying. A container would dramatically decrease the costs for tool use, increase the practical size of the toolkit, allow for transporting raw materials, and allow delayed consumption of some foods. This may be a crucial missing datum as we speculate on the origin of tool use. Here I will assume that carrying devices were not part of the toolkit of the first stone tool users, but may have been invented as early as the first-appearance of *Homo erectus* (*sensu lato*).

Living Apes Best Inform Our Conceptual Models

While living humans may be uniquely unique, and therefore somewhat uninformative for reconstructing the origin of tool use, the gap between apes and fossil hominins is manageable. If we accept that our closest relatives, the apes, are more adept tool-users than once recognized (McGrew, 1992; Schick *et al.* 1999, Toth *et al.* 1994), and if we further accept that early hominins — rather than *Homo* (de Heinzelin *et al.*, 1999) — were the first stone tool users, apes and hominins are arguably similar enough to justify even referential models. That is, as Wynn and McGrew (1989) suggested, it seems likely that the first stone tool-makers had cogni-

tive and manipulative abilities that were quite similar to those of living apes, with only bipedalism as a notable difference (Wynn and McGrew, 1989). Nor is bipedalism particularly confounding. Chimpanzees use tools most often when sitting. Among hominins, bipedalism is temporally disassociated from stone tool use, having appeared three and a half million year before the first stone tools. Indeed, in a comprehensive review of bipedalism origins, Rose (1991) found that among active scholars, a link between tool use and bipedalism is promoted merely as a preadaptation for tool carriage, not as a cause for bipedalism. In short, habitual bipedalism is unlikely to have much altered the dynamics of tool use and tool manufacture from the condition seen in apes.

I will look to the apes for the components of a conceptual model that will consider the effects that food-getting strategies, relative arboreality, social dynamics, and sex differences on patterns of early hominin tool use.

What is the Source of Sex Differences?

Sex differences in early hominins, if such were present, likely stemmed from the same source that dictates sex differences in living nonhuman primates. Differences between the sexes may arise for four reasons (Hunt *et al.* in review): (1) The ‘sexes have different **reproductive demands**’ hypothesis posits that females must gestate, lactate and (among anthropoids) carry offspring, while males may guard territories, guard females, or both. These different demands mean females and males have different dietary needs and different locomotor costs, which in turn will affect foraging behavior and anatomy. (2) The ‘**social rank**’ hypothesis holds that sex differences may arise when one sex is consistently socially dominant, and thus free to monopolize highly desired food items. (3) The ‘**body size**’ hypothesis stresses that when the sexes differ in body size, their nutritional needs, their mobility in the canopy, and their ability to open food items yields further sex differences. (4) The ‘**paternal investment**’ hypothesis indicates that, when males have high confidence in paternity or significant inclusive fitness benefits, they may defer to mates and/or offspring at feeding sites as a parental investment. Such competition avoidance may either reducing reduce or increasing increase sex differences. Each of these selective pressures may have affected early hominins.

Tool Use Can Only Be Understood in the Context of Other Ecological Variables

Conceptual models rely on identifying linked variables. For example, among frugivorous primates, incisor breadth is correlated with the diameter of the species’ average food item (Lucas *et al.*, 1986). I will make use of many such links as I discuss early hominin

tool use. Identifying differences between humans, apes and early hominins is our first order of business.

Whereas humans use tools in a wide variety of contexts, even among chimpanzee populations that use tools, and not all do, stone tools are used in only a few contexts. Only one is very common, nutcracking, and stone tools are used to process only a handful of species (Boesch and Boesch-Achermann, 2000). Likewise, among early hominins, stone tool use and manufacture must have begun as a relatively minor food processing technique in an already complicated and well-integrated foraging regime. Tool use could only have arisen if it was compatible with foraging strategies already in place. That is, stone tools must have increased net caloric return when it was introduced into an already long list of food-getting strategies. It cannot have reduced the efficiency of in-place strategies beyond some critical point, and costs must have been low relative to benefits. Among possible costs are transport effort, caloric expenditure during tool use, costs of searching for raw material, costs of manufacture, risks of injury, risk of predation, and risks of intraspecific agonism. Benefits depend on the encounter rate of items requiring stone tools, and include the increase in calories harvested per unit time using tools, and decreases in risks during harvesting. Costs and benefits will differ according to the diet, habitat use and foraging strategies. For example, a central-place forager that included meat in its diet might cache tools at its home base. If carcasses were carried home to share, tool use would require no additional transport costs, no additional exposure to predators, and little risk of tool loss (and therefore raw material and labor loss). For a nomadic, arboreal, frugivorous, forest-living ape, risks and costs are quite different. As we sift through possible the selective pressures acting on early hominins, we must consider that tool use likely arose in hominins that were principally frugivores.

ANALYSIS

What Was the Early Hominin Diet? Trace Element Evidence

Sponheimer and Lee-Thorp (1999) found that $\delta^{13}\text{C}$ values for three *Australopithecus africanus* specimens were most similar to a fossil hyena, suggesting that they were strongly dependent on C_4 plants, or animals that ate them. Note that among the animals that eat such plants are termites. One hominin had a C_3 signal suggesting it had consumed fruit, herbs or leaves. Australopithecines, these data suggest, were generalists compared to sympatric species, exhibiting $\delta^{13}\text{C}$ range more variable than 18 of 19 comparison taxa, among them baboons, vervets and *Notochoerus capensis*. Australopithecine $\delta^{13}\text{C}$ levels, however, were not unique: monkeys that range into open habitats, vervets and baboons, had similar levels. The authors concluded

that australopithecines ate between 25-50% C₄ foods. Australopithecine δ¹³C levels then are consistent with Backwell and d'Errico's (2001) interpretation of bone artifacts as termiting tools, even if the link is highly inferential.

Early Hominin Diet Inferred From Dental Size, Tooth Shape and Dental Microwear

Kay (1985) and Teaford and Unger (2000) found that in extant primates large molar areas correlate with high proportions of seeds, nuts, or other hard items in the diet. Molar areas also correlate with percentage of fruit in the diet (Lucas *et al.*, 1985). Compared to living primates, early hominins are 'megadont' — their cheek teeth are large (McHenry, 1984; Kay, 1985). In a regression of cheek-tooth area against body weight among living apes, *A. afarensis* fell 22% and *A. africanus* 32% above the regression line (Kay, 1985). Other australopithecines have similarly large molar surface areas, including *A. anamensis* and *Ardipithecus ramidus*, compared to chimpanzees (Teaford and Ungar, 2000). Thus, tooth size suggests a diet high in fruit, in seeds, or both.

Early hominin tooth shape accords well with dental dimensions. Early hominins lack long shearing crests that are correlated with leaf eating among extant hominoids (Teaford and Ungar, 2000). Teaford and Ungar interpret molar morphology in early hominins as evidence against carnivory. Instead, tooth shape suggests a diet of fruit or hard-coated seeds.

Thick enamel (Teaford and Ungar, 2000) is found among living frugivores such as capuchins and orangutans (Kay, 1985), whereas terrestrial primates such as gorillas and baboons have thinner enamel. In comparisons of closely related dyads such as gorilla/chimpanzee or siamang/gibbon, frugivores had thicker enamel. Across the primates, folivores have the thinnest enamel, whereas primates that consume hard, brittle foods have the thickest enamel, and frugivores are intermediate. Enamel microstructure (decussation) also suggests hard-object feeding (Kay, 1985; Teaford and Ungar, 2000). Thick enamel in early hominins suggests a diet of hard-husked fruit and/or hard-coated seeds.

Incisor size is correlated with food item diameter (Lucas *et al.*, 1985) and other physical characters. Small incisors among *A. anamensis*, *A. afarensis* and *A. africanus*, similar in relative size to gorillas, suggests they fed on smaller fruits than do chimpanzees and orangutans (Hylander, 1975; Teaford and Ungar, 2000).

Molar microwear has not been analyzed in early hominins, but *A. africanus* microwear (Walker, 1981; Teaford and Walker, 1984; Grine and Kay, 1988; Kay and Grine, 1988; Teaford, 1994) suggests they were frugivores. Kay and Grine (1988) found that *A. africanus* microwear feature width fell between howlers and capuchin monkeys. Pit:scratch frequency comparisons place them between orangutans and chimpanzees (Kay and Grine, 1988). Table 1 presents feeding records for these four taxa. Using these diet data, Hunt (1998) offered a best-guesstimate early hominin diet by averaging the diets of the species with microwear signatures most similar to early hominins (updated in Table 1). The results suggest that fruit made up nearly half the early hominin diet, that leaves were a critical food item, and that piths, insects, flowers seeds and bark were also included in the diet.

Early hominins, even the less robust species, had considerably thicker mandibular corpora than living hominoids (Chamberlain and Wood, 1985; recent finds reviewed in Teaford and Ungar, 2000). Among living primates, the Pitheciini (*Chiropotes*, *Cacajao* and *Pithecia*) have the most robust mandibles (Kinzey, 1992). Their diet is high in hard-husked fruits and seeds (Anapol and Lee, 1994; Kinzey, 1992; Boubli, 1999).

A. afarensis incisor microwear data seem indicate a lowland gorilla-like wear pattern that included gritty plant parts, perhaps grass stems, roots and rhizomes, in addition to fruits (Ryan and Johanson, 1989). The undulating pattern of wear on *A. afarensis* incisors indicates a stripping function, consistent with leaf stripping (Puech and Albertini, 1984; Puech, 1992). I argue that these data may also suggest that fruits eaten by early hominin were so small that they were ingested without incisal processing with the incisors. This would mean that leaves, as the second most common item in the diet,

Table 1

Species	Insects	Leaf	Meat	Fruit	Piths/ Herbs	Flowers	Bark	Seed
<i>Pan</i> ¹	5.6	10.3	1.0	57.0	22.6	0.7	0.0	0.0
<i>Alouatta palliata</i> ²	0.0	64.0	0.0	12.0	0.0	18.0	0.0	0.0
<i>Pongo</i> ³	1.0	26.0	0.0	58.0	—	—	13.0	2.0
<i>Cebus apella</i> ⁴	15.0	0.0	0.0	51.8	3.5	1.3	0.0	16.1
Early hominins?	5.4	25.1	0.3	44.7	6.5	5.0	3.3	4.5

Table 1 — Early hominin diet as suggested by molar microwear

¹Hunt (1989); feeding time, based on 3,891 feeding records of *Pan troglodytes schweinfurthii* at Mahale.

²Glander (1978); feeding time

³Rodman (1984); feeding time, Kutai, Kalimantan 40,022 min. observation

⁴Janson, 1985; proportion of total kJ intake. Nectar made up 12.3% of kJ intake.

would be the only microwear signature in the incisors.

The trace element analysis reviewed above suggests directions for fine-tuning. High C_4 levels in *A. africanus* (Sponheimer and Lee-Thorp, 1999) pushes the early hominin diet in the direction of that of at least some chimpanzees. Mahale chimpanzees included a very high proportions of the grass *Pennisetum purpureum* (Hunt, 1989) in their diet in 1986-87, very near the 25% level the early hominin C_4 data suggest. Chimpanzees also consume termites, presumably a C_4 food.

Although all data bearing on early hominin diet are not in complete accord, taken together they produce a rather consistent picture. Weighing each of these lines of data, we may synthesize them to conclude that a) approximately half of the early hominin diet was fruit, principally small-diameter, hard-husked or seedy fruit (e.g., *Grewia*, *Harungana*), that b) leaves made up as much as a quarter of the diet (note incisor microwear data above) and were an important fall-back food, c) that seeds and hard husked fruits (given dental morphology and microwear) were the second most important dietary item (though not the second highest in proportion), d) that grasses were perhaps equally important (also consistent with microwear data, I argue), e) gritty food items, perhaps underground storage organs, made up at least part of the diet, and f) that early hominin diets were quite varied and included insects, meat, herbs, blossoms and bark, in addition to the staples suggested above.

Evidence Suggests Early Hominins Were Woodland-Living and Dependent on Arboreal Foods

The broad, shallow and cone-shaped (Schmid, 1983) torso of *A. afarensis* resembles that of chimpanzees, and is unlike the barrel shape characteristic of *Homo*. Hunt (1992) interpreted this shape as a stress-reducing adaptation that decreases compression on the ribcage during unimanual suspension (i.e., arm-hanging). Hunt (1991a, b, 1992) argued that the raised-arm set of the chimpanzee shoulder joint is an adaptation to arm-hanging and/or brachiation (arm-swinging locomotion), since no other behavior requires the complete abduction of the humerus. He argued that other positional behaviors hypothetically linked to the arm-raised set of the ape shoulder joint either a) do not require full abduction (e.g., vertical climbing), b) are found in monkeys that are incapable of full abduction, yet are nevertheless capable vertical climbers, or c) on closer examination, actually do involve some form of arm-hanging or brachiation, either unimanual suspension, actual brachiation or some other arm-raised suspensory positional behavior (e.g., quadrumanous, or four-handed, climbing).

The arm-raised set to the joint is manifested most clearly in chimpanzees in the observation that when resting they often spontaneously raise one or both arms

above the head. When grooming, they often fully abduct the humerus to engage in hand-clasp grooming. The scapular glenoid fossa of australopithecines is also cranially oriented (Robinson, 1972; Stern and Susman, 1983), giving the shoulder joint an upward tilt intermediate between *Pan* and humans. Inouye and Shea (1997) showed that smaller humans have more uptilted joints, and went on to argue that this is evidence the feature has no function. I argue instead that the allometry itself is an adaptation. It suggests that humans have an evolutionary history of contrasting behaviors between smaller and larger individuals; specifically, it suggests smaller individuals were better adapted to unimanual arm-hanging than larger individuals.

Early hominins show evidence of vertical climbing adaptation. Origin and/or attachment areas of biceps, latissimus dorsi, extensor carpi radialis and brachioradialis muscles, used to perform a pull-up action during vertical climbing, were large. Although there is evidence of only very limited great toe gripping adaptations, the hip shows evidence of a long moment arm for the hamstrings (Stern and Susman, 1983), which would increase the power of thigh extension, presumably during vertical climbing. Inferred large deltoid muscles, if analogous to those in chimpanzees, were used to raise when reaching out to pluck fruits while arm-hanging and during vertical climbing.

The convex joint surface of the *A. afarensis* and *A. africanus* medial cuneiform indicates a rudimentary gripping capacity for the big toe (Stern and Susman, 1983; Deloison, 1991; pers. obs.; Clarke and Tobias, 1995). The diameter of a support which the reconstructed grip the foot could accommodate was considerably less than that of extant apes. The early hominin gripping capacity would be useful for gripping moderate-sized (•5 cm) supports during vertical climbing. Evidence for a large, ape-like peroneus longus muscle suggests powerful great-toe flexion. Together these features suggest early hominins ascended using narrower supports than do living apes, or vertical-climbed less often. I argue they utilized shorter trees that less often required vertical climbing, and that the climbing bouts were shorter in duration.

A large calcaneus in *A. afarensis* (Latimer and Lovejoy, 1989) suggests that terrestrial locomotion was nearly exclusively bipedal. A large calcaneus, however, is no barrier at all to arboreality (Hunt, 1998).

A plantar set, or at least greater mobility (Latimer and Lovejoy, 1990) of the ankle joint, compared to humans, would have allowed greater plantar flexion (pointing the toe) in early hominins. Gombe and Mahale chimpanzees plantar-flexed their feet when they used their toes grip a branch to support body weight with the hind limb in tension. If females were more arboreal, and more suspensory, one would expect greater plantar flexion among females, and indeed this has been observed (Stern and Susman, 1983). Consistent with the suspensory anatomy of the ankle, early hominins have long,

curved pedal phalanges (Tuttle, 1981). Gripping with the lateral four toes but not involving the great toe was seen in Tanzanian chimpanzees in concert with unimanual suspension (arm-hanging). Such pedal gripping increased stability among slender terminal branches (Hunt, 1994b). Australopithecine fingers are curved, robust, and exhibit flexor sheath ridges, evidence that they had a powerful, chimpanzee-like grip, a capacity used by apes during arboreal arm-hanging and vertical climbing.

A more convex articular surface of the proximal tibia and a anterior-posteriorly compressed distal articular surface of the femur in *A. anamensis* (Leakey *et al.*, 1995), *A. afarensis* (Stern and Susman, 1983) and *A. africanus* (Berger and Tobias, 1996) suggests an emphasis on flexibility rather than stability in the hindlimb. Flexibility is useful during arboreal locomotion.

Although the os coxae of australopithecines are human-like in appearance, the pelvis is considerably wider than necessary for giving birth to an ape-sized neonatal head, or indeed even a human-sized neonatal head. Hunt (1994b, 1998) suggested the wide pelvis lowers the center of gravity, thereby improving balance on unstable substrates such as tree branches. Short hindlimbs have been speculated to serve the same function (Kummer, 1991). Such a broad pelvis decreases locomotor efficiency and increases skeletal and ligamentous stress. Short hindlimbs further decrease locomotor efficiency (Jungers, 1982, 1994).

These features were present for more than four million years among early hominins, thereby rendering it extremely unlikely that they persisted without function. Short hindlimbs, a wide pelvis, and flexibility of the knee are maladaptive in an exclusively terrestrial biped. The null hypothesis that early hominin behavior anticipated that of their descendents for millions of years, rather than that it reflected their own anatomy is, to quote Eckardt (1981) again, nuller than most.

In summary, recent finds only re-emphasize conclusions made a decade ago: “although bipedalism may have been virtually the only terrestrial locomotor mode in [early hominins], poor bipedal mechanics and compromises that improve arboreal competence suggest a role for locomotor bipedalism that is relatively reduced compared to modern humans early hominids may not have been reluctant, half-evolved bipeds, but rather they had a fully evolved, unique adaptation for both terrestrial and arboreal bipedal gathering that was unlike that of any extant species, including humans. The persistence of arm-hanging features in later hominids...suggests that this adaptation may have remained relatively unchanged, even in *Homo habilis*...until the evolution of a more locomotion-oriented, near-modern postcranial morphology in *Homo erectus*.” (Hunt, 1994b).

Evidence Suggests the Early Hominin Habitat was an Open Forest/Woodland/Savanna Mosaic

At all early hominin sites published to date, associated fauna (Table 2) include both dry, open habitat taxa (elephants, giraffe, hyena) and taxa that are largely confined to more densely wooded, waterside or well-watered habitats (hippos, mustelids, colobus monkeys). Even colobus monkeys are range into open canopy woodlands. In short, there is no evidence early hominins were forest living, and much evidence that, compared to chimpanzees, they were a dry-habitat, woodland taxon. The tool-using *A. garhi* habitat may have been drier and more open than earlier early hominins. Although a finer-grained analysis that closely considers species frequencies may ultimately improve the resolution of our habitat description, at present the best we can say is that early hominins lived near relatively open forests of as yet undetermined density and canopy height, and that they also lived near more open woodland and savanna habitats. The faunal list is very similar to that of the dry-habitat chimpanzees at Semliki, Uganda (Hunt and McGrew, 2002).

Chimpanzees are Ascent-Minimizers

Hunt (1994a) found evidence that when budgeting energy expenditures, larger chimpanzees are more tightly constrained to minimize vertical climbing than are smaller individuals (Table 3). He used multiple regression to factor out social rank effects and showed that large chimpanzee males fed lower in the forest canopy, were found on the ground more often, utilized shorter-stature species of trees, and ascended significantly less frequently than did small males. This observation conforms to theoretical expectations that vertical ascents are energetically more costly for larger than for smaller animals. Since early hominins — like chimpanzees — were large compared to other primates, we expect that large male early hominins were particularly constrained to minimize ascents. Arboreal resources were more costly to acquire for males compared to females, due to energetic constraints, and were more dangerous to acquire, since the risk of falls was greater. Very large species are under some pressure to reduce climbing to the absolute minimum; that is, to become terrestrial full-time. If early hominins budgeted their energy expenditure as do chimpanzees, they climbed as little as they could, but as much as they had to.

Why Climb Into Trees, Then? A Lesson From The Chimpanzee

Mahale chimpanzees spent 61% of their active period on the ground (N=11,896). While it may be tempting to characterize chimpanzees as terrestrial primates, it would obscure the fact that they are utterly dependent on arboreal food resources. Despite the precariousness of movement and support among the terminal branches

Table 2

Closed Habitat Fauna							
	hippo	crocodile	turtle	mustelid	colobus monkey	wild boar ⁸	
<i>Sahelanthropus</i> ¹	X	X	X	otters	X	X	
<i>Orrorin</i> ²	X	X	X	otters	X	X	
<i>Ardipithecus</i> ³	X	X	X	otters	X	X	
<i>A. anamensis</i> ^{4,4}	X	X	X	X	X	X	
<i>A. afarensis</i> ⁶	X	X	X	X	X	X	
<i>A. garhi</i> ⁷	X	X	X	X	—	—	
Semliki	X	X	X	X	X	(other suids)	
Dry Habitat Fauna							
	equid	elephant	giraffe	hyena	kob	baboon	rhino
<i>Sahelanthropus</i> ¹	X	X	X	X	X	—	-
<i>Orrorin</i> ²	X	X	X	X	X	—	X
<i>Ardipithecus</i> ³	-	X	X	X	—	X	-
<i>A. anamensis</i> ⁴	X	X	X	X	X	X	X
<i>A. afarensis</i> ⁵	X	X	X	X	X	X	X
<i>A. garhi</i> ⁶	X	X	X	—	X	X	—
Semliki	(historic)	X	(Holocene)	X	X	X	—

Table 2 — Fauna associated with early hominins, compared to fauna sympatric with chimpanzees in a dry habitat (X = presence; — absence)

¹Vignaud *et al.*, 2002

²Pickford and Senut, 2001

³WoldeGabriel *et al.*, 1994

⁴Leakey, M. *et al.*, 1998

⁵Macho *et al.*, 2003

⁶Johanson *et al.*, 1982

⁷de Heinzelin *et al.*, 1999

⁸*Nyanzachoerus*

Table 3

Large Males	Small Males
Ground	Above ground
Lower in canopy	High in canopy
Small trees	Large trees
Vertical climb less	Vertical climb more

Table 3 — Body size and chimpanzee habitat use (after Hunt 1994a)

Table 4

Feature	Behavior Inferred	Inferred Stratum Use
1. Dietary generalist trace element signal	Omnivory	Arboreal or terrestrial possible
2. Molar, premolar area	Fruit, seed eating	Some arboreality required
3. Molar morphology	Fruit, seed eating	Some arboreality required
4. Enamel thickness	Fruit, seed eating	Some arboreality required
5. Enamel microstructure	Hard foods, likely seeds	Arboreal or terrestrial possible
6. Molar microwear	Fruit diet	Arboreal feeding
7. Mandibular robusticity	Hard-husked fruit or seed diet	Indeterminant
8. Incisor microwear	Folivorous diet	Arboreal or terrestrial possible
9. Incisor size	Small fruit, seed or leaf diet	Arboreal feeding
10. Large biceps, brachioradialis etc.	Elbow, arm extension	Climbing
11. Large deltoid	Abduction	Suspensory feeding, climbing
12. Torso shape	Arm-hanging posture	Arboreal armhanging
13. Scapula shape, raised-arm set	Arm-hanging posture	Arboreal armhanging
14. Curved fingers	Arm-hanging posture	Arboreal armhanging
15. Short (vs. apes) fingers	Gripping small supports only	Indeterminant
16. Robust fingers, powerful grip	Arm-hanging, vertical climbing	Arboreal armhanging
17. Plantar set of ankle	Hindlimb suspension	Arboreal armhanging
18. Long toes	Arboreal support gripping	Arboreal climbing, armhanging
19. Curved toes	Arboreal support gripping	Arboreal armhanging
20. Large calcaneus	Terrestrial bipedalism	Bipedal locomotion
21. Long forelimbs, brachial index	Arm-hanging, fruit harvesting	Arboreal climbing, armhanging
22. Large biceps, brachioradialis	Vertical climbing locomotion	Arboreal climbing
23. Hamstring mechanical advantage	Vertical climbing locomotion	Arboreal climbing
24. Flexible knee joint	Arboreal gripping	Arboreal armhanging, climbing
25. Slightly divergent great toe	Climbing, gripping branches	Arboreal climbing
26. Powerful great toe grip	Vertical climbing locomotion	Arboreal climbing
27. Wide pelvis	Improves arboreal balance, decreases locomotor endurance	Arboreal feeding
28. Short hindlimbs	Improves arboreal balance, decreases locomotor endurance	Arboreal feeding
29. Reduced pelvic ligaments	Terrestrial locomotor endurance reduced in re <i>Homo</i>	Walking range small
30. Habitat reconstruction	Savanna and woodland	Indeterminant

Table 4 — Early hominin morphological features and inferred behaviors

of trees, Mahale chimpanzees spent 7.1% of their active period there (N=840). They did so for one reason only: their food is there—Mahale chimpanzees fed 87.8% of time they were among terminal branches. Thirty-two percent of the Mahale chimpanzee active day was spent in the tree core (i.e., any part except terminal branches; N=3835), and 50% of that time was spent feeding. Feeding made up only 28% of their terrestrial activity. All told, 70% of chimpanzee activity in trees was feeding. Chimpanzees enter trees not because they prefer arboreality, but because their more preferred food, fruit, is found there (Hunt, 1998).

It is assumed that in more open habitats chimpanzees might spend more time on the ground. We have a convenient test, since it is more open at Gombe than Mahale (Collins and McGrew, 1985). Gombe spent *less* of their time on the ground than Mahale chimpanzees, 47.2% (N=3,056) versus 60.7% at Mahale. Nutritional demands do not decrease when the habitat is more open.¹

Early Hominins Are Sexually Dimorphic

Sexual dimorphism of approximately 50% (f/m body mass) is suggested for *A. anamensis* (Ward *et al.*, 2001), a level somewhat greater than that posited by

McHenry (1992) for australopithecines as a whole. Recently Reno *et al.* (2003) are flimsy (Ramos and Hunt, *in prep.*) suggested sexual dimorphism in early hominids was not significantly different from that of modern humans. Their body mass dimorphism reconstruction was based on femoral head diameters estimated from other skeletal elements. Reference to the elements themselves yields a dimorphism estimate around 70%, or in line with previous estimates.

Early Hominin Ecomorphology

Reviewing early hominin morphology and inferred ecology, evidence that they were a semi-arboreal, frugivorous species is pervasive (Table 4). Associated fauna suggest their habitat included forest. As a primatologist, it is difficult to imagine such apes foregoing resources in the forest, whether they spent the majority of their time in more open areas or not. Baboons, for example, use both forest and savanna when the two are contiguous. Of 29 notable early hominin features (Table 4), ten are adaptations to arboreal suspensory behavior, eight are associated with vertical climbing, and eight more suggest at least some arboreal behavior. Two suggest both greater arboreal balance and reduced locomotor endurance. It is significant that among living apes, more arboreal species (*Hylobates* spp., orangutans) are more bipedal, albeit it in the trees, than more terrestrially adapted species (*Pan* spp., Gorilla), which characteristically knucklewalk on the ground (Hunt, 1991a). Terrestriality *per se* seems not to encourage bipedality.

Of 30 lines of evidence pertaining to early hominin diet and habitat use, 22 are consistent only with an arboreal lifeway. None suggests exclusive terrestriality, since only the very most open habitats, where woody plants grow to only two or three meters in height, could allow hominins to gather fruit without climbing trees. There is much to suggest early hominins were dependent on arboreal food resources, in particular ripe fruit, and that they spent considerable time in the trees, though almost certainly less time than extant chimpanzees or Asian apes.

In summary, early hominins were an ape unlike any living ape (Table 5), but they were not uniquely unique. Other than bipedalism, they share their most significant attributes with one ape or another. Early hominins were Great Ape sized (similar to *Pan* or *Pongo*), had a Great Ape level of sexually dimorphism (like *Gorilla* and *Pongo*), occupied a habitat at the very limit of ape dryness and openness (perhaps slightly outside the *Pan* range), spent more time on the ground than chimpanzees but less than mountain gorillas, ate fruit (like *Pan* or *Pongo*), piths (like *Pan* or *Gorilla*), hard objects such as nuts and seeds (like *Pongo*) and supplemented their diet with leaves, like all apes. Their claim to uniqueness would be that they utilized underground storage organs, as no ape does, and walked on the ground bipedally.

Sexual Dimorphism Implies A Hamadryas–Or Gorilla-Like Organization

Great sexual dimorphism among early hominins suggests high levels of male-male competition. If hominins were ripe fruit specialists, as are chimpanzee (Wrangham *et al.*, 1998) and orangutans (Leighton, 1993), as both referential modeling and dentofacial morphology suggest, they lacked strong female bonds (Wrangham, 1980, 1986). In the absence of female bonding, sexually dimorphic primates such as hamadryas baboons and gorillas have instead strong bonds between males and females. Orangutan- or gorilla-like sexual dimorphism implies that males defended breeding units relying not on strength in numbers as is the case in chimpanzees, with their male-bonded community social organization, but in groups small groups of two or three, and in the case of gorillas sometimes as a single individuals, where individual fighting skill rather than group coordination is important. The implied social system is similar to that of hamadryas baboons, where one-male breeding units coalesce into larger groups via bonds between several males. Females are either coerced into maintaining strict proximity to males (hamadryas), or are forced into proximity to protect infants from infanticidal extragroup males (gorillas). As the number of bonded males in a social group increases, successful defense depends on the strength of male bonds and an effective multi-male defensive strategy, rather than body mass, and sexual dimorphism is lower. A hamadryas or gorilla-like social system fits best with early hominins ecomorphology (Wrangham, 1986). In both hamadryas and gorillas breeding units travel as a rather tightly coordinated group, rather than in dispersed and fluid feeding parties, as are seen in chimpanzees. Single- or all-female groups seem precluded. All-male groups, however, are found in such societies, and are significant threats to infants and to the integrity of breeding units.

If early hominins had a hamadryas or gorilla-like social system, it would profoundly affect their foraging strategies. Rather than individual or small-group foraging parties, the entire social group must forage as a unit. In the gorilla female-choice society, females tend to limit copulation to a single male. In consequence, males have low sperm competition, small testes (Harcourt *et al.*, 1981) and high confidence in paternity. Males with high confidence in paternity can receive inclusive fitness benefits if they defer to females at feeding sites in order to increase female reproductive success. Such deference means that sex differences will be driven more by body size effects and reproductive needs effects than to by rank effects. Peripheral to arguments presented here, but possibly of interest, visible estrus (sexual swellings) is unlikely in a female-choice social organization, and copulation rates are expected to have been low.

Table 5

Species	Female ¹ Mass (kg)	Sexual Dimorph.	Neocortical ratio ²	Home Range (ha)	Habitat ¹	Aboreality	Diet ¹
<i>Hylobates</i>	6.6	96.6 ¹	2.1	49 ³	For	100% ¹	Frt, Leaf
<i>Pongo</i>	35.7	45.7 ¹	-	70 ³	Moist For	90% ¹	Frt, Leaf
<i>G. g. gorilla</i>	71.5	47.2 ¹	2.7	2170 ⁴	For	30% ⁵	Pith, Frt
<i>Pan</i>	41.4	75.4 ⁶	3.2	2150 ³	For, Wood	50-60% ⁷	Frt, Leaf
Hominins	25-55 ⁸	50-75 ⁸	>3.2	?	Wood?	10-30%?	Frt? Seed?

Table 5 — Ecology and physical attributes of apes and early hominins

¹Fleagle, 1999; Frt=Fruit,; For=Forest, Wood=Woodland; Dimorphism = female mass/male mass

²Dunbar, 1993

³Dunbar, 1992

⁴Tutin, 1996

⁵Estimated in Hunt, 2004

⁶Wrangham and Smuts, 1980

⁷Gombe and Mahale range; Hunt, 1989, Table 5.31

⁸McHenry, 1992; Ward *et al.*, 2001

Sex Differences in Chimpanzee Diet

In a review of chimpanzee diet data and presentation of new data Hunt and colleagues (Hunt, 1993; Hunt *et al.* in review) noted that female chimpanzees eat more invertebrates (mostly termites, some ants, a small proportion of unidentified invertebrates), more seeds, and more *Garcinia huillensis* fruit than males. These differences were largely due to rank-effects, since female selection of invertebrates and seeds paralleled rank differences among males. Females ate a wider variety of leaves, and ate them slightly more often than males (Goodall, 1986). Female selection of leaves was argued to be a result of reproductive demands, rather than rank effects, since high ranking males were shown to have eaten more leaves than low ranking males. Furthermore, Hunt *et al.* reviewed evidence that even in species where females were dominant to males, females tended to eat more leaves. Among three guenon species, *C. nictitans*, *C. pogonias* and *C. cephus*, females ate a higher proportion of protein-rich leaves when pregnant than otherwise (Gautier-Hion, 1980). Cook and Hunt (1998) suggested that this protein/calcium preference among females extends to humans.

Males ate more piths and stems (predominantly stems of *Pennisetum* grass), more meat, more *Dioscorea* spp. fruits, more *Harungana madagascarensis* fruit (a small, palatable fruit found in large patches), more *Psychotria peduncularis* fruit (a large-patch, 1 one m tall shrub), and more miscellaneous fruit (*Cordia* spp. mostly). Hunt and colleagues showed that high ranking males ate more fruit and less pith than low ranking males, suggesting to them that females ate lesser amounts of fruit due to male-female competition. In support, they showed that when females were in parties with males the proportion of fruits in their diet dropped dramatically. Hunt's short-term observations were consistent with long-term records at Gombe that showed

that males engaged in hunting dramatically more often than females. Males took the prey in 288 of 336 records (Goodall, 1986; McGrew, 1992). Among notable sex differences were that males were overwhelmingly more likely to take dangerous colobus monkeys, whereas females were biased toward juvenile and infant bush pigs and the least dangerous prey, bushbuck.

Sex Differences in Chimpanzee Positional Behavior

Hunt *et al.* found that female chimpanzees used a flex-legged sitting posture, engaged in unimanual suspension (arm-hanging), squatted and transferred (slow suspensory movement among terminal branches) more often than males. Hunt (1992) found that high ranking males monopolized larger, more stable perches, including large-based, hammock-like interwoven tangles of branches. Males knucklewalked and sat with legs extended significantly more often. Females had a more diverse positional repertoire than males, eleven positional modes constituting 90% of male positional behavior, versus fifteen modes for females.

Armhanging was found to be a fruit gathering and, to a lesser extent, leaf gathering posture; 88% of all armhanging was observed during fruit gathering (Hunt, 1989). Counter-intuitively, males ate more fruit than females, but armhung less. The cause for this incongruity is that males found a way to eat fruit when sitting, whereas females ate fruit while armhanging significantly more often than males. Males were significantly more likely to utilize armhanging when feeding on fruits in large trees with multiple feeding sites, whereas females tended to use armhanging when feeding in small fruit trees.

Sex Differences in Chimpanzee Canopy Use

Female chimpanzees are more arboreal than males (Doran, 1993; Hunt, 1993), and females fed and moved among terminal branches significantly more often, 21.5% of the time, versus 15.6% of the time for males (Hunt *et al.* in review). Whereas feeding males spent nearly half of their time on the ground (48.5%), feeding females spent only 35.9%, a significant difference.

Sex Differences in Chimpanzee Activity Budgets

Females spent more time feeding than males, more time resting, and less time grooming. Hunt *et al.* attributed this difference to male monopolization of low-handling time food items. Female travel was significantly more often in the context of moving between feeding sites, whereas male knucklewalking episodes ended more often in rejoining a social group.

Sex Differences in the Order Primates

In their review, Hunt *et al.* found that among species where females are higher ranking than males, females devote less of their activity budget to feeding than males. Among species where males are dominant, females tended to spend more time feeding. Four taxa did not conform to this pattern. In vervet, gelada, gorilla and orangutan, males allocated more of their time-budget to feeding than did females. In primate species in which sexual dimorphism was similar to that in early hominins, either males exhibited a selectivity for fruit, females showed a selectivity for leaf, or both.

Of 24 taxa where sex differences were reported, females showed a preference for flowers, leaves and invertebrates in 17 cases, classes of items that tend to contain high levels of protein and calcium. Males selected these items in only two species (vervet, capuchin). Among four primate species that eat meat (bonobo, baboon, capuchin and chimpanzee) males ate more meat; in no cases did females eat more meat.

Explaining Chimpanzee Sex Differences

There is a pattern to sex differences in chimpanzee diet and behavior (Hunt *et al.*, in review; Table 6). Fruits eaten in abundance by females were those found in small, isolated trees. Travel costs likely decrease energy return from such small patches. Many of these same fruits are small-diameter, thus requiring more whole-body movements and more picking motions per unit weight harvested. Invertebrates are small, are often concealed, and often require tools to harvest. They are a low-risk food item. Whereas they require little energy to harvest, compared to meat they have a low nutrient return per unit time. Blossoms and shoots must be picked individually and are therefore likewise a high handling-time item. Seeds must be gathered individually and opened individually. Often they require the use of

tools. In short, female diet lists are rich in high-handling time food items.

In contrast, items eaten more often by males tended to be large fruits, items that could be harvested without climbing because the items are found on the ground or in low trees or bushes, and items found in large patches. Fruits, compared to most other dietary items, are calorie-rich. Some patches were large because the trees themselves were large, but others constituted a large patch because numerous smaller trees were found in dense stands. Meat is harvested in large packages, compared to invertebrates. A supporting phenomenon was observed by Goodall (1986), who reported that Gombe females ate more insects than males at most times of the year, but during the brief periods of greatest abundance, when the resource is large and concentrated, males ate them more often (Goodall, 1986: 258). Males, it seems, specialize on dietary items that have low handling times, either because the foods are in large packages, or because they are nutrient-dense, or because they are themselves large. Hunt *et al.* suggest that males spent less time feeding because they specialized on items that could be harvested quickly.

Despite their lower quality diet, females spent more time feeding and did it with more arboreal and acrobatic positional behaviors. They harvested foods arboreally, which requires greater energy expenditure because this demands ascents, greater effort to stabilize postures due to irregularly placed and unstable supports, and the need for challenging arboreal locomotion. Positional modes used significantly more often by females, armhanging and squatting, are more acrobatic than the predominant male positional mode, sitting. Armhanging is of particular interest, since it is a distinctively ape positional mode. The only obvious reason for females to work harder to get worse food is that they may be forced into such a regime by competition from males.

Leaves are also a high handling time item, since they must be picked individually and since chimpanzees appear to be very selective about which individual leaves are acceptable. Leaf eating therefore is slow going. Despite this, evidence suggests that female preference for leaves is due to reproductive demands. Females select leaves for their high density of protein and calcium.

Hunt *et al.* concluded that across the primates, females include more fruit in their diet when their social rank allows it, but that female preference for leaves is independent of social rank. Female diets resemble those of males more in species where males have a high confidence in paternity, and therefore might be deferring to females as a form of paternal investment. While male deference might reduce sex differences, males must maintain good condition to defend against interloper, infanticidal extragroup males.

Chimpanzees must also be under selection for paternal investment, since they defend a territory on which females depend, and their reproductive success in

Table 6

Male	Female
Large patches	Small, isolated patches
Terrestrial	Arboreal
Large items	Small items
Plant products with sugars, digestible hemicellulose	Plant products high in protein, calcium ¹
Few secondary compounds	Secondary compounds ²

Table 6 — Sex differences in chimpanzee food item characteristics.

¹Females ate more leaves, which have relatively high levels of protein (Gautier-Hion, 1980) and calcium (Leighton, 1993; Rogers *et al.*, 1990)

²Blossoms, seeds and leaf can contain high levels of secondary compounds (McKey *et al.*, 1981; Marks *et al.*, 1988)

Table 7

Item	Greater in:	Cause(s) in <i>Pan</i>	Inferred hominin sex difference ²
Invertebrates	Female	Rank, Repro	Females eat more invertebrates
Seeds	Female	Rank, Repro	Females eat more seeds
Leaf	Female	Repro, Rank	Females eat more leaf
Small-patch fruit	Female	Rank	S.U., P.I.
Small diameter fruit	Female	Rank	S.U., P.I. (or Females > due to Size)
Piths	Male	Repro, Size	Males eat more pith due to Size
Large diameter fruit	Male	Rank, Repro	Males > (Size, Rank) (small P.I., S.U. effect)
Terrestrial fruit	Male	Rank, Repro, Size	Males > terrestrial fruits due to Size, Rank
Large-patch fruit	Male	Rank, Repro, Size	S.U.
All fruit	Male	Rank, Repro	Males eat more fruit due to Repro, Rank
Meat	Male	Rank, Repro, Size	Males due to Size, Repro, Rank
Sit (extended)	Male	Rank	P.I.
Walking speed	Male	Repro	S.U.
Knucklewalk	Male	Repro	S.U.
Terrestrial	Male	Rank, Repro, Size	Males more terrestrial due to Size, Rank
Stand	Female	Rank	Males stand more due to > terrestriality
Arm-hang	Female	Rank	Females armhang more due to > arboreality
Transferring	Female	Rank	Females transfer more due to > arboreality
Squat	Female	Rank	Females squat more due to > arboreality
Terminal branches	Female	Rank	Females use t.b. more due to > arboreality
Arboreality	Female	Rank	Females more arboreal due to Size
>Time spent feeding	Female	Rank, Repro	Possibly greater in females due to Repro
Rest	Female	Male Repro	P.I, S.U.
Groom	Male	Repro	Females greater; protection from infanticide
Travel between feeding patches	Female	Repro	S.U.

Table 7 — Statistically significant chimpanzee sex differences, inferred causes, and inferences for early hominins¹

¹After Hunt *et al.*, in review. **Rank** = rank effects, **Repro** = reproductive demands, **Size** = body size effects,

²**P.I.** = no differences or small differences inferred due to high paternal investment, **S.U.** = no differences inferred because groups are presumed to travel as a single, unfissionable unit.

almost entirely dependent on the fecundity of females within their community range. Chimpanzees differ from gorillas because they must compete with intragroup males as well as extragroup males. They are expected to behave somewhat more selfishly than gorilla males, gibbon males, or perhaps even orangutan males, all of which have societies where males have higher confidence in paternity.

A Conceptual Model for Early Hominin Foraging Patterns

Table 7 summarizes the conceptual components of an early hominin foraging model, including which of rank-effects, body size-effects, reproductive demands effects and paternal investment might drive early hominin sex differences. Early hominin social units, at least as reconstructed here, were cohesive groups quite unlike the fluid, fission-fusion grouping seen among chimpanzees. This means that chimpanzee sex differences that are allowed by or result from males traveling in all-male groups, from males and females traveling separately, or from females foraging alone would not be found in early hominins.

There are no grounds to suggest that early hominin reproductive demands differed from those of chimpanzees and other living primates. Accordingly, early hominins might be expected to conform to the trend in chimpanzees for female food lists to have more high-handling time food items. If so, early hominin females might be expected to eat more invertebrates, more seeds, and more arboreal food items, compared to males, due to rank effects. Females are expected to eat more leaves due to reproductive demands. Males, free from the demands of pregnancy and lactation, and possibly required to engage in vigorous group defense, might be expected to monopolize low-handling time, high nutrient density items like fruit. Higher social rank but also larger jaw gapes and greater strength would reinforce the tendency for males to eat larger fruits and other larger items.

The greater costs and risks entailed in vertical climbing are argued to lower the net value of arboreal food items for males, and to increase the value of terrestrial fruits and other terrestrially harvested foods, such as piths. This effect is theoretically multiplied by rank effects, which are also expected to press females to be more arboreal and males more terrestrial. That is, males have a doubled reason to select fruits that can be harvested terrestrially: terrestrial fruits would be more valuable to them due to greater ascent costs and climbing risks for arboreal fruits, and males might monopolize terrestrial feeding sites due to their higher rank, even if the items were more valuable to females. Although Hunt *et al.* found no significant sex difference in vertical climbing between male and female chimpanzees, it would have been dramatically greater among female early hominins. Body size differences, rank differences and defense imperatives together reinforce one

another to suggest profound differences in arboreality between the sexes. This, I argue, is the explanation for allometry in shoulder morphology among early hominins (Inouye and Shea, 1997); it is an adaptation to sharp differences in arboreality between the sexes.

This in turn predicts greater frequency among females of squatting, arm-hanging, transferring, and other suspensory behaviors, those particularly among terminal branches. Arboreality would also provide females some protection from predators and, perhaps even more critically, some measure of protection from a sudden rush from an extragroup infanticidal male. Female arboreality would force larger and therefore less arboreally maneuverable males into a slower stalking strategy, leaving intragroup males time to come to the defense of mother and infant. Terrestriality would place intragroup males in an advantageous position to defend offspring and females from males or predators that must approach on the ground, assuming open habitats. Males might be expected to approach terrestrially even in closed habitats, as we know is the case with chimpanzees (Goodall, 1986).

Unencumbered by nursing and more capable of overcoming prey defense due to large body size, males might be expected to capture more meat than females. Meat-sharing as a paternal investment might be expected to reduce differences in consumption rates somewhat compared to chimpanzees, but even so males likely ate more meat.

These observations receive some support from the fossils. Where we can compare male and female skeletal elements, the female fossils have many more features associated with arboreality (Stern and Susman, 1983), suggesting that the trend for male terrestriality seen in chimpanzees was even more exaggerated in early hominids.

Sex Differences In Chimpanzee Tool Use

At the three sites (Gombe, Mahale, and Tai) where chimpanzee tool-using has been observed most frequently, female chimpanzees used tools more often than males. Boesch and Boesch (1981, 1984, 1990) observed that females cracked more nuts per minute, needed fewer blows to crack nuts, cracked more total nuts, and were more competent with heavier hammers (Boesch and Boesch, 1981, 1984, 1990). Males and females crack *Coula* nuts in equal proportions when the nuts are dry, and therefore easy to open, but when they are fresh and difficult to open, females opened nearly twice as many as did males (Boesch and Boesch, 1984). Cracking nuts in trees is a skill acquired relatively late, and which requires complicated coordination of two, three and four limbs. Females used tools in this challenging context over ten times more often than males (Table 8). Differences between males and females were greatest for *Panda* nuts, the most difficult nuts to crack. Panda nuts require both an adequate anvil and a stone hammer to open. Stones hammers are rare, which

means nut-crackers must invest time in carrying hammers to anvils, and they must remember hammerstone locations. Females were 2.4 times as likely to engage in Panda cracking as males (Table 8). As a general expression of lesser male competence, males were also more likely to choose a tool that was inefficient for the task at hand. In short, the more difficult the technique, the more likely it was that females were the ones that did it.

McGrew (1979) found that females fished for termites three times as many hours as males (166.3 v. 50.8), had more than twice as many individual termite bouts (372 v. 123), and spent 3 times as great a proportion of their active period termite fishing (4.3% v. 1.4%). Females were more likely to dip ants using an ant wand, a collecting regime that requires delicate two-handed coordination. Seventy-five percent of females were seen to ant-dip, but only 45% of males did so. Fecal samples confirmed a sex difference (56% of female samples contained insect parts, 27% of male samples). Similar observations were made at Tai (Boesch and Tomasello, 1998) and Mahale (Nishida and Uehara, 1980; Uehara, 1984). In addition to using tools to open nuts arboreally, females also harvested ants arboreally much more frequently than males (Nishida, 1973; Nishida and Hiraiwa, 1982).

Drinking tools are thought to be used more often by females than males (Sugiyama, 1995). Two cases of unusual tool use were engaged in by females, a tool used to prey on a squirrel (Huffman and Kalunde, 1993), and stepping sticks (Alp, 1997).

Males seem to use wooden probes to extract marrow (Boesch and Boesch, 1989), but since females eat meat less often than males, it is not clear that this is a meaningful sex difference.

Stones (66%) and other objects thrown at perceived threats are the only tools used more often by males than females, but it is a profoundly male behavior: all 44 throws mentioned by Goodall were by males (Goodall, 1964; McGrew 1981).

Of the tools commonly used by chimpanzees such as missiles, termite fishing tools, and nut-cracking tools, tools that could be called collecting tools were used by females between 1.3 and 11.3 times more often than males (Table 8). Missiles, in contrast, were used by males alone. Females use tools more often, in more dif-

ferent ways, in more difficult circumstances, and more innovatively than do males.

The Female Diet List Makes Tool Use Particularly Valuable to Females

Whether it is termiting tools, or hammers and anvils, females use tools with greater frequency, greater competence, and obtain more calories from their use. Hunt (1993) suggested that the reason for this difference is that sex differences in diets and foraging behavior serve to make tool-use relatively more valuable to females.

Termites, small fruits, shoots, blossoms, seeds and Panda nuts are quite different food items, but each requires a considerable time- and/or energy- investment before payoff, compared to items preferred by males. The male diet list, in comparison, contains items that have low handling times. Large fruits have a high volume per surface area, which means that gathering and opening individual fruits yields greater mass per item. Larger items require fewer harvesting motions per unit weight, which decreases both gathering motions and between-feeding-site locomotion. As a source of protein, meat is a calorically dense (compared to leaves) and large (compared to insects). Fruits are calorically dense, and therefore require less harvesting investment than lower-quality items. Foods found in large patches (e.g., *Harungana*, grass stems) require lowered travel investment and allow increased harvesting rates. Terrestrial fruits require lesser investment in ascents, arboreal movement and balance during harvesting.

The more strenuous foraging regime and lower quality diet in females means they must work harder but end up with what is, by most measures, a worse diet. The male diet list means that males are, compared to females, more effective time minimizers. Females, by virtue of their lower feeding rates, are in a position to benefit tremendously from tool use, whereas male food handling times are already relatively low. When females reduce feeding time, they reduce energy expenditures and free up time to reallocate on care of offspring and productive foraging.

Females benefit from tool use more than males because it allows them to compensate for male monopolization of food items such as meat by using tools to

Table 8

	Coula ¹		Panda ¹	Termites ²	Missiles ²
	ground	tree			
Female	336	68	92	372	0
Male	255	6	37	123	44
F/M	1.3	11.3	2.4	3.0	—

Table 8 — Sex differences in chimpanzee tool use, pooled data

¹Boesch and Boesch, 1984

²McGrew, 1979

add nutritionally similar items such as nuts and termites to their diet. Since meat is preferable to termites, males have little motivation to use tools to harvest invertebrates or crack nuts.

In addition to these rank effects, body size effects are expected. Greater body mass and therefore greater strength means that some food items that females cannot open or process with the teeth or hands can be processed by males without tools.

Females appear to have compensated for their lesser strength and for being excluded from preferred foods and preferred feeding sites by increasing the time they allocate to foraging, and by using positional modes (e.g. arm-hanging and transferring) that allow them access to less desirable feeding sites where there was little competition from males. Tool-use partly ameliorates this disadvantage for females.

Reproductive demands also have a role in shifting the balance toward female food items. McGrew (1992) identified reproductive demands as determining lower female hunting rates. Females are less free than males to make large, short-term energy or time investments which would put them in poor condition, whereas males are freer to engage in bouts of intense activity that result in short-term energy deficits, followed by dramatic, short-term increases in feeding and resting budgets. Since hunting is often unsuccessful and usually dangerous, it is a food-getting strategy that has two risks: the risk of investing energy in the hunt without a return, and the risk of injury. Regarding the former, chimpanzees hunt less often when their core food, fruit, is in low supply, and hunt more when fruit availability is high, when they can afford to fail (Mitani and Watts, 2001). Nutrient demands of pregnancy, lactation and infant carriage are more constant than male reproductive demands. Foods that can be located more consistently,

even if they are poor quality, are more valuable to females.

In short, female chimpanzees use tools more than males because they receive a disproportionate benefit when they lower food handling-times, gain access to items unavailable without tools, or avoid dangerous food-getting practices such as hunting.

Connecting the Dots: Inferred Sex Differences in Early Hominin Tool Use and Diet

The thrust of much of McGrew's (1992) innovative reasoning concerning chimpanzee tool use is that in order to use chimpanzees as an effective model we must be thoughtful to separate what chimpanzees do from what they are capable of doing. They use termite tools, missiles, pry bars, seat sticks and tooth probes. We know from the lab that bonobo chimpanzees *can* produce a sharp edge from a cobble by flaking (Toth *et al.*, 1993; Schick *et al.*, 1999), and they can make effective use of carrying devices. Most presume that they do not manufacture stone tools in the wild because they are incapable of doing so. McGrew and his colleagues (e.g., Wynn and McGrew, 1989) make an implicit argument that chimpanzees do not make cutting tools because they would not increase net nutrient intakes. In support, in Gabon where stones are common chimpanzees do not use them to crack nuts (McGrew *et al.*, 1997). In other words, there may be jobs stone tools can do for chimpanzees, but the costs of using them make them impractical. In order to use tools full-time, chimpanzees would have to cache and retrieve them, carry them throughout their daily foraging regime, or discover (or remember) them just as they are needed. Because chimpanzees feed arboreally, carrying would necessitate constant short-term caching and retrieval. Arboreal walking and leap-

Table 9

Task	Sex of human forager	Sex of <i>Pan</i> forager
Hunting large fauna	Male	Male
Woodworking	Male	Females termite tools are sometimes wood
Fowling	Male	Either (Goodall, 1986: 262-3, 293)
Stoneworking	Male	Females use stones to open nuts
Bone/horn/shell working	Male	—
Mining and quarrying	Male	—
Bone-setting and other surgery	Male	Females use medicinal plants more
Butchering	Male	Male?
Honey-collecting	Male	~Equal (Goodall, 1986: 255)
Gathering small aquatic fauna	Male	—
Gathering vegetal foods	Female	Female
Preparing vegetal foods	Female	Female

Table 9 — Modern human and chimpanzee sex differences

ing would interfere with stone tool carriage. Early hominins faced these and other influences and constraints.

Table 9 lists tasks for which there are sex differences in modern humans, and identifies where similar sex differences have been observed in chimpanzees. We might have great confidence that when tasks have the same pattern of sex differences in humans and chimpanzees, early hominins had similar differences. Conceptual modeling can fine tune these extrapolations.

Among both humans and chimps (Table 9), males hunt the larger fauna. The mass of the prey, however, differs over an order of magnitude. Chimpanzee hunt prey up to perhaps 15-20 kg, which they can dismember without stone tools. Stone tools for butchery would have no utility unless prey size were exceed the size for which brute strength could dismember the carcass. Chimpanzees are sympatric with prey that is presumably attractive to them. For instance, they eat bushpig piglets, but they ignore adult bushpigs (Goodall, 1986). This suggests that the reason chimpanzees do not take larger prey is not because they cannot butcher them, but because they cannot kill them. As has long been speculated (Brace, 1968), the likeliest first hominin tool was a stout, hand held stick which could be used to dig up underground storage organs, fend off predators, deter aggressive conspecifics, and dispatch largish prey as a club or spear. I argue that chimpanzees do not carry such a tool not because they cannot manufacture the tool, but for the same reason they abandon nutcracking hammers, even though they are rare and valuable. Carrying a stick would hamper arboreal activity, and if left on the ground there is a retrieval cost. Chimpanzees conceive of detaching smaller plant material to make termite and ant fishing tools. A spear/digging stick/club is conceptually similar, only larger. Chimpanzees are enormously powerful and easily break one and two centimeter branches when making nests. Breaking off a five centimeter sapling is possible for male chimpanzees, and presumably early hominins. Such a stick, spear or club might last for years, so a significant investment to shape it with the hands and teeth might pay off.

Males, I argue, would find stick carriage less costly than would females, since they were hypothetically more terrestrial and therefore would bear fewer caching and retrieval costs. Males would also find spear use more beneficial, since they were more likely to encounter prey and predators, and in a better position to dispatch them since they were not burdened by carried infants.

Among chimpanzees stoneworking (Table 9) is unknown. Perhaps stone tool use is a less sophisticated precursor for stoneworking: stone tools is mostly a female affair. Females chimpanzees are more deft, better able to choose a correct tool, and better able to master tool use that requires sequential tasks (Boesch and Boesch, 1981, 1984; work reviewed in McGrew, 1992). This suggests that stone tools for shaping and sharpen-

ing spears were likely a male tool. In the absence of carrying devices, presumably but not certainly out of the early hominin cognitive realm, carrying raw materials and flakes would be costly and possibly impractical. Males might have engaged in opportunistic woodworking, discarding or abandoning flakes after spear-sharpening. Because caching and retrieving tools is time consuming and energy expensive, tool carriage is still expensive, even for males. When stone tools began to be carried rather than used opportunistically, tool carriage of a single, all-purpose tool that could serve both woodworking and butchering duty seems more likely than a large, diverse toolkit. Carrying devices, of course, would change that balance.

Whereas chimpanzee males range independent of females and offspring, and might therefore increase range even further to increase encounter rates with prey, male early hominins hypothetically traveled in unfissionable gorilla-like units. Butchering is a male activity among humans, but this may be due in part to the absence of females in the early stages of processing, in addition to rank-effects. For proto-tool-users, prey were most likely to be encountered by the group, and likely encountered on the ground. We know that early prey were large enough (de Heinzelin *et al.*, 1999) that butchering tools would have had some utility. Among early hominins, males were likely the hunters, and so had first access to meat. If similar to chimpanzees, males monopolized the larger, easier to process body parts. Males were large enough to manage some dismembering tasks manually, and in any case would have been in a position to command the larger, time-minimizing portions. Females were more likely to increase access and decrease handling times by using tools to process body parts males deferred to them. Butchery tools, then, were more likely to have been female tools. Scrapers used for extracting the last bits of nutritional residue from items seem to fit clearly within a female tool-use strategy. Marrow is an embedded food much like nuts, more time-intensive to harvest, and therefore likely to have been a female food. Given large body (and jaw) size, males could have processed some bones without tools. For tasks for which bone, horn and shell would be more available or better suited, the same trends should apply.

Among chimpanzees both males and females take nestlings, whereas among humans males are more likely hunters. Use of nets, traps and snares placed at dispersed sites and therefore requiring long distance travel to monitor may account for human sex differences. With no sex difference in fowling among chimpanzees, and the expectation that male and female early hominins did not differ in day-range, we are left with only arboreality as a factor. Birds harvested terrestrially (e.g. guinea fowl) are more likely to be encountered and killed by males, birds that are encountered arboreally would be likely preyed upon by females. Since chimpanzees kill and dismember birds without tools, and nets and traps

were unlikely, this resource likely affected tool use little.

Mining and quarrying (Table 9) requiring strength or large body size would seem to be a male early hominin task. Since most early hominin tools were made of cobbles, rather than mined raw materials, this task was probably insignificant.

Among chimpanzees, females used medicinal plants more often than did males (Wrangham and Goodall, 1987). Whereas bone setting and other surgery is quite different from collecting medicines, if there is any such thing as early hominin medicine, it seems unlikely that females would be more common practitioners.

Among humans, honey collecting is likely engaged in by males because it is risky. Since early hominins were more competent arborealists, sex differences were probably less pronounced.

“Gathering” of small aquatic fauna fits most closely with female gathering habits (McGrew, 1981), but its male bias among living humans leaves the issue undecided. Gathering and preparing vegetal foods was likely a female pursuit among early hominins, as it is among both humans and chimpanzees, and as fits with a conceptual model of females specializing on more highly processed and less desirable food items.

If early hominins harvested termites, as seems likely (Sponheimer and Lee-Thorpe, 1999; Backwell and d’Errico, 2001), a chimpanzee analogy suggests that termite fishing would be a female activity.

Female chimpanzees and female humans each process and gather more plant material than males. Tools used for such activities are much more likely to be female tools. Again, it seems unlikely that female proto-tool users would have persistent tool carriers, given the demands of arboreal harvesting, but could have used tools opportunistically, or used them in confined areas where plant resources are persistent and tools could be cached without great travel cost.

Tools used for any arboreal activity whatsoever seem clearly female tools, both from analogy with chimpanzees, and reconstructed canopy use. Tools used to strip bark or score trees to gather exudates would be female tools.

Experimental evidence (Toth, 1985) suggests that toolkits might differ as in Table 10. In cases where raw materials are carried, males are more likely carriers, since they are larger, more terrestrial, and in less danger when encumbered. Some tools are ambiguous. Hammerstones might be used as missiles. If so, the pronounced tendency for male chimpanzees to throw missiles in defense or in intragroup aggression (McGrew pers. comm., 1992) suggest this as a possibility for male use, but inferences above suggest this tool would be in the hands of females most of the time. Cleavers may have been used (Toth, 1985) for hide slitting, an inferred female activity, but also for heavy duty butchery, possibly a male activity. Woodworking, if the inference that males are more likely to carry spears and to shape and sharpen them, would seem to be a male activity.

Table 10

Tool	Inferred use (Toth, 1985)	Sex
Chopper	Flake production	Either
Polyhedron	Flake production	Either
Bifacial discoid	Flake production	Either
Core scraper	Flake production	Either
Cleaver	Hide slitting, heavy duty butchery, woodworking	Either?
Acute chopper	Woodworking	Male
Large acute flake scraper	Heavy duty butchery, light woodworking	Male
Handaxe	Heavy duty butchery	Male
Pick	Heavy duty butchery, defense	Male
Unmodified stone	Missile	Male?
Small acute flake scraper	Hide scraping	Female
Steep flake scraper	Light woodwork, hide scraping	Female
Flake	Hide slitting, heavy and light butchery	Female
Hammerstone	Bone breaking, nut cracking	Female
Anvil	Bone breaking, nut cracking	Female

Table 10 — Early hominin tool use and manufacture sex differences

CONCLUSION

Early hominins are different enough from living apes that early prospects that they might be slotted into one or another ape socioecological niche have been disappointed. However, with fine-grained conceptual modeling, we can reconstruct more than might appear at first glance. Diet, social system, foraging strategies, and male-female differences are susceptible to reconstruction. We might have predicted that relatively small-brained early hominins would have exhibited few sex differences in foraging strategies. Among the inferences we can draw from analogy with living primates are:

- Dental microwear, tooth morphology, relative dental dimensions, facial morphology and trace-element analysis suggest that half of the early hominin diet was fruit, principally small-diameter, hard-husked or seedy fruit, and that leaves made up less of the diet than in living apes (but still perhaps as much as a quarter of the diet) and were an important fall-back food. It is also likely that seeds were the second most important dietary item (though not the second highest in proportion), that animal protein including both invertebrates and meat were an important part of the diet (though not clearly more important than among chimpanzees), and that grass stems and pithy items including underground storage organs were important.
- Early hominins were partly arboreal, collected small fruits using an arm-hanging bipedalism, slept in trees at night, and retreated to trees when threatened by predators.
- Faunal lists suggest early hominins were adapted to and lived in a rather open woodland habitat, not a closed canopy or forest habitat.
- Chimpanzees seek to minimize ascents, and early hominins likely did too, more so for large individuals — adult males — yielding a clear sex difference in arboreality.
- Chimpanzees climb trees and arm-hang when feeding on their most important food, fruit. Early hominins were likely the same.
- Early hominin females were 70% the body weight of males, suggesting that early hominins had a gorilla-like social system with no bonds between females, strong bonds between breeding males and females in their breeding group, and secondary bonds between males that allowed group-male defense against attacker males attempting to displace breeding males or kill infants.
- Female chimpanzees engage in more acrobatic and varied locomotor and postural modes and do so among smaller branches, compared to males. Early hominins were likely similar.
- Female chimpanzee diets differ from male diets principally due to social rank differences, but females preferentially pursue protein independent of rank. Early hominins were likely the same.

- Female chimpanzee tool use patterns suggests early hominins females used tools in a greater variety of circumstances, obtained more calories than males from their use, and used them with greater frequency.
- Early hominins likely used stone tools for tasks that had a low return, for processing smaller items, for tasks that required finer work, and for tasks that required smaller tools.
- Early hominin males were more likely to be the makers of large, heavy duty tools, and tools used to process high-return items.
- Early hominin males were likely to have used tools appropriate for first-access to carcasses, and for heavy-duty butchery tasks.
- Early hominin females were more likely to have used tools for fine butchery at the end of carcass processing, for hide slitting (bite sized pieces of hide might yield some last nutrients, if chewed long enough), for marrow harvesting, for scraping, for processing plant foods (e.g., pith harvesting, underground storage organ peeling), for nut-cracking, and for any arboreal food-getting activities.
- Early hominin males are more likely to have used tools for dispatching prey, and as missiles or clubs to deter predators or aggressive conspecifics.
- Even the extremely simple toolkit most expect among early hominins should be expected to have differed between the sexes.

Rather than sex differences having developed after stone tool use began, it seems most likely that sex differences evolved in the common ancestor of humans and chimpanzees, if not even earlier. Chimpanzee-like sex differences likely continued and were elaborated upon as the foraging regime in early hominins became more sophisticated and dependent on tools.

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