ECOLOGICAL MORPHOLOGY OF *AUSTRALOPITHECUS AFARENSIS*

Traveling Terrestrially, Eating Arboreally

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1. INTRODUCTION

Kinzey (1976, 1977, 1978) was quick to appreciate the utility of integrating systematic ecological research with study of positional behavior and morphology, a synthetic area of scholarly pursuit now distinguished by its own appellation, ecological morphology (Wainwright and Riley, 1994). Primatologists so often focus on food and food-gathering behaviors as keys to understanding primate anatomy because primate activity budgets are dominated by feeding. Across habitats ranging from thicket woodland to closed canopy forest, chimpanzees consistently dedicate half of their activity budget to feeding (Table 1). The next most common activity, "resting," might as well be called "digesting." As a simplifying first-assumption, an ecological perspective takes the view that the hominoid body is a food-getting machine, and ignores the presumably lesser selective roles played by intraspecific aggression and predator avoidance (though predation may be more important for smaller primates: van Schaik, 1983; van Schaik and van Hooff, 1983; van Schaik et al., 1983a, b; van Schaik and van Noordwijk, 1989). This view holds as significant the rarity of predation on hominoids (Cheney and Wrangham, 1986), and that intraspecific agonism is less a threat to survival than is starvation.

For those who find this perspective comfortable, feeding hypotheses (Du Brul, 1962; Jolly, 1970; Tuttle, 1975, 1981; Rose, 1976, 1984, 1991; Stern, 1976; Wrangham, 1980; Tuttle et al., 1991; Hunt, 1994a) for the origin of bipedalism (and/or the divergence of apes and humans) are particularly appealing. Jolly's seed eating hypothesis (1970) maintained that the prevalence of grass seeds in dry habitats selected for a suite of human characteristics. The small diameter and even distribution of grass seeds, he argued, demanded sustained bipedalism during postural collection. Shuffling bipedalism was seen as a high-

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Table 1. Activity budgets for Gombe, Mahale, and Kibale chimpanzees

Activity	Gombe (Hunt, 1989)	Gombe* (Wrangham, 1977)	Mahale (Hunt, 1989)	Kibale (Ngogo) (Ghiglieri, 1984)
Food	49.0	55.7	46.9	57.3
Rest, socialize	36.2	30.3	40.3	31.5
Travel	14.8	13.9	12.8	11.1

*Males only

profile variation on gelada scooting, advantageous for moving between food resources while sustaining a higher reach. The manipulation of small-diameter seeds selected for considerable manual dexterity, preadapting hominids for tool use.

Savanna baboons were observed to be bipedal when feeding on small food items, though grass seeds themselves were not common (Rose, 1976, 1984, 1991). Wrangham (1980) noted that gathering fruit from bushes, in particular, elicited bipedalism among chimpanzees. He offered a locomotor corollary to Rose's small-object feeding hypothesis: bipedal locomotion saves energy by eliminating the action of raising the upper body to feed bipedally after walking between resources quadrupedally. Jolly agreed, suggesting that specialization on small-diameter fruits, rather than seeds, might have been the critical selective pressure that resulted in the evolution of bipedalism (Jolly and Plog, 1987). The small-object postural feeding hypothesis (Rose, 1976, et seq.) derived from the research of Jolly, Rose and Wrangham postulates that bipedalism evolved as a terrestrial feeding posture advantageous for reaching into trees, and that bipedal locomotion evolved to reduce energy costs when traveling between densely packed feeding sites.

Recently, Hunt (1994a, 1996) added an arboreal component to the small-object postural feeding hypothesis, noting that small-object feeding elicits bipedalism in trees as well as on the ground. The small diameter of supports in the small trees in which small-diameter fruits tend to be found appears to encourage bipedalism arboreally as much as fruit diameter. The data from which these conclusions were made are examined below in more detail than is available in Hunt (1992a, 1996).

2. METHODS

I observed chimpanzees for 571 hours at the Mahale Mountains National Park and for 130 hours at the Gombe Stream National Park (Hunt, 1992a). Sixteen thousand three hundred and three instantaneous, 2-minute focal observations were made on 26 well-habituated prime adults spanning all social ranks. Twenty-five positional behavior variables were monitored, including positional mode, behavioral context of the mode, and a number of feeding parameters. Two thousand eighty seven observations were made on Gombe baboons over 83 hours using identical methods.

I identified one of 65 locomotor or postural modes in a target animal at each 2-minute point. I recorded positional behavior, location in canopy, height, size of supports, proximity to others, and food type. Because the chimpanzees were well-habituated, I was able to make observations during all hours of the day, in all contexts, and with no decrease in quality of observation when individuals were on the ground.

Bipedalism was defined as posture or locomotion in which it was judged that more than half of the body weight was borne by the hind limbs in compression. If neither forelimb nor any other part of the body other than the hind feet touched a support, I labeled the mode "unassisted bipedalism." When a forelimb or other body part supported some but less than half of the body weight, I called the mode "assisted bipedalism." I put behaviors for which I judged that more than half of the weight was borne by an abducted forelimb in an "arm-hanging" mode; arm-hanging is not part of this analysis.

3. RESULTS

3.1. Contexts of Chimpanzee Bipedalism

Bipedalism was not a common chimpanzee behavior. Ninety-seven instances of bipedalism among 21 individuals were sampled in 700 hours of observation. No two observations were made in consecutive time-points. *Ad libitum* observations (i.e., observations on non-target individuals, observations between time-points) were used as supplemental evidence, but tables and figures include only systematic observations (i.e., focal individual, time-point samples). By far, the most common context of bipedalism was feeding (Figure 1).

"Move in patch" typically occurred when an individual moved from one harvesting perch in a fruit tree to another within the same tree. Not uncommonly, a target individual did not even cease chewing during the move. If this behavior is pooled with "feed," which seems reasonable, a full 80% of chimpanzee bipedalism was in the context of feeding. The feeding function of bipedalism is dramatically illustrated by comparing bipedal contexts to the daily activity budget. Whereas half of the typical chimpanzee day is occupied with feeding (Table 1), *over 80%* of bipedalism was in a feeding context. Bipedalism was clearly a feeding mode both on the ground and in the trees (Figure 2). Rose found that bipedalism among baboons had the same feeding function (Rose, 1976).

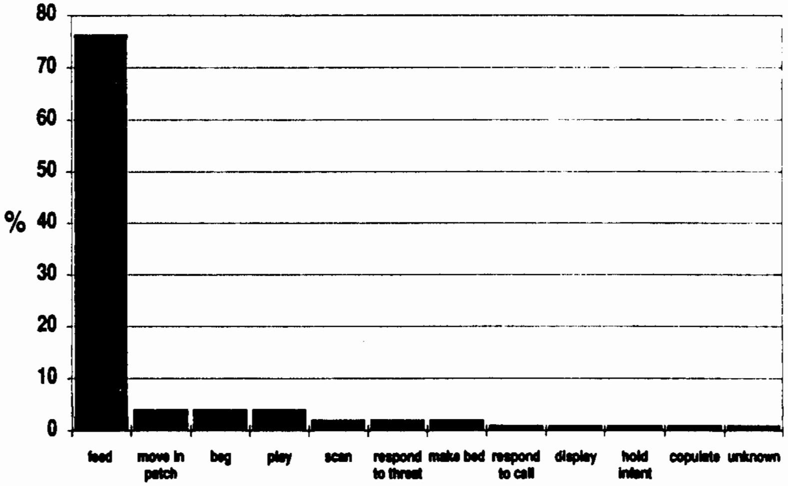

Figure 1. Contexts in which bipedalism was observed in Tanzanian (Gombe and Mahale) chimpanzees. Of 97 observations of bipedalism, feeding and moving within a feeding patch constituted 80.4% of all bipedal behavior.

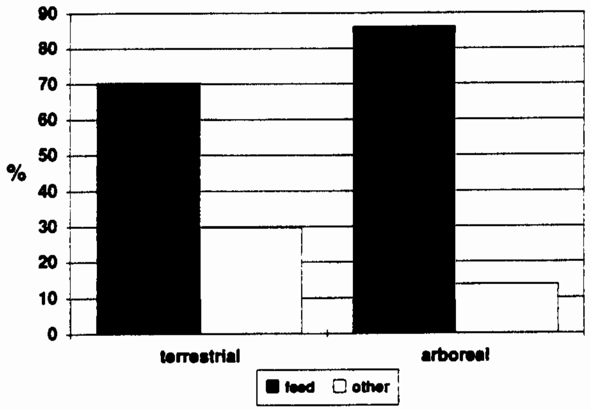

Figure 2. Percentage of bipedalism engaged in during feeding (dark columns) versus other activities (light columns) on the ground (left) and in trees (right). Note that bipedalism functioned as a feeding posture whether chimpanzees were on the ground or in the trees (N=97).

Perhaps the greatest surprise is that after feeding, the next two most common contexts of bipedalism are "beg" and "play" (Figure 1), two behaviors that have not been implicated as selective pressures for the evolution of bipedality (Rose, 1991). Chimpanzees stood bipedally occasionally to get a better view of their environment ("scan"); such scanning was sampled twice, totaling 4.1% of bipedal behavior. "Respond to threat" (4.1%) describes behavior in which an individual stood bipedally, often with one or both forelimbs lightly contacting a tree, to be ready to climb the trunk quickly if a displaying male or an altercation drifted in their direction. Chimpanzees were not uncommonly bipedal to free their hands to manipulate foliage while making a nest, or night bed (4.1%). Chimpanzees sometimes stood bipedally to listen to distant vocalizations (not sampled here, but observed *ad libitum*), and while responding to calls with their own vocalizations (2%). Display, though impressive when it occurs, is actually a rare behavior among chimpanzees (2%). Observations reported here do not include those made in feeding camp, where dominance displays in contests for provisioned food, or in response to unusually large social groupings, have allowed the frequent filming of bipedalism. Chimpanzees often support clinging newborns with a forelimb when walking, but utilizing both forelimbs for support and thereby requiring bipedalism ("hold infant") was rare (2%). Bipedal infant-carrying is probably so rare because infants become capable of gripping mother's fur within days of birth, after which little support is needed. I suspect, based on *ad hoc* observations, that mothers walk little the first few days after giving birth, reducing the need for helping a newborn to cling during its helpless phase. "Copulate" and "unknown" are rare contexts for chimpanzee bipedalism as well (2% each).

3.2. Postural versus Locomotor Bipedalism

Although postural behavior is more common than locomotor behavior in chimpanzees—85% of chimpanzee positional behavior is postural (Table 2)—this balance does not hold for bipedalism, where the postural component predominates. Postural bipedalism made up 95% of bipedal observations (Figure 3). This proportion is identical to that reported by Rose (1976) for baboons.

Table 2. Proportion of locomotion vs. posture among chimpanzees

Population	N	Posture	Locomotion
Mahale	11,471	84.8	15.2
Gombe	2,910	83.3	16.7

3.3. Is Bipedalism a Terrestrial Behavior?

Bipedalism is sometimes assumed to be a behavior naturally elicited by terrestriality. Chimpanzee behavior refutes this assumption. Chimpanzees were actually more likely to be bipedal when arboreal than when terrestrial; 61% of all bipedal behavior was arboreal (Figure 4). Nor is bipedalism limited to large branches in the tree core. Nearly 30% of bipedalism was observed among the terminal branches (Figure 4).

Although terrestriality did not elicit bipedalism, some might expect *locomotor* bipedalism to have been more common terrestrially than arboreally. That was not the case. Over 80% of locomotor bipedalism was arboreal. Of the 6 bipedal locomotor bouts in the sample, 5 were arboreal. Chimpanzees were moving arboreally within a feeding patch in 4 of 6 observations (Figure 1). The fifth observation was making a night nest. The sole terrestrial observation of bipedal locomotion was in the context of "playing" (Figure 1).

3.4. Forelimb-Suspension and Bipedalism Are Linked

Bipedalism was stabilized by an arm-hanging-like (=unimanual forelimb-suspension) support from a forelimb nearly 60% of the time (Figure 5). It appears that the inherent instability of bipedalism (Kummer, 1991) is amplified arboreally by the small, flexible nature of the support. While bipedal posture has two advantages—it increases the height

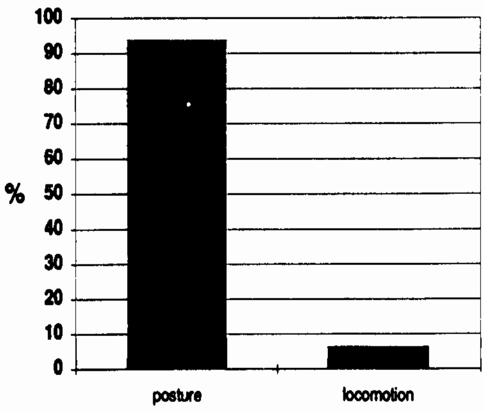

Figure 3. Percent of postural bipedalism compared to locomotor bipedalism. Although locomotion typically makes up 15% of all positional behavior, of 97 observations of bipedalism only 6 (6%) were locomotor.

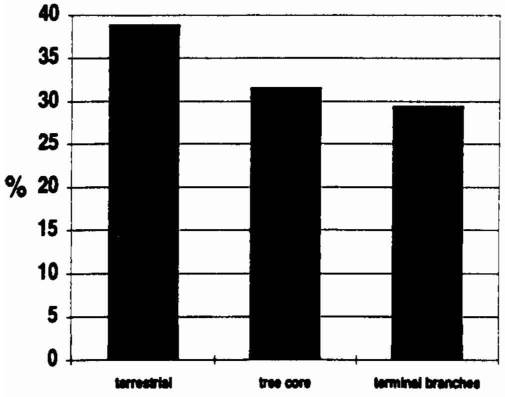

Figure 4. Percent of total bipedal bouts observed on the ground versus in the tree core (central part of tree), versus in the terminal branches (within 1 m of tree edge). Note that only 38% of bipedality was terrestrial. It was arboreality, not terrestriality, that most commonly elicited bipedalism among chimpanzees. Notably, bipedalism was nearly as common among tiny twigs in the terminal branches as it was in the tree core or on the ground. The common assumption that a stable substrate elicits bipedalism is clearly wrong.

of the reach and does not require a "gear-change" expense* (*sensu* Wrangham, 1980) when moving—it requires additional stabilization arboreally to be an effective harvesting posture. Assisted bipedalism involved stabilizing the body with the forelimb in a fully abducted forelimb-suspension gestalt.

The link between forelimb-suspension and bipedalism was most powerful among the terminal branches of trees. A forelimb oriented as in arm-hanging (though bearing less weight) stabilized bipedal posture in 93% of observations among terminal branches (N=27). Bipedalism occurred on significantly smaller branches than did other postures (12.2 cm vs. 15.0 cm, Mann-Whitney U test, U=123,620, P=0.0001, $N_{1,2}$=64,5375), probably because small trees offer few large branches stable enough for sitting or unassisted bipedal standing. In the tree core, or central part of the tree, 52% (N=23) of bipedalism was assisted by a forelimb. Arboreal bipedal locomotion was relatively rare (4.1% of all bipedal episodes), and consisted exclusively of short-stride-length shuffling.

Terrestrial bipedalism was less often assisted, presumably because the firm substrate did not require an extra stabilizing contact point. Terrestrial postural bipedalism was *un*assisted nearly 2/3 of the time, whereas bipedalism was assisted 3/4 of the time arboreally (Figure 6). During terrestrial gathering both hands were often used to harvest fruits. Not infrequently, one hand was used to pull down and hold an otherwise inaccessible fruit-bearing limb, so that the posture became a terrestrial arm-hanging-bipedalism. A few terrestrial bipedal bouts were locomotor bipedalism in the context of moving between feeding sites at the same tree (4.1%). That is, short-distance within-site shuffling, rather than long distance travel, was the most common context for locomotor bipedalism.

Fruit was the most common food resource harvested by bipedal chimpanzees (Figure 7). Among other foods harvested bipedally, only ants might be called common. Manipulation of an ant-dipping tool often required both hands, and therefore sites from which chimpanzees harvested ants tended to be those in which they could work while bipedal.

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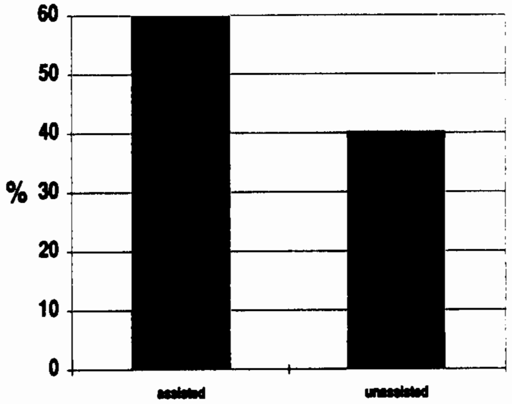
* That is, changing postural or locomotor mode entails some expense. In this case, the cost of raising or lowering the torso is an energetic expense that must be balanced against the increased energy expenditure required to locomote using an inefficient mode (bipedalism). If the difference between the energy expended to locomote bipedally versus quadrupedally is less than the energy expended to lower the torso to allow quadrupedal locomotion, and then raise the torso to a bipedal posture at a new feeding site, there is selection for the individual to locomote bipedally.

Figure 5. Frequency of assisted versus unassisted bipedalism. Nearly 60% of bipedalism in chimpanzees was assisted by a forelimb, most often in an forelimb-suspension-like manner. These figures do not include observations in which the forelimb was judged to be bearing more than half the body weight, a posture labeled arm-hanging (=forelimb-suspension). Supported forelimb-suspension made up another 3.6% of all positional behavior (N=11,393).



3.5. Characteristics of Foods Harvested Bipedally

Bipedalism occurred both terrestrially and arboreally when chimpanzees fed from *Garcinia huillensis, Harungana madagascarensis, Monanthotaxis poggei* and *Grewia* sp. Together these four species of trees constituted 27% of all bipedal feeding episodes and 48% of the bipedal episodes in which the plant material being eaten could be identified. At Mahale, *Garcinia huillensis* rarely reaches 15 m in height. It lives in forest edge habitats

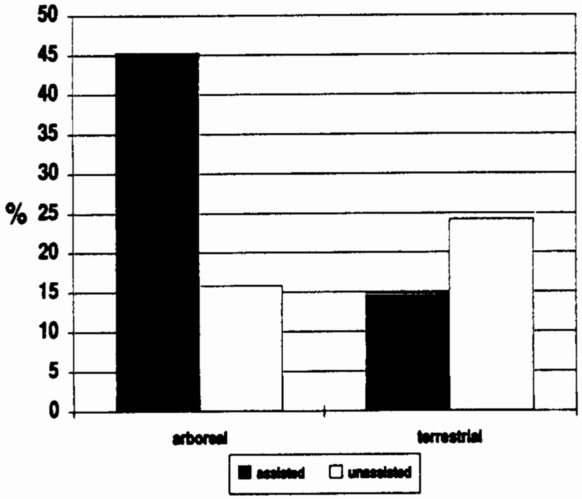


Figure 6. Frequency of assisted (=stabilized by a forelimb) and unassisted (support by hind limbs only) bipedalism in trees versus on the ground. Bipedalism is mostly unassisted on the ground, and mostly assisted in the trees. Unassisted bipedalism should be preferred because it allows a higher feeding rate, since both hands can be used for gathering (Rose, 1976). The higher frequency of assisted bipedalism among terminal branches is presumed to be due to the instability of bipedalism on small-diameter branches.

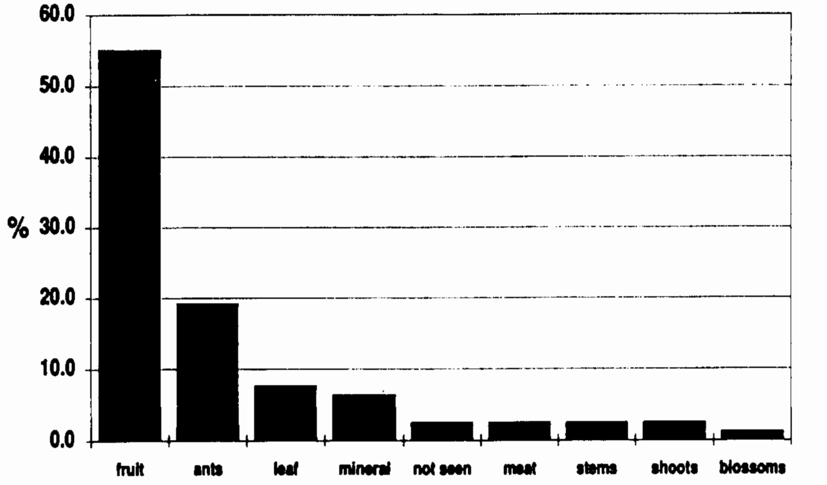


Figure 7. Food items harvested bipedally by chimpanzees. Note that aside from fruits, only ants are commonly harvested bipedally.

and lake-side environments. Its fruits are approximately 2 cm in diameter. *Harungana madagascarensis* is a many-branched understory tree ranging from several meters to 12 m in height. It is widely distributed in East Africa, typically in forest edge environments (Hamilton, 1982). Its fruits are 3–5 mm in diameter. It is typically found in monospecific stands (pers. obs.). *Monanthotaxis poggei* is a 1–2 m tall shrubby plant found in forest edge environments. It often occurs in dense stands. The fruits are approximately 1 cm in diameter. *Grewia* is a 5 m open-forest tree with 1 cm fruits.

All of these trees are short, forest-edge or open-forest trees. The fruits of each species are small (~2 cm, 0.4 cm, 1 cm and 1 cm respectively). The trees occur more often in monospecific stands than trees chimpanzees harvested fruits from in the more closed-forest part of their range. Three of the four (not *Garcinia*) are dry, fibrous, difficult to masticate fruits.

Although I did not sample bipedal gathering *both* arboreally and terrestrially in any other tree, other small trees with small fruits elicited bipedalism either arboreally or terrestrially much more commonly than did large trees. Bipedal food collecting was significantly more common among small (mature height of ≤ 15 m) trees (Figure 8) with small fruits (44 vs. 8, Fisher's Exact test, $P<0.001$, $\chi^2=27.8$, $df=1$), suggesting that fruit diameter and tree height are the critical factors eliciting bipedalism. It is difficult to distinguish between the effects of small trees and small fruits, since all but one small tree also had small (≤ 2 cm) fruit. When plant-foods gathered during bipedal bouts were identified, 28 of 33 fruits (85%) were ≤ 2 cm in diameter (Figure 9).

3.6. Why Do Chimpanzees Climb Trees?

Chimpanzee bipedalism and other behaviors might be argued to be poor predictors of behavior among the more terrestrial hominids. Chimpanzees may forage in trees because they prefer arboreality, whereas australopithecines might have preferred terrestriality. Chimpanzee foraging data suggest that chimpanzees go into trees not because they prefer them, but because their most preferred foods are found there. Early hominids may have been similarly constrained.

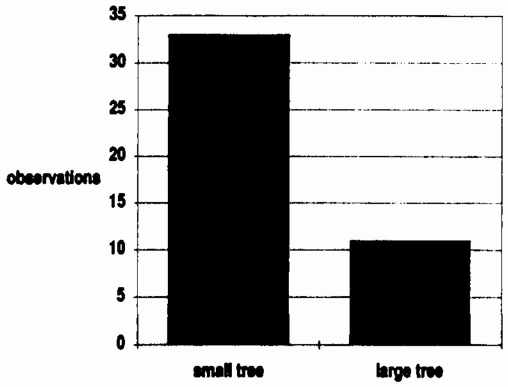


Figure 8. Although chimpanzees fed in small trees (N=1439) and large trees (N=1536) almost equally, most observations of bipedalism were in small trees.

Chimpanzees spent 70% of the time they were in trees feeding. Furthermore, chimpanzees entered terminal branches almost exclusively to feed; feeding constituted nearly 90% of terminal branch activity (Figure 10).

Because different chimpanzees spend differing amounts of time in trees, we may draw some generalizations about arboreality that can provide a model for canopy use in protohominids. Social rank, body size and sex appear to determine arboreality in chimpanzees (Hunt, 1992b, 1994b). Larger chimpanzees spent less time in trees than did smaller chimpanzees. In a multiple regression that included social rank, body size, and canopy height, with social rank factored out, large males positioned themselves lower in the canopy ($R=0.30$, $P<0.0002$, $N=6{,}600$).

When like-rank males of different body sizes are divided into 2 classes, large males fed from smaller tree species than did small males (Figure 11; large and small individuals

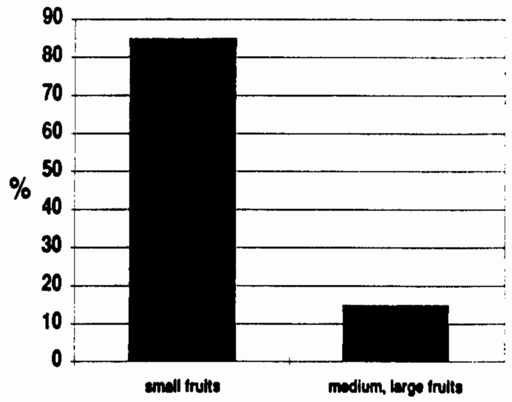


Figure 9. Frequency of bipedalism compared when eating small versus medium-sized and large fruits (N=33). Small fruits are associated with bipedalism.

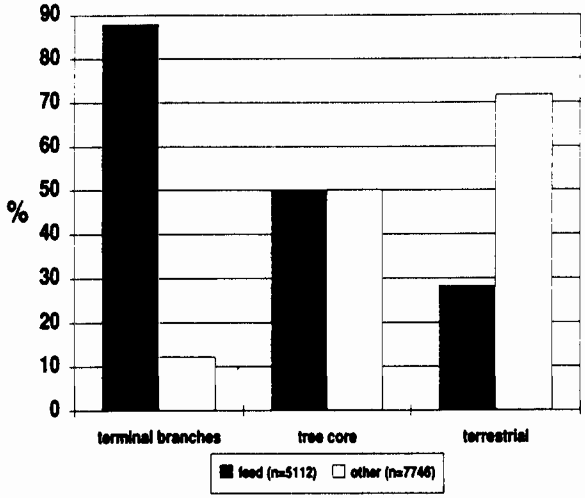


Figure 10. Frequency of feeding in different canopy locations. Chimpanzees do most of their feeding in trees, and they enter terminal branch sites almost exclusively to feed. Apparently there is little food on the ground that chimpanzees prefer.

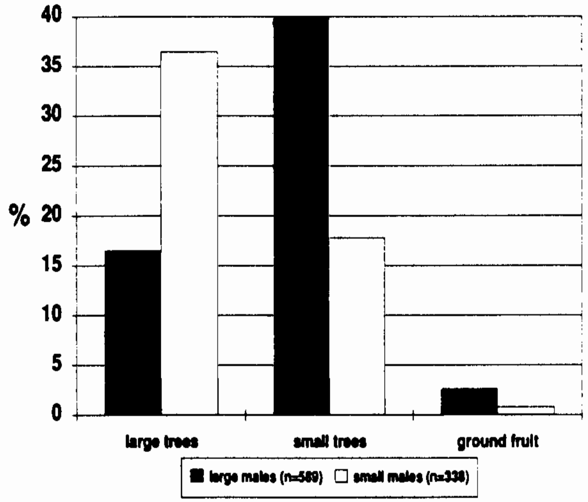


Figure 11. Comparison of feeding site preferences for large and small males, matched for social rank. Large males preferentially fed in small trees and on the ground. Large males minimized climbing, hypothetically because feeding sites lower in the canopy were more valuable to them.

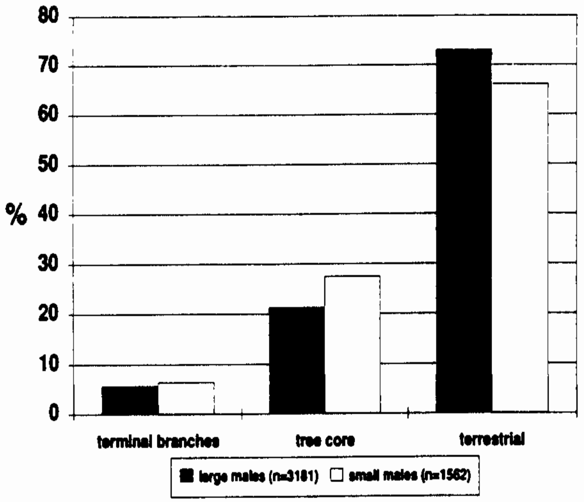


Figure 12. Comparison of canopy location between large and small males, matched for social rank. Large males spent more time on the ground.

were *matched for social rank*). *Matched for social rank*, large males spent more time on the ground than did small males (Figure 12). *Matched for social rank*, large males climbed less often, 0.8% of all behavior versus 3.2% for small males (χ^2=6.65, df=1, P=0.01, N=494, 476). The likeliest explanation for this pattern is that arboreal positional behavior is less demanding for smaller males.

Because these observations are limited to males, sex and infant care did not contribute to the differences. Individual males were matched for social rank, which means that body size alone caused these differences in canopy use. Comparisons of male and female chimpanzees show the same results, though it is not possible to adjust for infant-care and social rank differences. Females spend more time in the trees (Figure 13). It is likely that body size contributes to female arboreality by making arboreality less energetically demanding. Arboreality may also be predator-avoidance strategy for females, though the evidence from males suggests not.

4. AUSTRALOPITHECINE ECOLOGY: CRANIODENTAL EVIDENCE

Craniofacial shape, robusticity of the masticatory apparatus, cusp morphology, tooth size, enamel thickness, and incisor size are among the evidence that has been brought to bear on reconstructing australopithecine diets, most notably in a synthesis by Kay (1985). Although the correlation between each of these variables and diet is low, if considered together they provide a detailed model of australopithecine diet.

Molar dental microwear has not been examined in *Australopithecus afarensis*, leaving *A. africanus* microwear as an admittedly unsatisfactory stand-in (Walker, 1981; Teaford and Walker, 1984; Grine and Kay, 1988; Kay and Grine, 1988; Teaford, 1994). The

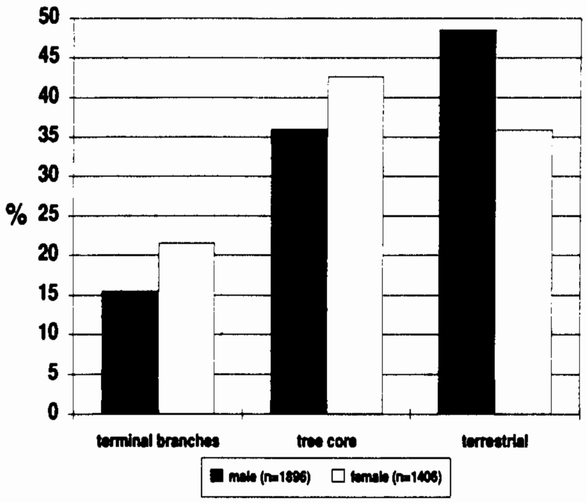


Figure 13. Comparison of canopy location in males and females. Females are more arboreal and spend more time among the terminal branches.

similarity of dentition of the two (Tobias, 1980), however, makes this unsatisfactory proxy more acceptable. Walker (1981) interpreted the *Pan*- or *Mandrillus*-like microwear of both *A. africanus* and *A. robustus* as meaning they were frugivores. Kay and Grine (1988) found that in both microwear feature width and relative frequency of pits versus scratches suggested the same thing. Molar microwear feature width falls between *Alouatta palliata* and *Cebus nigrivittatus* (Kay and Grine, 1988). Pit:scratch frequency comparisons place them between orangutans and chimpanzees (Kay and Grine, 1988). With the exception of howlers, these primates eat fruit at least 57% of the time (Table 3). Howlers concentrate on leaves. All four species include at least 10% leaves in their diet. With the exception of pith/herbs for chimpanzees, other dietary items are uncommon.

Pit frequencies for *Australopithecus* fall intermediate between orangutans and chimpanzees suggesting a low frequency of seed-eating and oral nut-cracking (Kay and Grine, 1988; Table 3). Orangutans open nuts orally, though it is not clear how common the behavior is; chimpanzees rarely crack nuts orally. Other evidence suggests that nut-cracking was not common in australopithecines. Peters (1987) argued that a small modelled gape in australopithecines and a relative lack of crenulations suggest low levels of nut-cracking. Although some nut-cracking cannot be ruled out, a small gape and unpitted teeth suggest that *A. africanus* and *A. robustus* were not specialized for this dietary item. A high frequency of pitting is also found in animals that eat foods that have adhering grit (Teaford and Walker, 1984; Teaford, 1994). The low frequency of pitting in australopithecine molars makes the utilization of roots and tubers and other below-ground resources with adhering grit unlikely.

Table 3. Primate diets

Species	Insects	Leaf	Meat	Fruit	Piths/herbs	Flowers	Bark	Other
Pan troglodytes[1]	5.6	10.3	1.0	57.0	22.6	0.7	0.0	–
Alouatta palliata[2]	0.0	64.0	0.0	12.0	0.0	18.0	0.0	0.0
Pongo pygmaeus[3]	1.0	26.0	0.0	58.0	–	–	13.0	2.0
Cebus spp.[4]	20.0	15.0	0.0	65.0	0.0	0.0	0.0	–
Mean	7.0	29.0	0.3	48.0	6.0	5.0	3.0	1.0

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

[2] Glander (1978); feeding time.

[3] Rodman (1984); feeding time, Kutai, Kalimantan 40,022 min. observations.

[4] Hladik and Hladik (1969); dry weight of stomach contents; records for *Cebus nigrivittatus* are 100% fruit (Fooden, 1964).

Macrowear adds an exclamation point to indications of some leaf-eating in australopithecines. In *A. afarensis* the incisors are unevenly worn so that the occlusal surface has an undulating appearance in frontal view (Puech et al., 1984). Such wear results from stripping, such as pulling a twig through the mouth to remove leaves.

An objective but somewhat crude estimate of the australopithecine diet might be gained by simply averaging the frequency of dietary items in primates that have microwear most similar to australopithecines (Table 3). Frugivory is suggested, with leaves as an important secondary component of the diet.

Dental microwear of *A. africanus* narrows the possible australopithecine diet somewhat from what is indicated by dental morphology.† Among primates, summed (i.e., I1 and I2) incisor size is correlated with food object size and are larger in frugivores than gramnivores or folivores (Hylander, 1975; Kay and Hylander, 1978). Primates that eat small fruits have small incisors. Fruits require incisal penetration of an often fibrous and/or abrasive husk; leaves do not. The extra wear on incisors cause by fruit processing requires larger incisors to maintain a functioning incisal edge in older animals. A regression of the natural logarithm of maxillary incisor width and log body weight for 57 primates yields a regression line with good separation between principally frugivorous cercopithecines and principally folivorous colobines (Hylander, 1975; Kay and Hylander, 1978). Australopithecines fall below both the regression line for apes alone (Kay 1985) and for pooled primates (Kay and Hylander, 1978; using McHenry, 1992 body weights).

The two earliest hominid species are not represented by lateral incisors, and cannot be directly compared to Kay and Hylander's (1978) results. Both, however, have I^1's quite near the mean of *A. afarensis* (10.63 mm, White et al., 1981). The I^1 of *Ardipithecus ramidus* is 10.0 mm (White et al., 1994), and the I^1 of *A. anamensis* is 10.5 mm (Leakey et al., 1995). The small early australopithecine incisor dimensions as expressed in their relation to the primate and ape regression line suggest that they consumed smaller food items than extant primate frugivores, including orangutans and chimpanzees.

Australopithecus afarensis molar areas fall above the regression line of cheek tooth area compared to body mass (log-log plot) for hominoids (Kay, 1985). The residual is nearly equidistant between orangutans and *A. africanus* (McHenry, 1984; Kay, 1985), and well above the values for chimpanzees. Among extant primates, species that open nuts and seeds and/or eat hard-to-masticate fibrous fruits have large molars (orangutans and capuchins, Kay, 1981, 1985).

Australopithecines have thick enamel (Kay, 1983), even thicker than the thickest-enamelled of extant primates (i.e., mangabeys, capuchins, and orangutans). Thick enamel is correlated with consumption of hard and brittle foods (Teaford, 1985) such as seeds,

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† Newly discovered fossils (*Ardipithecus ramidus*, White et al., 1995; *A. anamensis*, Leakey et al., 1995) are yet to be thoroughly evaluated, but where possible they are discussed. Otherwise, discussion centers on the more abundant and better studied fossils of *A. afarensis* and *A. africanus*.

nuts or hard-husked fruits. Thick enamel also occurs among mammals that consume foods that are abrasive, or foods that have adhering grit, as subterranean items do. Chimpanzees and gorillas have thin enamel with well-developed shearing blades (Kay, 1981), a morphology correlated with folivory and believed to function to finely comminute leaves into a fine, more digestible gruel. Because australopithecines have thicker enamel and shorter shearing blades than do chimpanzees and gorillas (Kay 1983), their diet must have contained considerably fewer leaves and piths than does the diet of African apes.

Compared to apes, *A. afarensis* has taller, more squared-off, more robust zygomae (White et al., 1981). The diameter of the mandibular corpus is also greater. A forward shift of the zygomae and thickening of the mandibular corpus mean that australopithecines could produce greater occlusal forces than those of extant apes, or could sustain high masticatory pressures for longer (Jolly, 1970). Feeding on hard-to-masticate items is suggested. Reduced prognathism suggests a reduced gape for australopithecines compared to apes.

If we consider all of this evidence at once, a rather precise modelling of the australopithecine diet is possible. Small incisors and the small gape, compared to living apes, suggest that australopithecines consumed smaller food items than do African apes or orangutans. Molar microwear suggests that australopithecines rarely engaged in nut-cracking, and that they did not consume below-ground foods. Their microwear suggests a frugivorous diet supplemented with piths or leaves. Their low-cusped molars with short shearing blades, however, offer contrary evidences, suggesting a lower proportion of piths and leaves. Large, thickly enameled molars suggests a specialization on fibrous fruits. A robust face suggests hard to masticate food items, again implying a specialization on fibrous fruits. Australopithecine craniodental fossils unambiguously suggest a diet high in small-diameter, fibrous fruits. The proportion of leaves in the diet is less clearly indicated, but it seems likely they were an important dietary item, though one clearly less important than fruits.

5. AUSTRALOPITHECINE POSITIONAL BEHAVIOR

5.1. Postcranial Evidence for Arm-Hanging.

The australopithecine torso is broad, shallow and cone-shaped (Schmid, 1983, 1991), the glenoid fossa cranially oriented (Robinson, 1972; Stern and Susman, 1983), the cross sectional area of the vertebral column quite small (Robinson, 1972; Jungers, 1988), and the brachial index chimpanzee-like (Kimbel et al., 1994). These features are adaptations to arm-hanging (Hunt, 1991a).

The australopithecine wrist is mobile (McHenry, 1991a), an adaptation that reduces stress on the wrist when suspending from vertical supports (Hunt, 1991a). Thin twigs bend to vertical when chimpanzees hang from them, necessitating a mobile wrist to maintain grip.

5.2. Postcranial Evidence for Vertical Climbing

The bicipital groove in which the biceps tendon rests is large (Robinson, 1972; Lovejoy et al., 1982), implying a large biceps muscle. The supracondylar ridge (proximal attachment of the extensor carpi radialis and brachioradialis muscles) is huge (White et al., 1993). The large muscles implied by these skeletal features suggest an ability to perform a powerful pull-up action, seen in extant hominoids most often during vertical climbing (Hunt, 1991b).

The convex joint surface of the *A. afarensis* medial cuneiform indicates a rudimentary ablity to abduct the first toe (Stern and Susman, 1983; Deloison, 1991; pers. obs.) *contra* Latimer and colleagues (Latimer et al., 1982). *Australopithecus afarensis* also has long, curved toes (Tuttle, 1981; Stern and Susman, 1983) and an antero-posteriorly short, rounded lateral femoral condyle (in the smaller specimens; Tardieu, 1983; McHenry, 1986, 1991a). A strongly developed fibular groove for the tendon of the peroneus longus muscle suggests ape-like great-toe flexion (Tuttle, 1981; Deloison, 1991), as might be used to grip branches when standing arboreally or climbing. Alternatively, a robust peroneus longus muscle may stabilize a more mobile foot, or support a ligamentously poorly supported arch; if so, bipedalism would be that much less energetically efficient, since muscular support would be necessary for toe-off, rather than a non-energy-consuming ligamentous support. A plantar set, or at least greater mobility (Latimer and Lovejoy, 1990), of the ankle allows full plantarflexion of the foot. Gombe and Mahale chimpanzees plantarflexed their feet when they used their toes grip a branch to support body weight with the hind limb in tension. Curved pedal phalanges (Tuttle, 1981) and a *third* pedal digit longer than the first or second (Stern and Susman, 1983) are gripping adaptations. Such pedal gripping, especially with the lateral 4 toes only, is used by Tanzanian chimpanzees during arm-hanging to increase stability among slender terminal branches. Climbing adaptations in the hindlimb are not limitied to the foot. A long moment arm for the hamstrings (Stern and Susman, 1983) increases the power of hip extension, implying a better climbing adaptation than in modern humans.

5.3. Postcranial Evidence for Both Arm-Hanging and Vertical Climbing

The deltoid tuberosity is large and laterally flaring, suggesting a large deltoid (White et al., 1993; Kimbel et al., 1994), and the coracoid process (proximal attachment of biceps brachii and distal attachment of pectoralis minor muscle) is large (Robinson, 1972). Chimpanzees use the deltoid to raise the arm during vertical climbing and when reaching out to pluck fruits when arm-hanging.

Australopithecine fingers are curved and have large flexor sheath ridges (Stern and Susman, 1983). The fingers are more human-like than ape-like in length; but the thumb is short (=chimpanzee-like) with a chimpanzee-like articulation (Tuttle, 1981; McHenry, 1991a). Arm and leg length proportions are intermediate between those of modern humans and chimpanzees, even when the diminutive stature of the fossils is considered (Jungers, 1982, 1991). These features are adaptations to powerful gripping of cylindrical surfaces, such as occurs in chimpanzees only during arm-hanging and vertical climbing (Hunt, 1992a).

5.4. Postcranial Evidence for Bipedalism

In both general morphology and detail, the pelvis and the hind limb morphology of *A. afarensis* and later hominids indicate bipedalism (Johanson and Edey, 1981; Lovejoy, 1988; Latimer and Lovejoy, 1989, 1990; McHenry, 1991a). The lumbar vertebrae are lordotic (Abitbol, 1987), the sacral alae are expanded, and the pelvis has a very human gestalt (Lovejoy, 1988; McHenry, 1991a). The femur has a deep patellar groove, and at least some specimens have an elliptical lateral condyle. The calcaneus is essentially modern

(Latimer and Lovejoy, 1989). The great toe is robust and the foot has well developed transverse and longitudinal arches (Latimer and Lovejoy, 1990; Langdon et al., 1991).

5.5. Morphology at Odds with Refined Locomotor Bipedalism

Other features in *A. afarensis* suggest a bipedalism that is not as refined as that of modern humans. Although the os coxae are human-like in appearance, *A. afarensis* has smaller sacro-iliac ligaments than modern humans (Stern and Susman, 1983). The width of the AL 288-1 pelvis is proportionally greater than the femoral neck length, suggesting that when compared to modern humans, *A. afarensis* had a greater joint reaction force at the hip and a lower mechanical advantage for muscles that prevent the hip from collapsing when one foot is off the ground (Jungers, 1991). A relatively small acetabulum/femoral head in australopithecines compounds the stresses caused by wide hips, creating even more stress in the hip joint.

Wide hips also cause the moment arm of the body weight of *A. afarensis* to be increased over that of modern humans, increasing the stress on the diaphyseal/femoral neck junction when bearing weight (Hunt, 1994a) and decreasing energetic efficiency during walking by requiring greater muscular activity (Jungers, 1991). The extraordinarily wide hips of AL 288 (Berge and Kazmierczak, 1986; Rak, 1991) and STS 14 (Robinson, 1972) are not obstetric adaptations (Rosenberg and Trevathan, 1995; Stoller, 1995). The broad hips of these hominids are due mostly to an unusually broad pelvic inlet. The pelvic index averaged 77.6 for modern human females (Tague and Lovejoy, 1986), but is 57.6 in AL 288-1. Although a large biacetabular breadth in modern humans is a necessary adaptation for giving birth to large-headed offspring, cephalopelvic reconstruction of AL 288-1 shows a considerable gap between the fetal head and pelvic inlet walls opposite the acetabula (Figure 14). In other words, the pelvis of australopithecines is much broader than could possibly be necessary for parturition.

Other features suggest reduced locomotor competence as well. *Australopithecus afarensis* has quite short hind limbs for its weight and height, suggesting greater energy expenditure per unit distance traveled (Jungers, 1991). The lumbar vertebrae and lumbosacral articular surface of other australopithecines are small, whether in proportion to body weight, hip width or nearly any other measure that has been attempted (Robinson, 1972; Jungers, 1988, 1991; McHenry, 1991a; Rak, 1991).

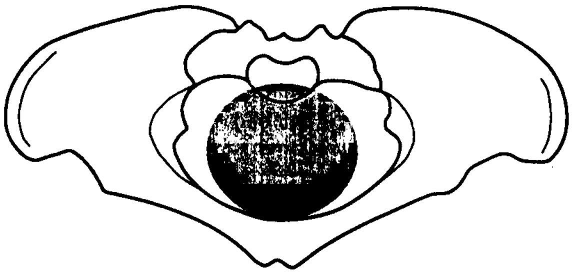

Figure 14. Reconstructed pelvis of *A. afarensis* (redrawn from Lovejoy and Tague, 1986 and from Lovejoy, 1988) with a hypothetical fetal head superimposed. The pelvis is much broader than necessary for parturition. Broad hips and short hind limbs are hypothesized to function to lower the center of gravity. A low center of gravity confers greater balance, which is particularly valuable when standing or moving on small and therefore unstable arboreal supports.

6. DISCUSSION

We can bring four lines of evidence to bear on the question of australopithecine bipedalism: (1) australopithecine craniodental data; (2) australopithecine postcranial anatomy; (3) the contexts that elicit bipedalism in living animals (chimpanzees in this case); and, (4) differences between large and small chimpanzees.

Molar feature width and low pitting argue strongly against nut-cracking or specialization on below-ground resources for australopithecines. Fruit and leaves are most consistent with their microwear, but these data conflict with dental morphology. Thick enamel, low molar shearing quotients, large molar areas and robust craniofacial morphology indicate a diet high in hard items, but not particularly high in leaves or piths. Because below-ground resources are precluded by the microwear data, and because nut-cracking is not strongly indicated, hard-husked and/or fibrous fruits that require extensive mastication fit best with the microwear data. Small incisor breadths indicate an australopithecine specialization on small diameter food items (Rose, 1976).

If australopithecines were frugivores, as these craniodental data suggest, they could forsake arboreality only if they lived in a habitat where most fruits were found in bushes shorter than about 2 m. Is there evidence that australopithecines had forsaken arboreality? In a word, no.

Above the waist, australopithecines are intermediate in morphology between chimpanzees and humans. Chimpanzees are adapted to unimanual suspension (arm-hanging) and vertical climbing. The positional repertoire of *A. afarensis* might then be reconstructed as containing about half as much arboreal activity as chimpanzees. Curved, powerful fingers accord well with an arm-hanging adaptation. Short fingers suggest that the supports from which *A. afarensis* suspended themselves were of smaller diameter than those commonly used by extant chimpanzees. Small trees with small branches are indicated as the most common feeding sites for australopithecines.

Below the waist, australopithecines had short limbs, long, curved toes, a more gripping great toe than that of modern humans, and extraordinarily wide hips. Short lower limbs bring the most massive part of the body, the torso, closer to the substrate, thereby lowering the center of gravity. Wide hips, especially in combination with the cone-shaped torso, lowers the center of gravity by increasing the mass of the lower portion of the torso, essentially allowing internal organs to rest lower in the torso. Both these features increase arboreal competence by making balancing on branches easier. Among apes, gripping toes are frequently used to stabilize the body. The strong toes of *A. afarensis* may have been used to grip small twigs during arboreal bipedal gathering.

Smaller joint surface areas and a less robustly ligamented pelvis than in modern humans indicate that *A. afarensis* was more prone to fatigue or injury during powerful and sustained bipedal locomotion. Bipedal carrying, with its imposition of greater stress on the musculoskeleton, must have been less common than it is in modern humans (Jungers, 1988, 1991; Hunt, 1994a). *Australopithecus afarensis* probably engaged in less sustained bipedal walking and less bipedal carrying than modern humans do.

Bipedalism is neither a locomotor behavior nor strictly a terrestrial behavior among chimpanzees; over 90% of Mahale chimpanzee bipedalism was postural, and more than half of all their bipedal episodes were arboreal. Among Mahale chimpanzees, bipedalism was overwhelmingly a feeding posture; 80% of all bipedalism occurred during feeding. Other behaviors that have been hypothesized to have exerted selective pressure on prebipedal protohominids to become bipedal—searching for predators, threatening, hunting—each constituted <5% of bipedal episodes among Mahale chimpanzees.

Chimpanzees fed bipedally from short trees with small fruits. Bipedal standing allowed individuals to reach higher in trees when feeding terrestrially, to bring more fruits within their reach. It also allows faster gathering (Jolly, 1970; Jolly and Plog, 1987). By using both hands, a flow of fruits can be maintained that takes full advantage of chimpanzee chewing capacities. This is particularly important for small fruits, since it is picking, not chewing, that constrains feeding rate. Terrestrial gathering is practical only when feeding from short trees or bushes. Even the lowest branches of trees >15 m were too high for the fruit to be reached. In some trees (e.g., *Harungana*) chimpanzees held the tree lower with one forelimb while they fed with the other. The effect was a terrestrial arm-hanging/bipedalism.

Small trees elicited bipedalism when they were fed from arboreally as well, but for different reasons. The small diameter of the branches discouraged sitting as a collecting posture. The small twigs in these trees bent to vertical under the weight of chimpanzees, making the substrate impossible to sit on. Among the terminal branches of these trees chimpanzees used as many contact points as possible. By extending the hip and fully abducting the arm they maximized the reach so that a larger number of branches were within grasp.

Short-stride-length arboreal movement and terrestrial bipedal shuffling are advantageous for collecting fine-grained resources such as small evenly distributed fruits in small trees. Frequent short distance (i.e., ~1 m) travel is necessary when harvesting small fruits both in the trees and on the ground. Feeding sites are depleted quickly so that postures that allow a switch to locomotion with little energy cost are preferred (Wrangham, 1980). Sitting postures during feeding are often engaged in on small-diameter supports, yet a squatting shuffling (gelada-style) to an adjacent branch is impossible. When bearing weight, terminal branch supports are often bent to such a degree that they are a meter or more lower than otherwise. Movement to adjacent small branches can be accomplished more effectively with bipedal locomotion, since it allows a hindlimb to be raised to the as yet unweighted level of the adjacent branch. Bipedal locomotion on small substrates is much like walking on an extremely soft cushion. Legs must be raised very high with each step. It is not practical for a harvester to avoid the costs of small branch collecting by breaking off a branch and retreating to a more stable perch, since any one branch contains too little food to constitute a meal. The combination of greater stability and easier transition to locomotion makes bipedalism a favored collecting strategy among small branches common among smaller trees.

Among chimpanzees, large individuals spent more time on the ground, less time among the terminal branches, and fed from smaller trees. Because vertical climbing is disproportionally more expensive for large animals (Taylor et al., 1972), the most straightforward interpretation of these data is that large individuals must balance the benefits of climbing (obtaining high-quality foods) with the costs of vertical ascent (a larger energy expenditure per unit weight, compared to smaller individuals). Because climbing is more expensive for big chimpanzees, arboreal foods are less valuable. As large-bodied primates to begin with, we might expect that compared to other primates chimpanzees prefer to minimize climbing, and large chimpanzees make more compromises to minimize climbing than do small chimpanzees. This leads to the expectation that adult male australopithecines should forage on the ground most often, since their body weight was nearly double that of females (McHenry, 1991b). Females might be expected to be more arboreal.

7. CONCLUSION

The synthesis of chimpanzee ecology and australopithecine functional morphology yields a postural feeding hypothesis that suggests that australopithecines were semi-arboreal, postural bipeds that specialized on gathering small, hard-husked fruit in short-statured trees.

Large males hypothetically found it more advantageous to gather terrestrially, whereas females were about half as arboreal as chimpanzees. Short hind limbs and wide hips are splendid adaptations for tree movement because they lower the center of gravity, increase stability, and improve climbing mechanics.

Bipedalism is hypothesized to have evolved initially in conjunction with arm-hanging, as a feeding posture effective for collecting small diameter fruits from small trees. Refinements to allow efficient bipedalism in the pelvis and hind limb of *A. afarensis* suggest that their terrestrial locomotion was fully bipedal, albeit less efficient than the bipedalism of modern humans. This suggests that their mode of travel on the ground was fully upright bipedalism.

Chimpanzees tend to travel terrestrially, and to feed arboreally. The woodland and open-forest habitat suggested for australopithecines would have required even more terrestrial movement than is found among extant chimpanzees. The ecological morphology of australopithecines suggests that they traveled bipedally terrestrially, but fed arboreally using a number of chimpanzee-like suspensory behaviors in addition to sitting and bipedal standing.

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REFERENCES

Abitbol M (1987) Evolution of the lumbosacral angle. Am. J. Phys. Anthropol. *72*:361–372.

Berge C, and Kazmierczak J-B (1986) Effects of size and locomotor adaptations on the hominid pelvis: Evaluation of australopithecine bipedality with a new multivariate method. Folia Primatol. *46*:185–204.

Cheney DL, and Wrangham RW (1986) Predation. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds.): Primate Societies. Chicago: University of Chicago Press. pp. 227–239.

Deloison Y (1991) Les Australopithèques marchaient-ils comme nous? In Y Coppens and B Senut, (eds.): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp. 177–186.

Du Brul EL (1962) The general phenomenon of bipedalism. Am. Zool. *2*:205–208.

Fooden J (1964) Stomach contents and gastro-intestinal proportions in wild-shot Guinan monkeys. Am. J. Phys. Anthropol. *22*:227–232.

Gantt DG (1983) The enamel of Neogene hominoids: Structural and phyletic implications. In RL Ciochon and RS Corruccini (eds.): New Interpretations of Ape and Human Ancestry. New York: Plenum Press, pp. 249–298.

Ghiglieri MP (1984) The Chimpanzees of Kibale Forest. New York: Columbia University Press.

Glander KE (1978) Howling monkey's feeding behaviour and plant secondary compounds: A study of strategies. In GG Montgomery (ed.): The Ecology of Arboreal Folivores. Washington: Smithsonian Inst. Press, pp. 561–573.

Grine FE, and Kay RF (1988) Early hominid diets from quantitative image analysis of dental microwear. Nature. *333*:65–68.

Hamilton AC (1982) Environmental History of East Africa: A Study of the Quaternary. London: Academic Press.

Hladik A, and Hladik CM (1969) Rapports trophiques entre vegetation et primates dans la foret de Barro Colorado (Panama). Terre et Vie *23*:25–117.

Hunt KD (1989) Positional behavior in *Pan troglodytes* at the Mahale Mountains and Gombe Stream National Parks, Tanzania. Ph.D. Dissertation., University of Michigan.

Hunt KD (1991a) Positional behavior in the Hominoidea. Int. J. Primatol. *12*:95–118.

Hunt KD (1991b) Mechanical implications of chimpanzee positional behaviour. Am. J. Phys. Anthropol. *86*:521–536.

Hunt KD (1992a) Positional behaviour of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. Am. J. Phys. Anthropol. *87*:83–107.

Hunt KD (1992b) Social rank and body weight as determinants of positional behavior in *Pan troglodytes*. Primates *33*:347–357.

Hunt KD (1994a) The evolution of human bipedality: Ecology and functional morphology. J. Hum. Evol. *26*:183–202.

Hunt KD (1994 b) Body size effects on vertical climbing among chimpanzees. Int. J. Primatol. *15*:855–865.

Hunt KD (1996) The postural feeding hypothesis: An ecological model for the evolution of bipedalism. S. Afr. J. Sci. *92*:77–90.

Hylander WL (1975) Incisor size and diet in anthropoids with special reference to Cercopithecidae. Science *189*:1095–1098.

Johanson DC, and Edey M (1981) Lucy: The Beginnings of Humankind. New York: Simon and Schuster.

Jolly CJ (1970) The seed-eaters: A new model of hominid differentiation based on a baboon analogy. Man. *5*:1–26.

Jolly CJ and Plog F (1987) Physical Anthropology and Archeology. New York: Knopf.

Jungers WL (1982) Lucy's limbs: Skeletal allometry and locomotion in *Australopithecus afarensis*. Nature. *297*:676–678.

Jungers WL (1988) Relative joint size and hominoid locomotor adaptations with implications for the evolution of hominid bipedalism. J. Hum. Evol. *17*:247–265.

Jungers WL (1991) A pygmy perspective on body size and shape in *Australopithecus afarensis* (AL 288–1, "Lucy"). In Y Coppens and B Senut (eds): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp. 215–224.

Kay RF (1981) The nut-crackers – A new theory of the adaptations of the Ramapithecinae. Am. J. Phys. Anthropol. *55*:141–151.

Kay RF (1985) Dental evidence for the diet of *Australopithecus*. Ann. Rev. Anthropol. *14*:15–41.

Kay RF, and Grine FE (1988) Tooth morphology, wear and diet in *Australopithecus* and *Paranthropus* from southern Africa. In F Grine (ed.): Evolutionary History of the Robust Australopithecines. Chicago: Aldine, pp. 427–447.

Kay RF, and Hylander WL (1978) The dental structure of mammalian folivores with special reference to Primates and Phalangeroidea (Marsupialia). In GG Montgomery (ed.): The Biology of Arboreal Folivores. Washington, D.C.: Smithsonian Inst. Press, pp. 173–191.

Kimbel WH, Johanson DC, and Rak Y (1994) The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. Nature *368*:449–451.

Kinzey WG (1976) Positional behavior and ecology in *Callicebus torquatus*. Yrbk. Phys. Anthropol. *20*:468–480.

Kinzey WG (1977) Diet and feeding behaviour of *Callicebus torquatus*. In TH Clutton-Brock (ed.): Primate Ecology. London: Academic Press, pp. 127–152.

Kinzey WG (1978) Feeding behaviour and molar features in two species of titi monkey. In DJ Chivers and J Herbert (eds.): Recent Advances in Primatology, Vol. 1. London: Academic Press, pp. 373–385.

Kummer B (1991) Biomechanical foundations of the development of human bipedalism. In Y Coppens and B Senut (eds): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp. 1–8.

Langdon JH, Bruckner J, and Baker HH (1991) Pedal mechanics and bipedalism in early hominids. In Y Coppens and B Senut (eds): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp. 159–167.

Latimer B (1991) Locomotor adaptations in *Australopithecus afarensis*: The issue of arboreality. In Y Coppens and B Senut (eds.): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp. 169–176.

Latimer B, and Lovejoy CO (1989) The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. Am. J. Phys. Anthropol. *78*:369–386.

Latimer B, and Lovejoy CO (1990) Hallucal tarsometatarsal joint in *Australopithecus afarensis*. Am. J. Phys. Anthropol. *82*:125–133.

Latimer B, Lovejoy CO, Johanson DC, and Coppens, Y (1982) Hominid tarsal, metatarsal and phalangeal bones recovered from the Hadar formation: 1974–1977 collections. Am. J. Phys. Anthropol. *53*:701–719.

Leakey MG, Feibel CS, McDougall I, and Walker AC (1995) New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature *376*:565–571.

Lovejoy CO (1981) The origin of man. Science. *211*:341–350.

Lovejoy CO (1988) The evolution of human walking. Sci. Am. *259*:118–125.

Lovejoy CO, Johanson DC, and Coppens Y (1982) Hominid upper limb bones recovered from the Hadar Formation: 1974–1977 collections. Am. J. Phys. Anthropol. *57*:637–649.

McHenry HM (1986) The first bipeds: A comparison of the *A. afarensis* and *A. africanus* postcranium and implications for the evolution of bipedalism. J. Hum. Evol. *15*:177–191.

McHenry HM (1991a) First steps? Analyses of the postcranium of early hominids. In Y Coppens and B Senut (eds): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp. 133–141.

McHenry HM (1991b) Sexual dimorphism in *Australopithecus afarensis*. J. Hum. Evol. *20*:21–32.

McHenry HM (1992) Body size and proportions of early hominids. Am. J. Phys. Anthropol. *87*:407–431.

Peters CR (1987) Nut-like oil seeds: Food for monkeys, chimpanzees, humans and probably ape-men. Am. J. Phys. Anthropol. *73*:333–363.

Puech P-F, and Albertini H (1984) Dental microwear and mechanisms in early hominids from Laetoli and Hadar. Am. J. Phys. Anthropol. *65*:87–92.

Rak Y (1991) Lucy's pelvic anatomy: Its role in bipedal gait. J. Hum. Evol. *20*:283–290.

Robinson JT (1972) Early Hominid Posture and Locomotion. Chicago: University of Chicago Press.

Rodman PS (1984) Foraging and social systems of orangutans and chimpanzees. In PS Rodman and JGH Cant (eds.): Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys, and Apes. New York: Columbia University Press, pp. 134–160.

Rose MD (1976) Bipedal behaviour of olive baboons (*Papio anubis*) and its relevance to an understanding of the evolution of human bipedalism. Am. J. Phys. Anthropol. *44*:247–261.

Rose MD (1984) Food acquisition and the evolution of positional behaviour: The case of bipedalism. In DJ Chivers , BA Wood, and A Bilsborough (eds.): Food Acquisition and Processing in Primates. New York: Plenum Press, pp. 509–524.

Rose MD (1991) The process of bipedalization in hominids. In Y Coppens and B Senut, (eds): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp. 37–48.

Rosenberg KR, and Trevathan W (1995) Bipedalism and human birth: The obstetrical dilemma revisited. Evol. Anthropol. *4*:161–168.

Sarmiento EE (1988) Anatomy of the hominoid wrist joint: Its evolutionary and functional implications. Int. J. Primatol. *9*:281–345.

Schmid P (1983) Eine Reconstrucktion des skelettes von A.L. 288–1 (Hadar) und deren konsequenzen. Folia Primatol. *40*:283–306.

Schmid P (1991) The trunk of the Australopithecines. In Y Coppens and B Senut, (eds): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp. 225–234.

Stern JT, Jr (1976) Before bipedality. Ybk. Phys. Anthropol. *19*:59–68.

Stern JT, Jr, and Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. Am J. Phys. Anthropol. *60*:279–317.

Stoller M (1995) The Obstetric Pelvis and Mechanism of Labor in Nonhuman Primates. Ph.D. Dissertation, The University of Chicago.

Tague RG, and Lovejoy CO (1986) The obstetric pelvis of A.L. 288–1 (Lucy) J. Hum. Evol. *15*:237–255.

Tardieu C (1983) L'articulation du genou. Analyse morpho-fonctionelle chez les primates. Application aux hominides fossiles. Paris: Centre National de la Recherche Scientifique.

Taylor CR, Caldwell SL, and Rowntree VJ (1972) Running up and down hills: Some consequences of size. Science *178*:1096–1097.

Teaford MF (1985) Molar microwear and diet in the genus *Cebus*. Am. J. Phys. Anthropol. *66*:363–370.

Teaford MF (1994) Dental microwear and dental function. Evol. Anthropol. *3*:17–30.

Teaford MF, and Walker AC (1984) Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. Am. J. Phys. Anthropol. *64*:191–200.

Tobias PV (1980) A survey and synthesis of the African hominids of the late Tertiary and early Quaternary periods. In L Konigsson (ed.): Current Argument on Early Man. Oxford: Pergamon, pp. 86–113.

Tuttle RH (1975) Parallelism, brachiation and hominoid phylogeny. In WP Luckett and FS Szalay (eds.): The Phylogeny of the Primates: A Multidisciplinary Approach. New York: Plenum, pp. 447–480.

Tuttle RH (1981) Evolution of hominid bipedalism and prehensile capabilities. Phil. Trans. Roy. Soc. *292*:89–94.

Tuttle RH, Webb DM, and Tuttle NI (1991) Laetoli footprint trails and the evolution of hominid bipedalism. In Y Coppens and B Senut (eds.): Origine(s) de la Bipédie chez les Hominidés, Cah. Paléoanthrop. Paris: Editions du CNRS, pp.187–198.

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour *87*:120–143.

van Schaik CP and van Hooff J (1983) On the ultimate causes of primate social systems. Behaviour *85*:91–117.

van Schaik CP, van Noordwijk MA, Boer RJ de, Tonkelaar I den. (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques. Behav. Ecol. Sociobiol. *13*:173–181.

van Schaik CP, van Noordwijk MA, Warsono B, and Sutriono E (1983) Party size and early detection of predators in Sumatran forest primates. Primates. *24*:211–221.

van Schaik CP, and van Noordwijk MA (1989) The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. Behav. Ecol. Sociobiol. *24*:265–276.

Wainwright PC, and Reilly SM (1994) Ecological Morphology: Integrative Organismal Biology. Chicago: University of Chicago Press.

Walker AC (1981) Diet and teeth—dietary hypotheses and human evolution. Phil. Trans. Roy. Soc. London B. *292*:57–64.

White TD, Johanson DC, and Kimbel WH (1981) *Australopithecus africanus*: Its phyletic position reconsidered. S. Afr. J. Sci. *77*:445–470.

White TD, Suwa G, and Asfaw B (1994) *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature *371*:306–312.

White TD, Suwa G, Hart WK, Walter RC, WoldeGabriel G, de Heinselin J, Clark JD, Asfaw B, and Vrba E (1993) New discoveries of *Australopithecus* at Maka in Ethiopia. Nature *366*:261–265.

Wrangham RW (1977) Feeding behaviors of chimpanzees in Gombe National Park, Tanzania. In TH Clutton-Brock (ed.): Primate Ecology. London: Academic Press, pp. 503–538.

Wrangham RW (1980) Bipedal locomotion as a feeding adaptation in gelada baboons, and its implications for hominid evolution. J. Hum. Evol. *9*:329–331.

21

TIME AND ENERGY: THE ECOLOGICAL CONTEXT FOR THE EVOLUTION OF BIPEDALISM

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1. INTRODUCTION

This paper is concerned with explanations for the evolution of bipedalism. Its general point is a very simple one—that the occurrence of bipedalism is context specific. The pattern of hominid evolution, as much as that of any other lineage, reflects the costs and benefits of the way an animal is structured and behaves, and this ratio is entirely dependent upon when and where it is occurring. Historically the context for bipedalism has been the general characteristics of the environment—savanna grasslands, open environments, patchy woodland versus forest. This remains important, but here we shall add a new consideration, that of time budgets, which provides a more specific ecological context for considering the energetics of bipedalism.

The paper will first discuss the various contexts that do need to be taken into account when considering the origins of bipedalism. It extends a model developed earlier (Foley, 1992), based on a cost-benefit analysis, which suggested that the advantages of bipedalism should be placed into the specific ecological context of the Pliocene hominids. That context was specifically the effect of more arid, seasonal and open environments with more patchy and dispersed resources. The major change predicted in the model was an increase in day range length, and that the energetics of bipedalism are directly linked to increased ranging area (Foley, 1992). In quantitative terms, it was suggested (Foley, 1992: Figure 5.3) that bipedalism allowed a 50 kg hominid to exploit a day range of 16 km for the same energy as a male chimpanzee (45 kg) uses for the maximally observed day range length of 10 km (Rodman, 1984), a result that Leonard and Robertson (1997) have recently replicated. The earlier model will be developed here to incorporate a new element,

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