

Arboreal Bipedalism in Wild Chimpanzees: Implications for the Evolution of Hominid Posture and Locomotion

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ABSTRACT Field observations of bipedal posture and locomotion in wild chimpanzees (*Pan troglodytes*) can serve as key evidence for reconstructing the likely origins of bipedalism in the last prehomimid human ancestor. This paper reports on a sample of bipedal bouts, recorded ad libitum, in wild chimpanzees in Bwindi Impenetrable National Park in southwestern Uganda. The Ruhija community of chimpanzees in Bwindi displays a high rate of bipedal posture. In 246.7 hr of observation from 2001–2003, 179 instances of bipedal posture lasting 5 sec or longer were recorded, for a rate of 0.73 bouts per observation hour. Bipedalism was observed only on arboreal substrates, and was almost all postural, and not locomotor. Bipedalism was part of a complex series of positional behaviors related to feeding, which included two-legged standing, one-legged standing with arm support, and other intermediate postures. Ninety-six percent of bipedal bouts occurred in a foraging context, always as a chimpanzee reached to pluck fruit from tree limbs. Bipedalism was seen in both male and female adults, less frequently among juveniles, and rarely in infants. Both

the frequency and duration of bipedal bouts showed a significant positive correlation with estimated substrate diameter. Neither fruit size nor nearest-neighbor association patterns were significantly correlated with the occurrence of bipedalism. Bipedalism is seen frequently in the Bwindi chimpanzee community, in part because of the unusual observer conditions at Bwindi. Most observations of bipedalism were made when the animals were in treetops and the observer at eye-level across narrow ravines. This suggests that wild chimpanzees may engage in bipedal behavior more often than is generally appreciated. Models of the likely evolutionary origins of bipedalism are considered in the light of Bwindi bipedalism data. Bipedalism among Bwindi chimpanzees suggests the origin of bipedal posture in hominids to be related to foraging advantages in fruit trees. It suggests important arboreal advantages in upright posture. The origin of postural bipedalism may have preceded and been causally disconnected from locomotor bipedalism. *Am J Phys Anthropol* 129:225–231, 2006. © 2005 Wiley-Liss, Inc.

The origin of bipedalism is central to understanding hominid evolution. Models of the earliest bipedal posture and locomotion hypothesized terrestrial knuckle-walking (Washburn, 1968), vertical climbing (Prost, 1980; Fleagle et al., 1981; Gebo, 1996), arboreal brachiation preceding terrestrial knuckle-walking (Keith, 1923), terrestrial bipedalism with facultative climbing/arboreality (Jungers, 1982; Stern and Sussman, 1983), and efficient terrestrial bipedal walking (Lovejoy, 1988; Johanson et al., 1982). Recent fossil finds increased our understanding of the earliest hominids (White et al., 1994; Clarke and Tobias, 1995; Leakey et al., 2001; Pickford and Senut, 2001; Brunet et al., 2002), without resolving the question of adaptive advantages of bipedalism in the last prehomimid ancestor of apes and hominids. Whichever postural modes characterized the immediate precursors to the Hominidae, they were presumably preceded by those of an ape ancestor that engaged in behavior patterns that favored increased bipedalism.

How and why natural selection favored the transition to bipedal posture and locomotion are likewise ongoing subjects of scholarly debate and conjecture. Hypotheses to explain the advent of bipedalism range from energetics of locomotion (Rodman and McHenry, 1980; Leonard and Robertson, 1997; Steudel, 1994, 1996) to feeding (Jolly, 1970; Rose, 1976) to thermoregulation (Wheeler, 1984; Falk, 1990) to carrying for purposes of food provisioning

(Bartholemew and Birdsell, 1953; Washburn, 1968; Lovejoy, 1981) to social displays (Jablonski and Chapin, 1993). None of these has unassailable logic or empirical support.

As Hunt (1994, 1996) pointed out, hypotheses for the advent of bipedalism that involve behaviors in which prehomimids may have frequently engaged offer the most plausible explanations for the adaptive shift from quadrupedal to bipedal posture. Tuttle (1975, 1981) and Rose (1984) argued that bipedalism likely arose from the energetic advantages gained by an ape that occasionally moved bipedally between arboreal feeding sites. Hunt (1994, 1998) extended the foraging hypothesis, based on his observations of arboreal bipedal small-fruit feeding

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by free-ranging chimpanzees in Gombe and Mahale National Parks, Tanzania. He reported two postural foraging modes associated with bipedalism: 1) standing on arboreal substrates while plucking small fruits from overhead, often assisted by one-armed support, and 2) standing bipedally on the forest floor while reaching up to pull down low-hanging fruit-laden branches. In both cases, wild chimpanzees used bipedal posture to enhance access to fruits. These findings by Hunt (1994, 1998) support a strong arboreal component to the behavioral repertoire of both the last common ancestor and the earliest hominids.

In the only other field study of chimpanzee bipedal behavior, Doran (1993) reported 15 bipedal bouts in a 7-month study in Tai National Park, Ivory Coast. Seven of these 15 instances occurred in trees, all in the context of feeding. Doran (1993) did not note whether the study subjects were foraging for leaves or fruit while standing bipedally.

The behavioral ecology of chimpanzees can provide key insights into the possible beginnings of bipedal posture and locomotion in the earliest hominids. Although chimpanzees are rarely bipedal, the context for this behavior is of great interest to both primatologists and paleoanthropologists. Hunt (1998) found that chimpanzees rarely engaged in bipedal posture (0.17 times per hour of observation), and that most of these bipedal events occurred in the context of foraging.

This paper reports on the arboreal bipedal behavior of a population of chimpanzees that exhibits a high frequency of upright foraging posture. Data on bipedalism are presented to explain why this population is more bipedal than others that were studied. Models of the evolution of hominid bipedal posture are then considered in the light of arboreal bipedalism data.

STUDY SITE AND METHODS

The study site is located in the eastern (Ruhija) sector of Bwindi Impenetrable National Park in southwestern Uganda (approximately 0°53'–1°08' South and 29°35'–29°50' East). Bwindi is a range of rugged hills, with elevations ranging from 2,000–2,350 m, and annual rainfall averaging 1,100–2,400 mm (Butynski, 1984). The local climate is characterized by two dry seasons lasting from May–July and from late December–February. The national park protects the last remaining large (313 km²) tract of wet montane forest in East or Central Africa; the study site is composed of about 25 km² of the higher elevations of the park. The forest is composed of at least 163 tree species, with great elevational zonation in species occurrence (Butynski, 1984). *Parinari*-dominated forest, *Chrysophyllum*-dominated upland forest, *Newtonia*-dominated forest, swamp, and a small bamboo zone are the most widely distributed forest types (Bitariho, 1999). More detailed descriptions of the vegetation are given in Bitariho (1999), Stanford and Nkurunungi (2003), and Nkurunungi (2004).

Research on chimpanzees in Bwindi began in late 1996, as part of a study of the sympatric ecology of chimpanzees and mountain gorillas (*Gorilla g. beringei*). Behavioral and ecological data on the Ruhija community are collected daily by a team of research assistants. Data collected for this paper were entirely observational and were collected ad libitum by the author in the course of instantaneous 5-min scan behavioral sampling during field seasons between May 2001–July 2003.

The Ruhija chimpanzees are not habituated to close approach on the ground; due to their wariness and the

very dense undergrowth, nearly all observational data were collected while they were in trees. The chimpanzees can be approached to within 20 m when they are in feeding trees. An unusual feature of observation conditions in Bwindi is that the ruggedness of the terrain means that many observations are made in narrow ravines, in which the observer sits on a steep slope and observes study subjects in trees 20–50 m directly across the ravine. Observations of arboreal bipedalism were facilitated by these conditions, because observers were situated at eye-level with the animals, rather than on the forest floor beneath them.

Branch diameters were estimated to the nearest centimeter visually through binoculars, and tree heights and crown diameters were estimated to the nearest meter, using range-finders and (for crown diameters) straight-line measurements made on the ground. Bipedal posture and locomotion were recorded in the course of sampling a range of behavioral data; other positional behavior variables were not recorded. Bipedalism occurred as part of a complex and fluid set of behaviors. Bipedalism was recorded whenever a chimpanzee stood with most of its weight supported by its legs for at least 5 sec; the 5-sec criterion was chosen because it meant the animal held the position for at least 3 sec after rising onto its legs. Following Hunt (1998), this bipedal posture by Bwindi chimpanzees was called “unassisted bipedalism.” If the chimpanzee used one or both arms to support itself on branches, but most of its body weight still appeared to be supported by its legs, it was considered to be engaging in “assisted bipedalism.” The latter occurred most often, and described the positional behavior of Bwindi chimpanzees when they were engaged in arboreal bipedal feeding.

RESULTS

One hundred seventy-nine bipedal bouts of 5 sec or more were observed among 13 individuals in 246.7 total observation hours (0.79 bouts/hr). This was a markedly higher frequency than was reported in the only long-term study of chimpanzee bipedalism at Gombe and Mahale (Hunt 1994, Table 1). The mean duration of bipedal bouts was 11.9 sec, with a range from 5 sec (the minimum duration for which an event was recorded) to 66 sec. The majority of bipedal bouts were brief: 110 of 179 bouts (61.4%) were 5–8 sec in duration, and only two bouts lasted more than 1 min (Fig. 1). Both bouts lasting more than 60 sec occurred on the same day, by two males, as they foraged in a large *Ficus* sp. tree laden with fruit.

All bipedalism observed was in trees, on substrates >5 m above the ground, and usually >15 m above the ground. Although it is possible that chimpanzees were bipedal on the forest floor as well, we never observed this, and observation conditions at Bwindi were so poor due to dense undergrowth that we would have been unlikely to observe ground bipedalism. The shuffling locomotor bipedalism that Hunt (1994) reported for chimpanzees, which some researchers (Wrangham, 1980) believed to be evolutionarily important for early bipeds, was not observed. The only bipedal walk recorded in this study was by one female, who took several bipedal steps assisted by arm support on a large-diameter branch in a *Ficus* sp. crown.

Bipedalism was employed in an array of positional behaviors that shifted frequently and fluidly between bipedal and quadrupedal states. A feeding chimpanzee

TABLE 1. Comparison of Bwindi chimpanzee bipedal bouts with those recorded by Hunt (1994, 1998) in Mahale

Site	Observation hours (N)	Bipedal bouts/hour	% postural
Bwindi	246.7	0.73	99.4
Mahale	571.0	0.17	84.8

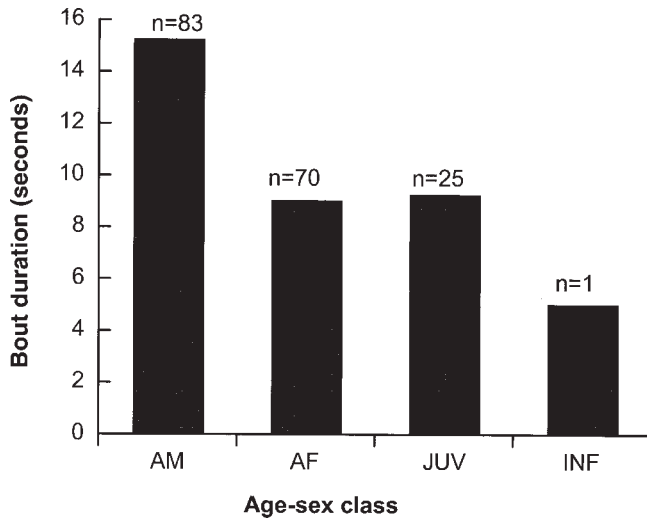


Fig. 1. Bipedal bout duration by age-sex class, for all bouts 5 sec or more.

might engage in two-legged assisted bipedalism and, while reaching for a more distant tree limb or fruit, lean into one-legged assisted bipedalism. As the animal's body moved forward toward the sought-after branch, the arms took on the majority of body support, and the chimpanzee moved into an arm-hanging posture, or brachiated to the next tree limb. The fluidity and frequency with which chimpanzees moved among unassisted bipedal, assisted bipedal, and quadrupedal climbing and standing postures belied the dichotomous way in which the distinction between quadrupedal and upright postures is often depicted. Arm-hanging and arm-aided support were key components of bipedal feeding; at least one arm helped support the animal during some portion of a bipedal bout in 169 of 179 (94.4%) episodes of observed bipedalism.

Ecological context

All 179 instances of bipedalism were recorded while chimpanzees were foraging in large trees. All but one instance occurred as postural rather than locomotor bipedalism, and 96% of all instances occurred in a feeding context (Table 2). All bipedal bouts were observed in three tree species: *Ficus* sp. (probably *F. natalensis*), *Chrysophyllum* sp. (probably *C. gorungosanum*), and *Olea capensis*. All three species are common at the study site, although the distribution of large *Ficus* sp. is patchy, and few individuals are in fruit at the same time (Nkurunungi, 2004). *Chrysophyllum* sp. is an abundant tree that grows in stands. All are important food species for chimpanzees (Stanford and Nkurunungi, 2003). Chimpanzees were more frequently bipedal in *Ficus* sp. than in the other two species (Fig. 2; $t = 5.85$, $df = 3$, $P < 0.01$).

Both the *Ficus* sp. and *Chrysophyllum* sp. are very large emergent trees, commonly reaching higher than

TABLE 2. Summary of context of bipedalism for different age-sex classes¹

	Feed	Stand	Walk	Total
AM	81	2	0	83
AF	64	5	1	70
JUV	25	0	0	25
INF	1	0	0	1
Total	171	7	1	179

¹ AM, adult male; AF, adult female; JUV, juvenile; INF, infant (see text for definitions of age-sex classes).

40 m in height. No measure was attempted of the distribution of fruit in the tree crown. Chimpanzees appeared to forage bipedally most often when feeding in the upper portion of the crown, reaching up to branches emergent in the sunlight, and perhaps containing harder-to-reach ripe fruit. When *Ficus* sp. fruit crops ripened, chimpanzee parties moved into the crowns to feed and remained there all day long until the fruit was visibly depleted, often nesting nearby and returning to the same large tree for up to 12 consecutive days. Most observations of bipedalism were made during a foraging party's intensive use of such large fruit crops. Both these tree species possess large limbs with diameters up to 50 cm that serve as broad substrates on which chimpanzees stand while plucking fruits from the next branch overhead. Bipedalism was also recorded on branches of smaller diameter, however, particularly when feeding in *Olea capensis*.

Branch size was an important influence on bipedal frequency and duration. Bipedal bout frequency showed a significant positive correlation with branch diameter (Fig. 3; $r^2 = 0.691$, $P < 0.001$). Bipedal bout duration showed a weaker but significant positive correlation with branch diameter (Fig. 4; $r^2 = 0.275$, $P < 0.05$). Bipedalism occurred only on branches over 10 cm in diameter, and most bipedal bouts occurred on branches over 15 cm in diameter. Smaller branches were visibly bent and shaken by the weight of adult chimpanzees standing briefly on them.

Fruit size was expected, as in Hunt (1994, 1998), to be an important determinant of bipedal foraging. But whereas Hunt (1994, 1998) reported that small fruit selection was positively correlated with bipedal posture (from forest-floor foraging sites), fruit size at Bwindi showed a nonsignificant relationship with both bipedal bout frequency and duration (Fig. 5). *Olea capensis* bears larger fruit than *Ficus* sp., and *Chrysophyllum* sp. bears larger fruit than either of the other tree species.

Age-sex class differences

Adult males were not bipedal significantly more often than other age-sex classes (two-tailed t -test, $t = 1.15$, $df = 3$, $P > 0.10$). Their bipedal bouts were, however, of significantly longer duration than those of other age-sex classes (Fig. 6; $t = 6.77$, $df = 3$, $P < 0.05$). Bipedalism was recorded for all age classes, although it was seen only once in an infant (individuals under estimated 5 years of age). I recorded 25 bipedal bouts for juveniles (individuals of estimated age 5–14 years, comprising only three individuals). On three occasions, females stood and fed bipedally with infants clinging to their backs. Animals were observed feeding bipedally in close proximity, suggesting some social facilitation of the behavior.

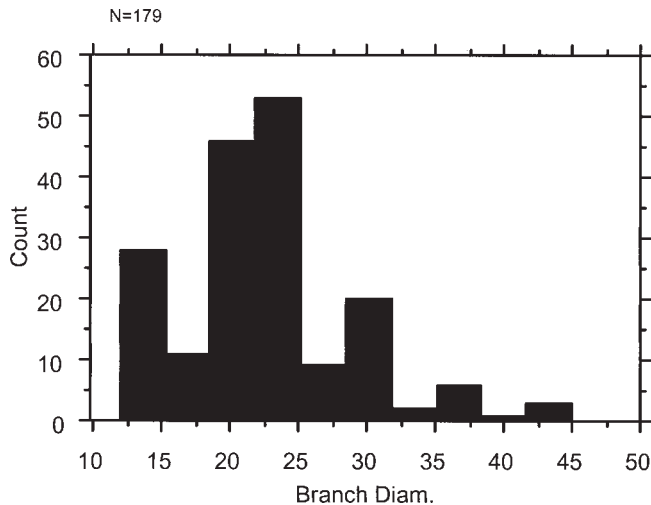


Fig. 2. Range of branch diameters used as bipedal foraging substrates.

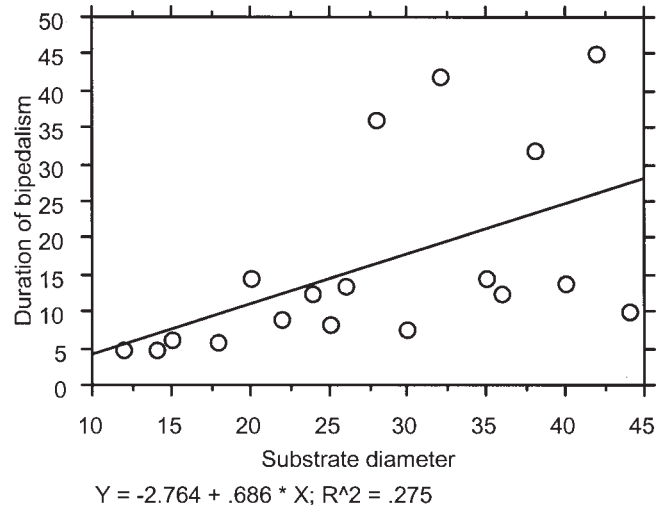


Fig. 4. Bout diameter in relation to branch diameter.

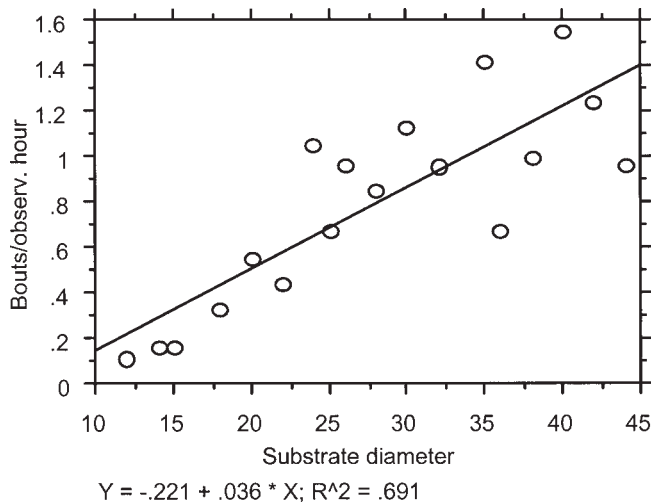


Fig. 3. Bout frequency in relation to branch diameter.

Social facilitation

Although there appeared to be some degree of social facilitation of bipedal foraging, in that chimpanzees were seen foraging bipedally next to one another, nearest-neighbor proximity was not significantly correlated with either bipedal bout frequency ($r^2 = 0.011$, $P = 0.15$) or bout duration ($r^2 = 0.018$, $P = 0.11$).

DISCUSSION

Comparison with other studies

Some important similarities exist between this study and those in Gombe and Mahale National Parks by Hunt (1996, 1998). In Gombe, Mahale, and Bwindi, bipedal posture was strongly associated with arm-hanging and arm-support (Hunt, 1996, 1998). Hunt (1996, 1998) argued that this was because the small, unstable substrates on which arboreal bipedalism occurred were inherently poorly suited to unassisted bipedal standing. As Wrangham (1980)

noted, bipedal foraging eliminates the need for continual posture changes while moving or feeding. It also increases the arm reach of the forager in many situations (Hunt, 1998).

Fruit size harvested during bipedal standing was also similar between sites. The primary fruit eaten bipedally was *Ficus* sp.; these were generally 1 cm or less in diameter. The fruits of the four understory trees that were eaten bipedally according to Hunt (1998) were 1–2 cm. The second most-eaten fruit at Bwindi, *Chrysophyllum* sp., produced larger fruit (3–5 cm diameter). Branch diameter and foraging height were significantly positively correlated with bipedal fruit-eating at Bwindi, whereas fruit size and smallness of branch diameter were the main correlates of bipedal foraging in Mahale and Gombe.

Important differences between the studies' findings exist as well. Bipedalism was observed among Bwindi chimpanzees only in arboreal contexts. The study subjects in Gombe and Mahale (Hunt, 1994, 1998) employed bipedal posture and locomotion as often in trees as they did on the ground. Other differences exist between the results of Hunt (1994, 1998) and this study. Hunt (1994, 1998) observed arboreal bipedalism primarily when chimpanzees fed in small trees. All four tree species in which Mahale and Gombe chimpanzees foraged bipedally were understory trees, whereas all three species in which Bwindi chimpanzees foraged bipedally were tall emergent trees >15 m. In Hunt (1994, 1998), chimpanzees foraged arboreally in the same understory tree species from which they also plucked fruit while standing bipedally on the forest floor. In Bwindi, no terrestrial bipedalism was seen, although as noted earlier, the dense undergrowth would have precluded observing such behaviors. Differences in observation conditions between the two sites may confound some apparent empirical differences in the data, as discussed below.

Chimpanzees in Hunt (1998) used arboreal bipedal behavior primarily on smaller substrates. Bipedalism in Mahale and Gombe occurred most often on the smaller-diameter terminal ends of fruit-laden branches. In Bwindi, such branches were rarely used for bipedal behavior, although the animals sometimes stepped upon such smaller substrates in the course of moving through a tree crown while feeding. Bwindi bipedalism was primarily a large-

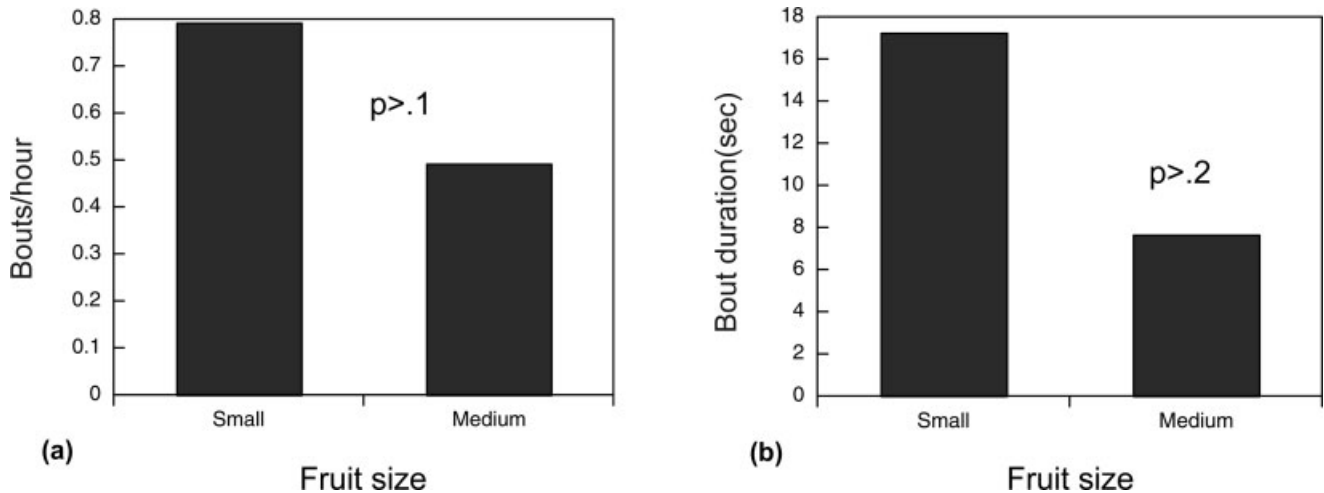


Fig. 5. Feeding bout frequency (a) and duration (b) in relation to fruit size.

branch behavior, used to move between or reach between fruit patches >15 m above the ground.

Why are Bwindi chimpanzees so bipedal?

The frequency of bipedalism among Bwindi chimpanzees requires an explanation. Although the frequency of bipedal bouts relative to other positional behaviors is no doubt exaggerated in this study because all observational data were collected in trees and not on the ground, the number of bipedal bouts was substantially higher than that recorded in the most detailed naturalistic chimpanzee study (Hunt, 1994) that explicitly examined bipedalism. Several hypotheses are offered to explain the high level of bipedalism seen among Bwindi chimpanzees.

Observation conditions. Bwindi chimpanzees may be no more bipedal than chimpanzees elsewhere; observed frequencies of bipedalism differ among chimpanzee study sites due to varying observation conditions. It is possible that the unusual observation conditions at Bwindi induced by rugged terrain produce more readily observed bipedalism than in other chimpanzee study sites. Researchers typically conduct observations of chimpanzee arboreal behavior from the ground below (sometimes far beneath) study subjects. At Bwindi, the narrow, steep-sided ravines on which large fruits often grow mean that most observations of arboreal bipedalism are made at eye-level from 20–50 m away, where vertical changes in posture are easier to observe and foliage is less often an obstruction. If this hypothesis is correct, chimpanzees at other sites are also more bipedal than has been appreciated, but observation conditions are less than ideal for readily observing this. Some sites where chimpanzees were watched extensively are, however, topographically similar to Bwindi, such as Gombe National Park in Tanzania. Hunt (1998) observed arboreal bipedal behavior at Gombe, although little mention was made by other researchers of Gombe chimpanzees being bipedal.

Forest structure. The forest at Bwindi may consist of more arboreal substrates conducive to bipedalism than other chimpanzee study sites, perhaps due to the steep terrain or particular composition of tree species. There is little evidence of this, although detailed vegetation com-

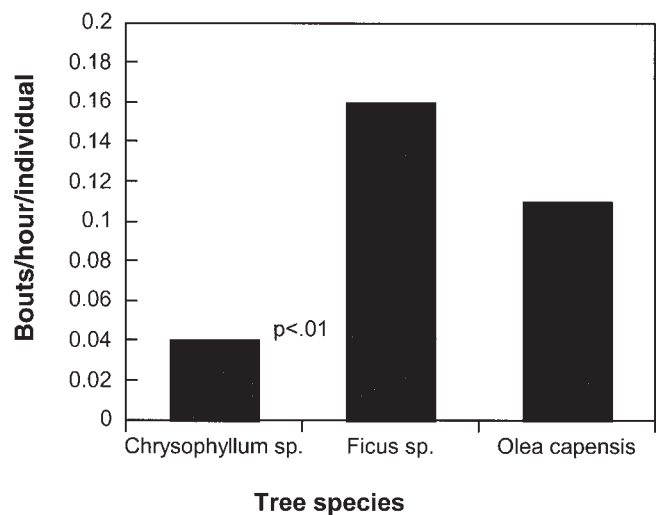


Fig. 6. Bout duration in relation to tree species.

parisons with other forest tracts are still in progress (Nkurunungi, 2004; Nkurunungi et al., 2004). The initial observations I made of arboreal bipedalism at Bwindi occurred in large *Ficus* sp. trees growing at steep angles from steep ravine slopes. This led Stanford (2002) to hypothesize that the frequency of bipedalism in the Ruhija chimpanzee community was due to an unusual number of large-diameter, parallel horizontal substrates on which feeding chimpanzees could stand upright, reaching to branches above to pluck fruit. This turned out to be a small sample bias, however. Further observations in the same forest suggest no such bias toward odd-angled trees, and this study took place among three fruit tree species of varying dimensions and growth angles.

Disabilities. Chimpanzees with upper body or arm injuries, such as snare-induced wounds or amputations, might be more likely to forage bipedally. At Gombe, a polio epidemic in the 1960s crippled the arm of one adult male (Faben), leading him to walk bipedally on a frequent basis (Bauer, 1977; Goodall, 1986). Snare wounds and amputations are common in chimpanzees in Ugandan forests: in at least one site, the Budongo Forest

Reserve, more than one-third of all adults are missing at least one hand or foot as a result (Waller and Reynolds, 2001; Quiatt et al., 2002).

There are few snare wounds or disabilities of any kind among Bwindi chimpanzees, which presumably is related to the relatively low number of snares (compared to other chimpanzee study sites in southwestern Uganda) that are found by ranger patrols in the study site. Two individuals (one of them among the 13 in whom bipedalism was observed) possessed a severe snare wound. It is therefore unlikely that snares have any effect on bipedal posture at Bwindi.

Cultural tradition. Bipedalism among Bwindi chimpanzees may be a cultural tradition. Traditions are widespread in chimpanzee behavior and are not necessarily ecologically adaptive (Whiten et al., 1999). Bipedal foraging may not be adaptive or ecologically more efficient (in terms of fruit-harvesting rate) than other modes of feeding. Although bipedalism was not discussed previously as a learned tradition, Bwindi chimpanzees exhibit other traditions not commonly seen in wild chimpanzees. For instance, in one Bwindi chimpanzee community to the north of the study community, chimpanzees sometimes build ground nests. These nests are made in areas where elephant, gorillas, and leopard do not occur, and have been reported since the 1950s (Albrecht and Dunnett, 1971).

If arboreal bipedal foraging is a cultural tradition, we might expect to see it in immature animals whose mothers exhibit the posture more often than those whose mothers do not. In fact, of 26 instances of bipedalism by juvenile or infant chimpanzees, 14 instances were recorded for chimpanzees whose mothers also exhibited bipedal foraging. While it is possible that Bwindi chimpanzees are more bipedal than nearby chimpanzee populations due to a local cultural tradition, there is little evidence in this study to support or refute the hypothesis.

There is no persuasive evidence that any of the four hypotheses presented above is more likely to explain Bwindi bipedalism than the observation-conditions hypothesis. If intersite observation-condition differences explain the high incidence of Bwindi bipedalism, observers should be able to note bipedalism at other hilly sites, such as Gombe. Since there is little evidence of high frequencies of bipedalism at Gombe (personal observations; Hunt, 1994), it appears that bipedalism occurs at an unusually high frequency at Bwindi. Relatively poor conditions for observing arboreal bipedalism at other chimpanzee study sites may have yielded observational bias at those sites.

CONCLUSIONS

The behavior of wild chimpanzees suggests that several aspects of the positional behavior of earliest hominids may have been given less attention that they merit. First, arboreal bipedal posture is not dichotomous with arboreal quadrupedal posture. Bwindi chimpanzees moved fluidly between four-legged, three-legged, and two-legged postures while feeding in tree crowns. Their use of three-dimensional space in tree tops incorporated elements of positional behavior most often seen as binary states. This fluid quadrupedal-bipedal shifting may have occurred in the earliest hominids as well. Arguments about whether early hominids were fully adapted to bipedal walking, or facultatively arboreal, have been carried on for at least three decades (Susman et al., 1984; Lovejoy, 1988). Recent

evidence suggests that knuckle-walking may have been employed by the immediate ancestors of the australopithecines (Richmond and Strait, 2000). Chimpanzee bipedal behavior suggests that early hominids likely engaged in a fluid variety of positional behaviors and postures, but provides little evidence for the adaptive advantage of terrestrial knuckle-walking in the last common ancestor of apes and humans.

Modern gorillas are not often thought of as arboreal foragers, because of their bulky, terrestrially adapted anatomy and because the earliest field data on gorilla foraging came from a site (the Virunga Volcanoes) nearly lacking in fruit trees. But recent field observations (Tutin, 1996; Stanford and Nkurunungi, 2003) show that even adult male gorillas climb extensively into tall trees in search of desired plant foods. Given this long-unsuspected use by gorillas of arboreal substrates, and the occurrence of occasional bipedalism among chimpanzees, we should not underestimate the degree of behavioral plasticity, and of arboreality, likely to have occurred in early hominids.

Rose (1984) argued that there is no reason to view the origin of bipedalism as a progression from "poor biped" to "good biped." Instead, there was likely a diversity of forms of bipedalism in the earliest hominids. One such hominoid example may be *Oreopithecus bambolii*, a supposed bipedal ape (Köhler and Moya-Solá, 1997). The bipedal evidence from Bwindi, Mahale, and Gombe supports this view of early hominid evolution. Instead of viewing the earliest bipedal adaptation as the lowest rung on a posture/locomotion evolutionary ladder, it may be that early hominid species evolved a variety of forms of bipedalism in particular ecological contexts. We do not yet know how many taxa of early hominid species existed in the late Miocene/early Pliocene, but the number may be substantially more than have been described (Foley, 1991; Leakey et al., 2001).

Little evidence of extensive terrestrial locomotor adaptation exists in the morphology of modern chimpanzees, despite the fact that chimpanzees travel long distances primarily on the ground, using trees mainly for feeding and sleeping. In other words, chimpanzees do quadrupedally exactly what many paleoanthropologists believe australopithecines were adapted to do bipedally. Given the occasional incidence of chimpanzee bipedalism and their extensive terrestriality, we should not underestimate the degree of behavioral plasticity, and of arboreality, likely to have occurred in early hominids.

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