

Positional Behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania

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ABSTRACT The positional behavior of habituated adult chimpanzees and baboons was observed for 784 hr in a year-long study. Comparisons between species were made to establish the distinctiveness of chimpanzee positional behavior and habitat use. Brachiation (*sensu stricto*, i.e., hand-over-hand suspensory locomotion) was observed in low frequencies among chimpanzees, and its significance for chimpanzee anatomy is judged slight. Although no significant differences were found between sympatric baboons and chimpanzees in the proportion of time spent in the terminal branches, or in the mean diameter of weight-bearing strata, chimpanzees exhibited evidence of a terminal branch adaptation in that they, unlike baboons, used postures among smaller supporting strata different from those used among larger supports. Among chimpanzees, unimanual arm-hanging was most common among the smallest strata and was associated with smaller mean and median support diameter than other postures. Unimanual arm-hanging was the only common behavior among chimpanzees that usually involved complete abduction of the humerus. A number of behaviors often subsumed under the label "quadrumanous climbing" were distinguished in this study. Compared to baboons and other cercopithecoids, chimpanzees did not show increased frequencies of large-stratum vertical climbing, and their vertical climbing did not involve significant humeral abduction. Arm-hanging (i.e., unimanual suspension) and vertical climbing distinguish chimpanzee positional behavior from that of monkeys.

Apes share high intermembral indices, curved metacarpals and phalanges, long fingers, mobile shoulders, mediolaterally reduced scapulae, cranially oriented glenoid fossae, cone-shaped ribcages, anteroposteriorly flattened torsos with concomitantly long clavicles, strongly curved ribs resulting in more ventrally placed vertebral bodies, wide manubria of the sternum, reduced numbers of lumbar vertebrae, the lack of a tail (Keith, 1899; Schultz, 1930; Erikson, 1963; Susman, 1979), a distinctive pelvic floor (Keith, 1923) and a predominance of muscles that flex the elbow and raise (i.e., abduct or protract) the upper arm (Ashton and Oxnard, 1963; Napier, 1963a; Oxnard, 1963, 1967; Ashton et al., 1965; Tuttle, 1969). The anatomical similarity of the apes implies that they share a limited number of positional modes for

which these traits are evolved. Keith (1891, 1899, 1903) speculated that the morphological specializations of the gibbon were related to brachiation (*sensu stricto*),¹ and assumed that the then-unstudied African apes shared this adaptation (cf. Chivers, 1972; Andrews and Groves, 1976). The ascendancy of this paradigm inspired anatomists to interpret virtually every ape specialization as adapted to brachiation (e.g., Napier, 1963a,b, 1967; Erikson, 1952, 1954, 1957, 1963; Ashton and Oxnard, 1963, 1964a,b; Oxnard, 1963, 1967;

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¹The term brachiation (*sensu stricto*) means hand-over-hand suspensory locomotion, with or without a period of free flight. The qualifier distinguishes it from a liberal usage (*sensu lato*). Ricchet al brachiation is used even more restrictively to mean only gibbon-like brachiation with a period of free flight.

Benton, 1967, 1976; O'Connor, 1975, 1976; Napier, 1963a).

Avis (1962) demonstrated that when confronted with a variety of weight-bearing structures (WBS) apes more often brachiated beneath thin, unstable WBS, whereas monkeys preferentially locomoted on top of more stable WBS. Brachiation was thought to allow apes to gain access to food resources found among the small branches at the periphery of trees (Avis, 1962) and/or to travel more efficiently than Old World monkeys among the terminal branches by moving directly between adjacent feeding sites (Ripley, 1970; Ellefson, 1974; Rose, 1978). In one form or another the amalgamation of Keith's anatomical and Avis' ecological hypotheses has dominated ape positional behavior research to the present.

Not all anatomical evidence accorded with the brachiation paradigm. Many aspects of the African ape wrist and hand that had been supposed to be adaptations to brachiation were shown to be knuckle-walking adaptations (Tuttle, 1965, et seq.; Jenkins and Fleagle, 1975; Rodman, 1984; Grand, 1984). The contention that the mobile wrist of apes was an adaptation to brachiation (*sensu stricto*) (Gregory, 1916; Lewis, 1965 et seq.) was cast into doubt by evidence that gibbons, the preeminent brachiators, have the greatest ulnar-carpal articulation of all apes (Conroy and Fleagle, 1972). Cartmill and Milton (1977) demonstrated that lorises have a reduced ulnar-carpal articulation as an adaptation to slow (cautious) climbing, leading them to hypothesize that the large body size of apes necessitated a similar cautious climbing locomotion. Jenkins (1981) showed that Lewis' supposition (1965, et seq.) that a lesser articulation between the styloid process of the ulna and the triquetral and pisiform allowed wrist rotation was wrong, since wrist rotation occurs mostly in the midcarpal joint.

Field studies of positional behavior did not support a brachiation (*sensu stricto*) specialization in apes (Bingham, 1932; Donisthorpe, 1958; Schaller, 1963; Schaller and Emlen, 1963; Nissen, 1931; Goodall, 1963; Kortlandt, 1962, 1968, 1974; Reynolds, 1965; Carpenter, 1938; Schaller, 1961; Harrison, 1962), although evidence from some chimpanzee researchers was equivocal (e.g., Reynolds and Reynolds, 1965; Goodall, 1968). To accommodate these data it was reasoned that ape anatomy was adapted to behaviors

that were purported to be kinematically similar to brachiation (*sensu stricto*), such as vertical climbing, hoisting, arm-swinging, and, at least tacitly, any other humerus-abducted, forelimb-dominated behaviors, including postures (Washburn, 1973; Morbeck, 1972). Some researchers continued to refer to these behaviors as brachiation (see Andrews and Groves, 1976), but the term *quadrumanous climbing* has come to be preferred.

Although field research on wild primates was interpreted as supporting a quadrumanous climbing adaptation in apes (Fleagle, 1976a,b; Mittermeier and Fleagle, 1976; Fleagle and Mittermeier, 1980), the term suffers from the same liability as brachiation (*sensu lato*) since it conflates a number of kinematically diverse behaviors—including suspensory locomotion (Fleagle, 1976b, Fig. 2), quadrupedal walking on slightly inclined WBS (Fleagle, 1976b, Fig. 3), arm-swinging, transferring, scrambling, clambering, and vertical climbing—under a single nomen (Cant, 1986).

Of the various positional modes subsumed under quadrumanous climbing, vertical climbing has received the most intensive theoretical attention. Long arms were hypothesized to confer an advantage to vertical climbers by allowing them to ascend larger WBS than monkeys (Kortlandt, 1968, 1974; Cartmill, 1974; Tuttle, 1975; Jungers, 1976; Mendel, 1976; Stern et al., 1977; Fleagle et al., 1981; Jungers and Stern, 1980; Tuttle et al., 1979; Jungers and Susman, 1984). Stern et al. (1977) and Fleagle et al. (1981) showed that muscles that are larger in apes were as or more active in vertical climbing than in brachiation, indicating that they may have been maintained as an adaptation to the former. Fleagle et al. (1981) maintained that shoulder mobility was an adaptation to reaching up during climbing and concluded that vertical climbing is responsible for many of the synapomorphies (including shoulder mobility) in the hominoid clade.

Most students of ape positional behavior recognize that adaptation to suspensory posture is significant in all apes (e.g., Fleagle, 1988), yet its conflation with vertical climbing has obscured the extent of the adaptation and perhaps overemphasized the importance of vertical climbing. Brachiation (*sensu stricto*), vertical climbing, unimanual arm-hanging, hoisting, clambering, amoebic suspensory locomotion, arm-swinging, and

transferring are distinct behaviors, one or several of which may be the behavior or behaviors for which ape specializations were evolved. Here quantitative data on the positional behavior of chimpanzees and baboons are compared in order to determine which mode(s) distinguish chimpanzees from Old World monkeys.

METHODS *Study sites*

The Mahale Mountains and Gombe Stream National Parks are located on the shores of Lake Tanganyika, Tanzania (Nishida, 1968, Goodall, 1968). The principal differences between the two sites relate to the greater rainfall at Mahale (Hunt, 1989). The Mahale M group range is characterized by closed forest and vine tangles, whereas at Gombe there is less vine tangle and forest and more open woodland (Collins and McGrew, 1988). The greater forest floor cover at Mahale is the most remarkable difference between the two sites (personal observation).

Choice of baboons as a comparative species

Even in closely related species with very similar morphologies, greater body weight limits saltatory locomotion [e.g., hylobatids (Carpenter, 1940; Chivers, 1972; Fleagle, 1976b), galagos (Crompton, 1984), 7 Surinam monkeys (Fleagle and Mittermeier, 1980), and 8 African forest monkeys (Rollinson, 1975)]. Body weight is of particular interest in ape studies since hominoid morphology and positional behavior have often been hypothesized to be adaptations to their greater weight (e.g., Keith, 1891, 1923; Miller, 1932; Napier, 1963a,b, 1967; Lewis, 1965 et seq.; Ripley, 1970, 1976, 1979; Rose, 1973, 1974; Cartmill, 1974). Among all living nonhominoid primates only *Mandrillus sphinx* is closer in body size to the chimpanzee than the baboon is (Jungers, 1985). Nevertheless, baboons have typical cercopitheine anatomy, including restricted wrist mobility, restricted shoulder mobility, a ventrally oriented glenoid fossa, a low intermembral index, fewer thoracic and more lumbar vertebrae, a narrow, barrel-shaped (as opposed to cone-shaped) torso, and short manual digits with a large thumb (Jones, 1967; Benton, 1967, 1976; Corruccini and Ciochon, 1976; Lewis, 1972a; Swindler and Wood, 1973; Schultz, 1936, 1937, 1944, 1953, 1956, 1961, 1963, 1967, 1969; Erikson, 1952,

1954, 1957, 1963; Avis, 1962; Miller, 1932). Multivariate analysis of shoulder morphology places them in a cluster with other monkeys, separated from apes (Corruccini and Ciochon, 1976).

Study group and sampling method

Chimpanzees were observed for 571 hr at Mahale and 130 hr at Gombe. Here 14,866 instantaneous, 2-min focal observations (Altmann, 1974) on 26 well-habituated prime adults spanning all social ranks are analyzed (see Hunt, 1989 for more detail). At the 2 min mark the target was instantaneously sighted and values were recorded for 25 positional behavior variables (Hunt, 1989). Approximately equal numbers of observations were made in wet and dry seasons (7,984 vs 6,882) and on males and females (7,754 vs 7,112). Baboons at Gombe were observed for 83 hr resulting in 2,087 observations. Identical methods of data collection were employed for both species. The baboon home range was considerably smaller than that of the chimpanzees and located near the center of the Kasekela community range.

An attempt was made not to observe the same individual 2 days in a row in order to avoid potential positional bias associated with the collection of temporarily abundant fruit; of 147 chimpanzee follows, the same individual was followed 2 days in a row 7 times. None was followed 3 days in a row. Targets were discovered as early in the day as possible and followed for as long as possible or until they entered their night nest. Any purposeful decision to cease taking data was made at least an hour in advance, after which no other data were taken in the same day. No data were recorded in feeding camp, in staff camp (Goodall, 1986), or while the animals were mobile-provisioned (Nishida, 1979).

Data collected

The following variables are analyzed here:

1. *Location in tree*: the target was recorded as being on the ground, in the terminal branches (i.e., any part of the target's trunk within 1 m of the tree edge), or in the central part of the tree (i.e., not within 1 m of the edge). Note that a separate measure was kept for the size of the supporting structure (WBS); not all supports in the terminal branches are small.

2. *Contact with WBS (weight-bearing structure)* (typically recorded for posture only): it was noted which of the ischia, side, belly, back, or four limbs were supporting a significant portion of the body weight.

3. *Locomotor or postural mode*: in the course of study 65 different positional modes were observed; these were collapsed into 20 positional modes presented in Appendix A. Note that climbing means vertical climbing and that brachiation means hand-over-hand suspensory locomotion.

4. *Weight bearing structure (WBS) diameter*: the diameter of the supporting structure that the hand(s) and/or foot/feet were touching was estimated. If the sizes of WBS contacting the left and right cheiridia were similar in size but distinguishable, the left and right were averaged. If one was more than approximately double the size of the other, the size of the WBS judged to be bearing the most weight was recorded. Often the ischia contacted a large diameter WBS and the feet rested on smaller WBS; in such cases the diameter of the WBS of the body part(s) (feet versus ischia) bearing the most weight was recorded. When the WBS consisted of a number of intertwined branches of small diameter it was recorded simply as "tangle," such support was as stable as the largest WBS and was pooled with large WBS when appropriate (Hunt, 1989).

5. *Canopy level*: height above the ground was estimated in meters.

6. *Context or activity*: 116 different behaviors associated with positional behavior were recorded.

Continuous data were collected whenever a target animal was observed climbing, as follows:

1. *WBS diameter*: recorded for each distinct climbing bout.

2. *Angle of WBS*: angle above horizontal.

3. *Climbing mode*: flexed-arm climb, extended-arm climb, ladder climb, and pulse climb were recognized; see Appendix A for definitions.

Statistical method

Observations only 2 min apart are presumably highly dependent due to what might be called behavioral inertia, complicating statistical analysis. Many positional studies have chosen to omit statistical testing altogether. Cant (1987a,b) tested positional differences with χ^2 tests, which he

reasoned were the best choice despite the fact that behavioral inertia may violate the assumption that observations are independent. The procedure used here is similar. To minimize the dependence between data points, somewhat artificial "bouts" were created from instantaneous observations. The data were reduced by pooling sequential observations in which positional mode did not change. Analytical variables were averaged over the series of sequential bouts, and the resulting group of observations was considered a single observation or bout. For example, if there were 20 consecutive 2-min observations in which the same positional category (e.g., "sitting") was observed, the 20 samples would be collapsed into one observation and analytical variables such as canopy height, WBS size, and WBS angle would be averaged over the 20 observations, regardless of whether other variables changed. The artificial bouts were made up of a varying number of observations from one to scores (the mean number was 2.96). This collapsing or reduction produced a number of "bouts" that totalled approximately one third the number of observations in the raw data.

Reduced data sets were used for all statistical procedures (Fisher's exact tests, χ^2 tests and Mann-Whitney U tests). There was no need to reduce climbing data, since these were continuous. Fisher's exact tests were used when possible since they are more accurate than χ^2 tests on small samples (Gibbons, 1983); on larger samples Fisher's exact values asymptotically approach χ^2 values (Gibbons, 1983:120). Since Fisher's exact tests give only P values, χ^2 values are presented.

More observations were made in the middle hours of the day than early or late, a bias that introduced significant distortion since chimpanzees exhibited a marked daily cycle (Hunt, 1989). Chimpanzees spent more time feeding just after waking and in the last few hours before entering their night beds than at other times of the day (comparison on data reduced on context: hours 07-08 compared to 09-14, Fisher's exact test, $P < .01$; $\chi^2(1) = 4.9$; hours 15-18 compared to hours 09-14, Fisher's exact test, $P < .0001$; $\chi^2(1) = 68.8$). As a consequence raw measures underrepresent feeding positional behaviors. To compensate for time-of-day bias, data were standardized by hour of day for Table 1. Activities were calculated by the hour and proportions from each hour were averaged over the typical 12- or 13-hr daily schedule. Such standardization precludes statistical analysis,

and is therefore used only for Table 1. Stratified data on Gombe chimpanzees were suspect in some cases due to small sample sizes. In these cases observations are presented for Mahale chimpanzees only. In cases where values are nearly identical between sites, data are pooled for comparisons with baboons.

RESULTS

Table 1 presents the composite positional schedules (i.e., standardized for hour of day) for the Mahale and Gombe chimpanzee populations based on 11,393 and 2,700 2-min instantaneous focal observations respectively. Gombe baboon figures are mid-sex averages (there were 1,113 and 937 observations on males and females) standardized by hour.

Chimpanzees showed more variety in positional behavior than baboons. Standing, sitting, and walking made up nearly 95% of all baboon positional behaviors versus 79.2% in chimpanzees. Compared to baboons, chimpanzees sat more, lay more, arm-hung more (with and without support from the ischia and feet), palm-walked more, and vertical-climbed more, but stood (tripedal and quadrupedal standing pooled) less and walked less (all Fisher's exact tests on pooled Gombe and Mahale data, $P < .05$, $df = 1$).

Positional variation by WBS diameter and canopy location

There were no significant differences in WBS size usage between baboons and chimpanzees whether in feeding (Mann-Whitney U test, $U = 61,065$, $P = .16$, $n = 1117$; see Table 2) or nonfeeding contexts (Mann-Whitney U test, $U = 15,636$, $P = .82$, $n = 607$). Nor did chimpanzees spend more time in the terminal branches (Fisher's exact test, $P = .70$, $\chi^2 = .15$ for Gombe; $P = .61$, $\chi^2 = .22$ for Mahale; see Table 3) even though baboons spent significantly less time in trees compared to sympatric chimpanzees (Fisher's exact test, $P < .0001$; $\chi^2 = 38.6$) and Mahale chimpanzees (Fisher's exact test, $P < .0001$; $\chi^2 = 15.5$).

Whether measured by proximity to the edge of the tree (Table 4) or by WBS diameter (a more accurate measure of stability; see Table 5), positional behavior differed in chimpanzees according to the canopy structure. Sitting was the most common posture, regardless of WBS diameter. Unimanual arm-hanging both with and without support

TABLE 1. Positional behavior of baboons and chimpanzees compared

Species	Percentage of each behavior															
	Sit (in)	Sit (out)	Lie	Arm-hang	AH (Supp)	Stand	Squat	Cling	Bip. stand	Walk	Vertical climb	Run	Leap	Misc. susp.	Palm-walk	Bip. walk
Mahale Chimp	34.3	30.9	11.3	0.8	3.3	1.4	0.3	0.3	0.2	15.3	0.9	0.2	0.0	0.3	0.6	0.1
Gombe Chimp	22.5	37.0	12.7	0.7	3.8	3.6	1.0	0.3	0.3	16.1	0.9	0.3	0.0	0.0	0.5	0.1
Chimp mean	28.4	34.0	12.1	0.8	3.6	2.5	0.7	0.3	0.3	15.7	0.9	0.3	0.0	0.2	0.6	0.1
Baboon	22.5	34.6	3.2	0.0	0.0	14.5	0.5	0.3	0.0	23.2	0.5	0.4	0.2	0.0	0.	0.0

TABLE 2. Mean WBS diameter compared in chimpanzees and baboons

		Mean (cm)	n	SD
Feeding	Mahale chimpanzee	5.8	1,904	5.3
	Gombe chimpanzee	6.3	692	5.5
	Baboon	6.5	304	3.4
Nonfeeding	Mahale chimpanzee	13.4	1,475	9.9
	Gombe chimpanzee	10.8	275	6.5
	Baboon	11.6	162	12.9

TABLE 3. Percentage of time in each stratum level compared in baboons and chimpanzees

Context	Study group	n	Terminal branches	Central tree	Ground
Feeding	Baboon	851	11.3	27.6	61.1
	Gombe chimp	1,140	14.8	54.2	31.0
	Mahale chimp	3,972	16.8	40.0	43.2
Nonfeeding	Baboon	997	0.7	17.3	82.0
	Gombe chimp	1,554	0.6	41.8	57.6
	Mahale chimp	6,192	1.9	27.0	71.1
All	Baboon	2,082	5.2	22.6	72.2
	Gombe chimp	3,056	6.0	46.8	47.2
	Mahale chimp	11,896	7.1	32.2	60.7

TABLE 4. Percentage of each posture in Mahale adults by stratum level

Location	Posture								
	Sit (in)	Sit (out)	Stand	Armhang	Armhang w/support	Lie	Squat	Sit/recline	Armhang stand
Terminal branches (n = 749)	30.7	28.4	2.2	7.1	15.5	9.5	1.9	0.4	3.2
Central tree (n = 3,458)	35.9	40.1	1.0	0.9	4.7	13.9	0.8	1.6	0.5
Ground (n = 5,426)	39.8	34.0	2.4	0.5	0.0	21.5	0.1	1.5	0.1

from other parts of the body² was more common among the smaller WBS [Fisher's exact test, $P < .0001$; $\chi^2(1) = 93.6$, $n = 1,436$; see Table 5]. Unimanual arm-hanging had the smallest mean and median WBS diameter of all postures (Table 6; all contexts represented), followed by arm-hang with support and arm-hang/stand. These results are strong evidence that it was unimanual arm-hanging (all modes) that gave chimpanzees access to the smallest, terminal branches.

Tables 7 and 8 present locomotor modes by

proximity to edge of tree and by WBS diameter. Though sample sizes were small (only 34 surveys in the terminal branches) vertical climbing, palm-walking (both observed significantly more than brachiation, Fisher's exact test, $P < .05$ in both cases) and transferring (but not significantly, $P = .17$, Fisher's exact test on reduced data) were the most common locomotor behaviors in the terminal branches. Brachiation made up 8.8% of all locomotor behavior in the terminal branches and was observed in approximately the same frequency in the central parts of the tree (7.7%). Quadrupedal knuckle-walking had the highest median WBS diameter, followed by climbing, palm-walking, and running. Transferring was observed on the smallest WBS (Table 8).

²Suspensory modes in which half or more of the body weight depended on a fully abducted forelimb were pooled under the label "arm-hanging (all modes)." "Arm-hanging" means the entire body weight is suspended from one arm, whereas "arm-hanging with support" means that 50%+ is suspended from a forelimb, but that some of the body weight is supported with other body contact.

TABLE 5. Postural mode frequencies by WBS size in Mahale adults

Substrate diameter	Posture								
	Sit (in)	Sit (out)	Stand	Armhang	Armhang w/support	Lie	Squat	Sit/recline	Arm-hang stand
< 3 cm (n = 976)	35.0	36.9	2.2	2.3	16.9	2.0	1.5	0.3	1.9
3-10 cm (n = 1,328)	36.9	48.0	0.8	0.2	5.4	5.0	1.0	1.4	0.7
> 10 cm (n = 7,175)	38.4	33.9	2.3	0.0	0.4	22.6	0.3	1.7	0.3

TABLE 6. Mean and median substrate diameter by posture (Mahale only, all contexts)¹

	Posture								
	Sit (in)	Sit (out)	Stand	Arm-hang	Arm-hang w/support	Lie	Squat	Sit/recline	Arm-hang stand
Mean (in cm)	9.7	7.1	11.2	2.6	3.5	47.6	4.4	11.2	3.9
n	335	581	42	76	257	530	16	49	43
SD	17.0	9.7	17.3	1.5	5.4	33.3	3.4	4.2	5.6
Median (in cm)	5.1	5.1	5.1	2.5	2.5	35.6	2.5	10.2	2.5

¹Means and medians are given for the substrate diameter contacting the feet, except for arm-hanging, for which only the hand(s) contacted the stratum.

TABLE 7. Locomotor mode frequencies by stratum location in Mahale adults

Location	Locomotion						
	Quadrupedal knuckle-walk	Climb	Palmar walk	Bipedal walk	Brachiate	Transfer	Run
Terminal branches (n = 34)	0.0	32.4	29.4	2.9	8.8	20.6	0.0
Central tree (n = 143)	6.3	54.5	24.5	1.4	7.7	1.4	0.7
Ground (n = 1,557)	98.6	0.1	0.1	0.1	0.0	0.0	0.8

Locomotion in travel versus feeding

Quadrupedal knuckle-walking was the most common positional mode when moving between feeding patches and when traveling with no recognizable purpose (Table 9). In contexts where individuals moved within a patch while feeding ("Feed" in Table 9), knuckle-walking was still the most common locomotor mode, but palm-walking and climbing were observed in high frequencies as well. Transferring was also more common in feeding contexts.

Positional behavior during feeding

Of all feeding contexts (including moving within a feeding patch), 96.8% of all posi-

tional behavior was postural (Gombe and Mahale data pooled, $n = 5,038$). Chimpanzees fed 87.8% of the time when among the terminal branches (Table 10; data from Mahale chimpanzees only). Of unimanual arm-hanging 95.7% occurred during feeding bouts. In other humerus-abducted arm-hanging modes chimpanzees fed 89.4% and 84.6% of the time (Table 11). For arm-hanging (all modes), 90% of all observations were feeding.

Postural modes during food consumption or harvesting are tabulated in Table 12 (rows sum to approximately 100%). "Small" fruit species are those in which the height of adult trees was ≤ 15 m. No one postural mode appears to be specifically adapted to a nar-

TABLE 8. Locomotor mode frequencies by WBS size in Mahale adults

Location	Locomotion						
	Quadrupedal knuckle-walk	Climb	Palmar walk	Bipedal walk	Brachiate	Transfer	Run
< 3 cm (n = 57)	0.0	47.4	15.8	1.8	14.0	14.0	0.0
3-10 cm (n = 39)	2.6	43.6	35.9	0.0	10.3	0.0	2.6
> 10 cm (n = 1,615)	95.1	2.5	1.2	0.0	0.1	0.0	0.9
Median substrate size ¹	15.2(4)	7.6(84)	7.6(42)	5.1(2)	2.5(14)	1.3(8)	7.6(1)

¹Number of surveys in parentheses; tree observations only.

TABLE 9. Locomotion in chimpanzees while feeding and while traveling

Site	Activity	n	Knuckle- walk	Climb	Palm- walk	Bip. walk	Brachiate	Transfer
Mahale	Feed	123	57.7	13.0	21.1	1.6	4.1	2.4
	Travel	1,055	98.6	0.9	0.1	0.0	0.2	0.1
Gombe	Feed	34	58.8	11.8	20.6	5.9	0.0	2.9
	Travel	333	98.5	0.6	0.6	0.0	0.0	0.0

TABLE 10. Percentage of contexts for chimpanzees by stratum level (Mahale only)¹

Location	n	Context							
		Feed	Rest	Groom male	Groom ²	Looks	Move between patches	Move in patch	Travel
Terminal branches	763	87.8	5.1	0.8	1.2	0.8	0.5	1.2	0.0
Central tree	3,197	49.9	23.6	4.8	11.5	2.3	0.7	0.7	0.0
Tree	3,960	57.2	20.1	4.0	9.6	2.0	0.6	0.8	0.0
Ground	6,161	28.3	17.8	10.4	13.1	2.5	10.3	0.9	7.6
All levels ³	10,203	40.6	18.6	7.8	11.8	2.3	6.5	0.9	4.6

¹Not all contexts included; does not sum to 100%.

²Includes females, estrus females, juveniles, unidentified individuals, and autogrooming.

³Includes cases where there are no data on type of location within the tree.

row range of food items, but several trends are apparent. "Sit (in)" was the preferred posture while harvesting and eating stems of *Pennisetum purpureum*, perhaps because it is difficult to extend the legs among the closely set grasses. The "sit (out)" posture was used most often when eating fruit in small trees. This posture appeared to be particularly stable among small WBS because it increased diameter of the base of support by distributing weight over several branches. In larger trees large WBS were

more readily available and sit (in) and sit (out) postures constituted approximately equal percentages (21.4 vs 21.9%). Suspensory postures were used most often when feeding on fruit. Unimanual arm-hanging (without support) was most often used when feeding on fruit in large trees, whereas unimanual arm-hanging with support was used most often when feeding on fruit in small trees. It seemed that large trees were less likely to have tangles of interwoven vines or twigs that could be grasped with the feet

TABLE 11. Percentage of activities for chimpanzees by posture (sites pooled)¹

Posture	n	Context					
		Feed	Rest	Groom Male	Groom ²	Looks	Infant Care
Sit (in)	3,682	55.6	11.3	7.6	12.2	4.2	3.7
Sit (out)	3,918	50.9	12.8	9.0	18.2	2.4	3.4
Stand ³	186	34.4	3.2	4.8	5.9	16.1	1.1
Arm-hang	93	95.7	0.0	0.0	0.0	1.1	0.0
Arm-hang w/support	358	89.4	2.2	0.8	1.4	1.1	1.1
Lie	2,108	5.1	75.9	6.5	7.5	0.8	1.7
Arm-hang /Stand	52	84.6	0.0	0.0	0.0	0.0	1.9

¹Not all contexts included; does not sum to 100%.

²Includes females, estrus females, juveniles, unidentified individuals, and autogrooming.

³Listen, make nest, and rest in travel make up most of the rest of the contexts in this posture.

when hanging, and were more likely to have isolated branches so that arm-hanging (without support) was the only possible posture among the smallest strata.

Although lying was not a common feeding posture, when chimpanzees fed while lying the food item was most often fruit or insects. Sometimes chimpanzees carried a branch laden with fruit to a day nest or large trunk where they could lie, or fed lethargically on nearby fruit while lying in a day bed. While ant fishing individuals often lay to get closer to the anting aperture or to provide a stable position while leaving both hands free.

Squatting was observed often on vertical and subvertical (i.e., near-vertical) WBS. The WBS was grasped with the feet and the upper body was stabilized with an arm. Fruit found in small trees was harvested most often by squatting, perhaps because the trunk itself was the largest and most stable perch from which to feed.

Vertical climbing

Chimpanzees climbed significantly more often than baboons [Fisher's exact test; $P < .03$; $\chi^2(1) = 3.7$; Table 1], though the difference was small (0.9 versus 0.5%). The different frequencies of climbing may have been due to different strategies for ascending trees. Baboons often ascended by alternately leaping and walking on slightly angled WBS, whereas chimpanzees used less saltatory locomotor modes.

Ad lib observations suggested that chimpanzees preferentially entered trees by knuckle-walking on gently angled ($< 45^\circ$) large WBS (i.e., 15 + cm), or by palm-walking on somewhat smaller (5–15 cm) gently

angled WBS. If such means were not available chimpanzees vertical-climbed small (2–10 cm) vertical WBS, e.g., vines or adjacent small trees. Only if no large gently angled or small vertical WBS were available did chimpanzees climb large trunks. Over 85% of chimpanzee climbing bouts were on WBS 10 cm or smaller (Table 13; see also Fig. 1).

Two aspects of chimpanzee vertical climbing are worth emphasizing. First, chimpanzees did not fully abduct their humerus when climbing small, subvertical WBS, although when climbing graded into arm-hanging, the final reach before suspension often involved abduction. Second, the kinematics of baboon and chimpanzee vertical climbing differed little. When climbing small WBS the torso was held subvertical, angled forward so that the shoulders were closer than the hips to the WBS. Such a position appeared to balance the upper body so that propulsive force from the legs did not cause backward rotation. The arms assisted in elevating the body through flexure of the forearm and retraction (extension) of the humerus. The elbow was completely extended only very rarely when climbing small diameter WBS, remaining partly flexed even as the arm was raised above the head to its maximum extent. The elbow was elevated to perhaps 10 cm above the shoulder at most; the humerus was protracted (flexed) rather than abducted. That is, when elevated the humerus was held approximately parallel to the sagittal plane. A similar kinematic has been described in a laboratory setting (Larson and Stern, 1986). Despite the fact that baboons were not observed to fully abduct their hu-

TABLE 12. Percentage of food item harvested by posture

Posture	Food items												
	Insects	Blossom	Leaves	<i>Pennisetum</i>	Bark	Monkey	Shoots	Seeds	Stems	Pith	Fruit (large)	Fruit (small)	Fruit (ground)
Sit (in) (n = 1,637)	5.2	0.4	10.1	28.6	0.5	1.1	0.1	2.7	1.4	0.0	21.4	24.3	2.1
Sit (out) (n = 1,410)	6.5	1.1	10.6	14.4	0.1	0.0	0.3	1.4	1.9	2.9	21.9	36.0	2.0
Stand (n = 37)	5.4	2.7	13.5	16.2	10.8	0.0	0.0	0.0	0.0	0.0	27.0	18.9	5.4
Arm-hang (n = 66)	3.0	0.0	15.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	47.0	34.8	0.0
Arm-hang w/support (n = 224)	11.2	0.0	11.2	0.0	0.0	1.3	0.9	0.0	0.0	0.0	22.3	53.1	0.0
Lie (n = 48)	10.4	0.0	0.0	4.2	4.2	0.0	0.0	0.0	0.0	0.0	33.3	37.5	0.0
Squat (n = 32)	3.1	0.0	9.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	31.3	56.3	0.0
Arm-hang /stand (n = 32)	40.6	0.0	6.3	0.0	0.0	3.1	0.0	0.0	0.0	0.0	12.5	34.4	3.1

meri, and indeed seemed incapable of it, flexed-arm climbing made up a substantial part of their climbing repertoire (Table 14).

The mechanics of chimpanzee climbing were different on larger WBS. The chimpanzee foot can grasp a WBS of up to 10 cm in diameter with a power grip, but WBS substantially larger cannot be easily grasped (personal observation). On large diameter WBS an extended elbow climbing was evinced wherein a "leaning back" gestalt increased the friction between the tree trunk and the pes (Cartmill, 1974; Jungers, 1976; Jungers et al., 1982; Jungers and Susman, 1984). In such instances flexure of the forearm provided little or no propulsive force; extension of the spinal column and the hindlimbs and retraction of the humerus instead appeared to provide the climbing power. Stride length was extremely short; hands and feet were raised perhaps 10–50 cm at a time. This mode of climbing will be referred to as extended-arm climbing.

The extended-arm or large-trunk-climbing hypothesis predicts that chimpanzees climb larger WBS than baboons, a difference that should be pronounced given the larger body size of chimpanzees. Here there was no significant difference between chimpanzee (pooled Gombe and Mahale data) and baboon WBS diameters while climbing (Mann-Whitney *U* test, $U = 5163.5$, $P = .08$). Extended-arm climbing (see Table 14; Fig. 2) was observed in chimpanzees almost exclusively on WBS greater than 10 cm in diameter. Baboons showed a similar trend. Among baboons the extended elbow orientation was evinced during "pulse climbing," which was observed more often on large diameter WBS, whereas flexed-arm (hand-over-hand) climbing was associated with smaller WBS. Although baboons ascended by walking and leaping more often than chimpanzees, on extremely large vertical WBS both species used a type of climbing in which the elbow was completely extended.

DISCUSSION

Assessing the impact of positional behavior

Positional mode frequencies are an important consideration in assessing the evolutionary origin of positional anatomy. The more frequent a positional behavior, the greater the need for reinforcing the locomotor apparatus against positional-mode-specific injury and wear; the greater the need for shaping skeleton and muscle to prevent fa-

TABLE 13. Percentage of climbing bouts by WBS diameter

Site	n	WBS diameter in cm						
		2 and less	>2-4	>4-6	>6-8	>8-10	>10-20	>20
Mahale	101	9.9	40.6	27.7	6.9	3.0	9.9	2.0
Gombe	88	18.2	35.2	11.4	11.4	9.1	6.8	8.0

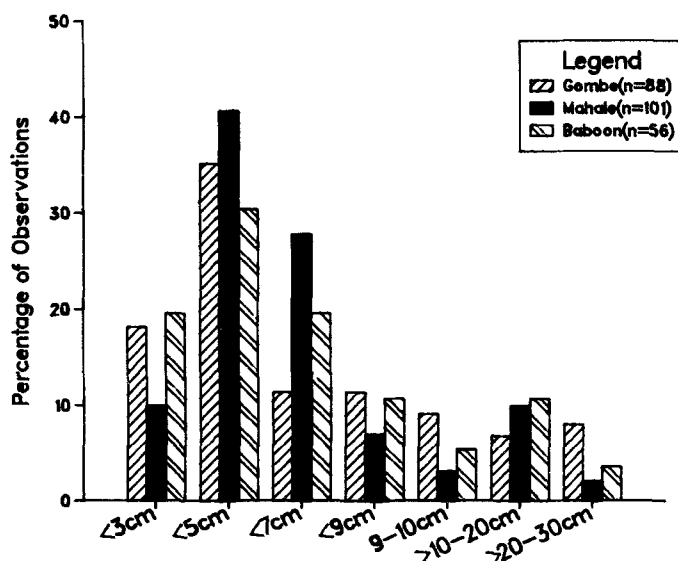


Fig. 1. Size of WBS in climbing compared in chimpanzees and baboons. Note that the size of WBS climbed

is quite similar in the two species. Neither species climbed strata larger than 20 cm frequently.

tigue; and the greater the opportunity for energy conservation if it is made more efficient. If the frequencies of various positional modes were the sole consideration in assessing positional adaptations, one would conclude that sitting is the most important positional behavior among chimpanzees (Table 1), and other positional behaviors, in order of decreasing importance could be said to be (2) quadrupedal knuckle-walking, (3) lying, (4) unimanual arm-hanging (all modes), (5) standing, (6) climbing, (7) squatting, and (8) palm-walking (other modes made up less than 0.5% each). Such an approach is clearly inappropriate. Certainly the frequency of a positional mode is an important selective force, but frequencies must be considered in comparison with other species to assess a morphological adaptation. Only by isolating a particular feature among species that also show a common behavior can function be

determined (Kay and Cartmill, 1977; Kay, 1984). In other words, the distinctiveness of the mode must be considered. Furthermore, the muscular effort required for a positional mode and the associated stress in the musculoskeletal system determine the anatomical adaptations required to allow it. Frequency, distinctiveness and physical stress must be considered together. That is, links can confidently be made between specific anatomical features and specific behaviors with a three-part protocol. First, the frequency of the behavior must be known in a representative sample of wild subjects; second, the distinctiveness of the behavior relative to other species must be demonstrated; and third, the physical stress involved must be established. Although the frequency of various positional modes was estimated rather accurately for chimpanzees (Table 1), measuring stress and distinctiveness is problematical. As a

TABLE 14. Percentage of climbing type by WBS diameter

Site	Climbing type	WBS diameter in cm						
		2 and less	>2-4	>4-6	>6-8	>8-10	>10-20	>20
Mahale chimp	Palmar-walk	0.0	2.7	3.7	28.6	0.0	10.0	0.0
	Knuckle-walk	0.0	0.0	0.0	0.0	0.0	10.0	0.0
	Flexed	100.0	97.3	96.3	57.1	100.0	50.0	0.0
Gombe chimp	Extended	0.0	0.0	0.0	14.3	0.0	30.0	100.0
	Palmar-walk	6.3	7.1	0.0	20.0	0.0	20.0	14.3
	Knuckle-walk	0.0	0.0	12.5	0.0	0.0	40.0	0.0
Baboon	Flexed	87.5	92.9	87.5	80.0	100.0	20.0	14.3
	Extended	0.0	0.0	0.0	0.0	0.0	20.0	71.4
	Walk	9.1	18.8	14.3	33.3	33.3	0.0	0.0
	Leap	18.2	12.5	14.3	0.0	0.0	20.0	0.0
	Flexed	63.6	37.5	28.6	16.7	33.3	0.0	0.0
	Pulse	9.1	31.3	42.9	50.0	33.3	60.0	100.0

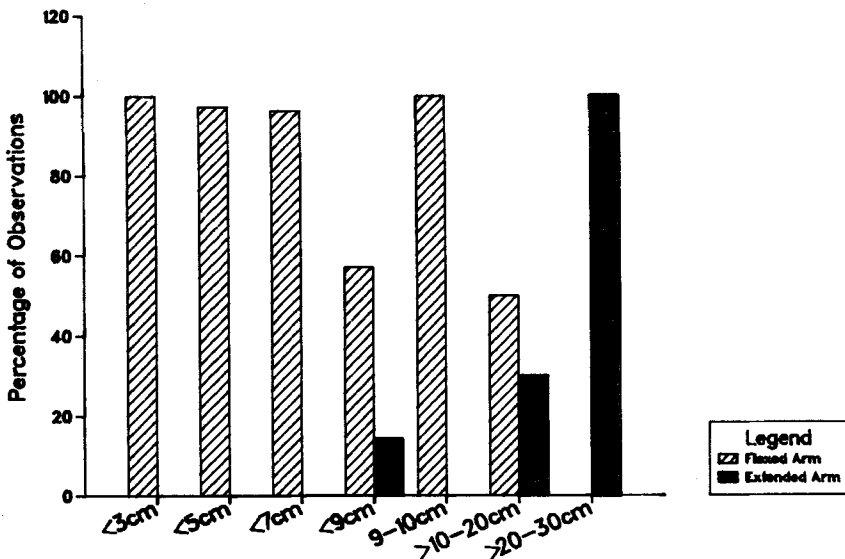


Fig. 2. Flexed vs extended arm climbing compared by size of supporting stratum. Data for this figure are given

in more detail in Table 14. Note that extended arm climbing is rare on substrates 10 cm and smaller.

first approximation, these latter factors are estimated as follows.

Physical stress

Although information derived from EMG study had been an important tool for explaining muscle function (Basmajian, 1965, 1972; MacConnail and Basmajian, 1969; Basmajian and Bazant, 1959; Basmajian and Stecko, 1963; Basmajian and Tuttle, 1973; Tuttle and Basmajian, 1974a,b,c; Tuttle et al., 1972; Stern et al., 1977, 1980; Susman and Stern, 1979; Tuttle et al., 1979;

Jungers and Stern, 1980; Stern and Susman, 1981; Stern et al., 1980), such information cannot be used to estimate physical stress when evolutionary issues are involved. Although high EMG activity in particularly large muscles does indicate great muscle, ligament, and bone stress, this simple association is complicated by the assumption that natural selection shapes the anatomy to reduce both muscular activity and structural stress in proportion to the frequency of the behavior (Basmajian, 1965; MacConnail and Basmajian, 1969; Cartmill et al., 1987). Positional behaviors for which animals are well

adapted are expected to produce less muscle activity and less stress in the skeleton and ligaments than behaviors for which the animal is poorly adapted. For example, during arm-swinging EMG potentials of some muscles are higher in a poorer brachiator (woolly monkey) than a better brachiator (spider monkey; Stern et al., 1977). Furthermore, joints evolve so that in posture ligamentous and skeletal elements, not muscles, bear body weight (Basmajian, 1965, 1972; Basmajian and Bazant, 1959; Basmajian and Greenlaw, 1968; Basmajian and Stecko, 1963; Cartmill et al., 1987). Theoretically, the more common the positional mode the greater the selective pressure to evolve this muscle sparing function. The consequence of this evolutionary response is that comparisons between species should follow the rather counterintuitive rule that less muscle activity accompanies behaviors for which an animal is particularly well adapted. In assessing which of two (or more) equally common positional modes should be accompanied by the greatest anatomical adaptations, the force applied to the WBS is the critical datum, rather than muscle activity or even stresses in the skeleton of any particular species. The latter can vary dramatically even in similar sized animals; the former must remain relatively constant regardless of how well adapted the animal is for the behavior.

As a preliminary method, force applied to the WBS for common chimpanzee positional modes was crudely estimated as high, medium, or low. Climbing was considered to entail high stress since it involves acceleration directly against gravity. Running and leaping were considered to entail high stress by virtue of their rapid acceleration. Other modes of locomotion were considered to have median force rankings (brachiating, walking, palm-walking, and bipedal walking). Postures (sitting, lying, unimanual arm-hanging, standing, squatting, clinging, and bipedal standing) were assumed to involve low stress.

Assessing distinctiveness

Distinctiveness was quantified by comparing chimpanzee positional frequencies to those of baboons. In Table 15 five positional modes that were significantly more common in chimpanzees than in baboons are bold faced. The proportion of chimpanzee to baboon percentages is presented in column 2 (percentage of the chimpanzee behavior di-

vided by the percentage of the same behavior in baboons; data from Table 1). Lying, for example, was 3.8 times more common in chimpanzees than baboons. Actual figures are given for cases where the frequency of the behavior was $< 0.1\%$ for baboons. Modes that were equal or more frequent in baboons cannot be considered to be distinctive chimpanzee behaviors. Proportions are ranked in column 3. The difference between chimpanzees and baboons in the percentages of each behavioral mode are presented in column 4. Column 5 (difference rank) ranks the behaviors in order from most distinctive to least distinctive.

Proportions and differences are each estimates of the distinctiveness of positional modes in chimpanzees, but each has its biases. Distinctiveness rank based on proportion may overrepresent rare behaviors when values are extremely low (e.g., 0.5 versus 0.1% gives a proportion of 5, but the values are so low that they may be insignificant nevertheless). Ranks based on differences may overemphasize the distinctiveness of common behaviors (e.g., the difference between 55 and 40% is greater than the difference between 10 and 0%, but is it more significant?). To moderate these biases distinctiveness will be assessed using the average rank of both methods (column 6, Table 15), and only for values that are significantly different. Of the 5 behaviors that are statistically more common in chimpanzees, the most distinctive to least distinctive are (1) lie, (2) unimanual arm-hang (all modes), (3) sit (in), (4) vertical climb, and (5) palm-walk.

Interpreting frequency, stress, and distinctiveness

To estimate the relative selective force exerted by each positional mode on the chimpanzee locomotor apparatus, the combination of frequency, stress, and distinctiveness must be considered together. The aim is to assess the likely importance of each positional mode in the evolution of distinctive chimpanzee morphological features. Below, each mode is discussed in order of highest to lowest frequency. Discussion is summarized in Table 16.

Sitting was the most common positional behavior in chimpanzees, constituting over 61% of their waking behavior (none of the data presented includes lying in a night nest). It was significantly more common in chimpanzees than baboons [Mahale and Gombe observations pooled, Fisher's exact

TABLE 15. *Distinctiveness of chimpanzee positional behaviors*

Positional behavior	Chimp/baboon proportion	Proportion rank ¹	Chimp-baboon difference (in %)	Difference rank	Average rank ²
Arm-hang ³	4.4/0	1	4.4	3	2
Lie ³	3.8	2	8.9	1	1.5
Climb ³	1.8	3	0.4	5	4
Squat	1.4	4	0.2	7	5.5
Sit (in) ³	1.3	5	5.9	2	3.5
Palm-walk ³	0.6/0	6	0.6	4	5
Bipedal stand	0.3/0	7	0.3	6	6.5
Susp. loco.	0.2/0	8	0.2	7	7.5
Bipedal walk	0.1/0	9	0.1	9	9
Cling	1.0	—	0.0	—	—
Sit (out)	0.98	—	-0.6	—	—
Walk	0.68	—	-7.5	—	—
Run	0.75	—	-0.1	—	—
Leap	0/0.2	—	-0.2	—	—
Stand	0.17	—	-12.5	—	—

¹For cases where the baboon figure is 0.0, the proportion is taken to be the percent of expression in chimpanzees.

²Proportion and difference ranks averaged.

³Positional modes in bold face are significantly more common in chimpanzees ($P < .05$; Fisher's exact test).

TABLE 16. *Distinctiveness, frequency, and stress for chimpanzee positional modes*

Positional behavior	Average distinctiveness	Frequency	Stress category
Sit (out)	—	0.340	Low
Sit (in)	3.5	0.284	Low
Walk	—	0.160	Medium
Lie	1.5	0.121	Low
Arm-hang	2	0.044	Low
Stand	—	0.025	Low
Climb	4	0.009	High
Squat	5.5	0.007	Low
Palm-walk	5	0.006	Medium
Bipedal stand	6.5	0.003	Low
Run	—	0.003	High
Cling	—	0.003	Low
Suspensory	7.5	0.001	Medium
Bipedal walk	9	0.001	Medium

test, $P < .0001$; $\chi^2(1) = 15.0$], and was third in average distinctiveness rank. As a posture, however, it falls in the lowest of the 3 tiered stress estimations presented above, and therefore probably presents little selective pressure in the form of injury. Furthermore, it is similarly common in other Old World primates for which there are quantitative positional information (Rose, 1974, 1977, 1978; Morbeck, 1977; Fleagle, 1978). Despite its high frequency and relatively high distinctiveness in chimpanzees, the low stress involved in sitting makes it unlikely to have been an important behavior in the evolution of distinctive chimpanzee anatomical traits.

Although posture made up over 80% of all chimpanzee positional behavior, knuckle-walking was the second most common positional mode (15.7%). Although the knuckle-walking mode of the African apes is unique among the primates, related morphological adaptations are expected to be limited to the manus and carpus, since selective pressures on other parts of the positional apparatus are presumably substantially similar to those in other primates. Whereas the knuckling aspect of chimpanzee walking is distinctive, walking was significantly more common in baboons [Fisher's exact test, $P < .0001$; $\chi^2(1) = 22.1$], indicating that walking may have less profound morphological implications for chimpanzees than for baboons and other monkeys. Quadrupedal walking is the most common locomotor mode in a number of primates [e.g., *Presbytis obscura* (Fleagle, 1980), *Saguinus midas*, *Saimiri sciureus*, *Chiropotes satanas*, *Cebus apella*, and *Alouatta seniculus* (Fleagle and Mittermeier, 1980)] and is very common in some other primates [*Galago crassicaudatus* (Crompton, 1984), *Saguinus oedipus* (Garber, 1984), *Alouatta seniculus* (Schon Ybarra and Schon, 1987), and *Colobus guereza* (Rose, 1978)]. Evidence that knuckling is responsible for many characteristics of the wrist and hand shared by the African apes (Tuttle, 1965, et seq.) is supported, but walking per se cannot be the behavior for which characteristic ape features are evolved since quadrupedal walking is less common in hylobatids (Chivers, 1972; Fleagle, 1976b,

1980; Srikosamatara, 1984) and orangutans (MacKinnon, 1974; Galdikas, 1978, 1979; Sugardjito, 1982; Sugardjito and van Hooff, 1986; Rodman, 1984; Cant, 1987a,b) than are other behaviors previously proposed to be responsible for ape ("brachiating") characteristics (Hunt, 1991).

Lying was the third most common chimpanzee positional mode; its frequency was significantly higher in chimpanzees than in baboons [Fisher's exact test, $P < .0001$; $\chi^2(1) = 40.1$] and its average distinctiveness rank was highest of any positional mode. However, in lying the weight of the body is distributed over large areas, reducing stress on any one body part. Adaptations for maintaining anatomical integrity during locomotion are likely to have preadapted the body for such a relatively nonstressful behavior. Lying requires little muscular activity to stabilize or balance the body and thus selection to improve efficiency is probably unimportant. Despite its high frequency and high distinctiveness, the low stress involved in lying (presumably the lowest of all positional behaviors observed) argues against its having been an important selective force for creating or maintaining the distinctive aspects of chimpanzee morphology.

Arm-hanging with support [Fisher's exact test, $P < .0001$; $\chi^2(1) = 34.7$], unimanual arm-hanging [Fisher's exact test, $P < .0001$; $\chi^2(1) = 15.7$], and arm-hang/standing [Fisher exact test, $P < .005$; $\chi^2(1) = 5.3$] were each significantly more common in chimpanzees (sites pooled) than baboons. Pooled arm-hanging modes, each of which was characterized by a fully abducted humerus, constituted 4.4% of all positional behavior, the fourth most common positional mode. The average distinctiveness rank of arm-hanging (all modes) was very high (second only to lying). Unlike sitting and lying, arm-hanging was both a distinctive chimpanzee posture and a behavior with physical demands unlike those of other positional behaviors. It is likely to have associated physical adaptations that distinguish chimpanzees from baboons, and, indeed, from all Old World monkeys for which there are quantitative data (Rose, 1974, 1977, 1978; Morbeck, 1977; Fleagle, 1978).

Standing constituted 2.5% of all positional behavior. Chimpanzees spent much less time standing than baboons [sites pooled; Fisher's exact test, $P < .0001$; $\chi^2(1) = 344.7$]; standing therefore cannot be responsible for chimpanzee specializations.

Climbing constituted 0.9% of all positional

behavior; it was significantly more common in chimpanzees than in baboons [Fisher's exact test, $P < .03$; $\chi^2(1) = 3.7$]. It is the second most common chimpanzee locomotor mode and the sixth most common positional behavior. It had an average distinctiveness rank of 4. It was placed in the highest stress category. Its high stress and distinctiveness support previous work postulating that this behavior is responsible for some chimpanzee specializations (Fleagle et al., 1981). There is, however, little support for the large-WBS-climbing hypothesis or for the contention that vertical climbing selected for ape humeral abduction abilities. Climbing WBS diameters and kinematics were not significantly different between chimpanzees and baboons. Vertical climbing constituted less than 1% of the total positional repertoire, and extended-arm climbing made up only 6.6% of that. It is possible, however, that extended-arm climbing might be a more common positional mode in other habitats, since Gombe and Mahale habitats had few emergents (Collins and McGrew, 1988), and therefore few resources that could not be harvested by climbing smaller trees or vines instead of large central trunks. Data presented here, however, indicate that extended arm climbing is not a distinctive aspect of the chimpanzee positional repertoire.

The frequency of squatting was 0.7% compared to 0.2% in baboons (Table 1). Its average distinctiveness rank was 5.5, or sixth of all positional behaviors. Its stress category was low. Considering its low stress, low frequency, and relatively low distinctiveness, its evolutionary significance for chimpanzee anatomy is probably low as well.

Palm-walking (0.6%) was significantly more common in chimpanzees than in baboons [Fisher's exact test, $P < .002$; $\chi^2(1) = 10.0$]. It had an average distinctiveness rank of 5 (fifth) and a stress estimation of medium. This behavior was different from knuckle-walking in the orientation of the manus (the long axis of which appeared to be rather perpendicular to the direction of movement, requiring that the wrist be supinated), in the extent of dorsiflexion of the manus and in the volar contact with the WBS. The medium stress rank and high distinctiveness rank are evidence that adaptations to this mode may be greater than those for squatting, but less than those for knuckling, arm-hanging (all modes), and climbing. More intensive study of the orientation of the manus during this locomotion

and of the stresses in the carpus and manus is warranted.

Bipedal standing, clinging, and running each was observed in chimpanzees 0.3% of the time. Although bipedal standing required supporting the substantial weight of the upper body against gravity, its low frequency and relatively low distinctiveness argue against it being an important chimpanzee adaptation. Clinging and running were not distinctive in chimpanzees (see Table 15).

Brachiation constituted 0.1% of all positional behavior. It is pooled with other humerus-abducted suspensory locomotion (transferring, dropping, clambering, and arm-swinging), together termed "suspensory locomotion." This pooled mode constituted 0.2% of all positional behavior. Its average distinctiveness rank was 7.5 (eighth) and its stress was medium. Suspensory behaviors necessitate suspending the body by one or both arms with the scapula rotated and the humerus abducted. Although the frequency of suspensory behaviors was low, the suspension of the body weight from a single forelimb may exert great stress on the shoulder and this mode may, therefore, have some evolutionary consequences.

Bipedal walking is the least common of the categories here presented. Its distinctiveness is low and stress is medium. Its rarity argues against any significant anatomical adaptations.

CONCLUSIONS

The first functional discussion of the positional adaptation of apes emphasized the impact that large body size had on mobility within the canopy (e.g., Avis, 1962; Rose, 1974, 1978; Ripley, 1967; 1970, 1979; Grand, 1972, 1984). The small size of available WBS in the most productive areas of fruiting trees was seen as the most significant evolutionary pressure selecting for suspensory locomotion. Data reported here support the suspensory (as opposed to locomotor) aspect of this paradigm. There were, however, no significant differences in mean WBS diameter between baboons and chimpanzees, indicating that chimpanzees may not have a greater competence on small WBS. Nevertheless, chimpanzees used suspensory postures in much greater frequency among the smallest WBS, and arm-hanging had the smallest average and median WBS of all feeding postures. The proportion of arm-hanging (all

modes) rose the most of any posture as WBS size decreased (Table 5). Arm-hanging (all modes) was seen in the context of feeding more than any other posture. This evidence strongly supports the hypothesis that suspensory behavior is an adaptation to harvesting fruits in the terminal branches and that suspension helps to retain positional competence on small-diameter WBS despite the larger body size of chimpanzees compared to monkeys.

Of all locomotor modes, vertical climbing, brachiation, and transferring were the most common among the smallest WBS. Small sample sizes make conclusions tentative, but it appears that climbing and transferring are preferred over brachiation among small WBS. These results conflict with the contention that brachiation (*sensu stricto*) provides increased competence or efficiency among small diameter WBS.

Consideration of the frequency, stress, and distinctiveness of each positional mode in chimpanzees permits a ranking of behaviors with respect to selective force on morphology. Of the common chimpanzee positional behaviors, the high frequency and distinctiveness of knuckling argue for a strong adaptive response in the wrist and hand, but knuckling cannot explain the most distinctive morphology of chimpanzees and other hominoids. Lying and sitting produce too little stress to have important adaptations. Other positional behaviors are regarded as less important either because they are not distinctive or not common. After lying and sitting (*sit in*), arm-hanging (all modes) was the most distinctive positional behavior of chimpanzees. Although its stress was categorized as low, its high frequency and high distinctiveness argue for substantial morphological adaptations. Although vertical climbing was observed at low frequency in chimpanzees and was considerably less distinctive than arm-hanging, it was in the highest stress category. Vertical climbing, however, was kinematically similar in baboons and chimpanzees, whereas arm-hanging was unlike any behavior observed in baboons, since it often involved complete humeral abduction.

Data presented here suggest that arm-hanging (all modes) and climbing are the two behaviors that most distinguish chimpanzees from baboons, and presumably from other monkeys as well. Functional anatomists should pay particularly close attention to

chimpanzee morphological complexes that are expressly involved in these two behaviors.

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APPENDIX A: POSITIONAL MODES

- i. *Sit (in)*: sitting with the weight supported by the ischia and one or two legs, of which the hip and knee were tightly flexed so that the heel(s) were near or touching the ischia and dorsal aspect of the thigh. The feet were judged to have borne an amount of the weight roughly proportional to that borne by the ischia. The trunk was orthograde.
- ii. *Sit (out)*: sitting with the legs extended, that is, the feet "out" so that the ischia bore most of the body weight. The feet were used mainly for balance, and did not appear to bear much more than their own weight. Sit/recline was included in this category; it was a

type of sitting in which the ischia bore most of the weight, but the elbow, back, stomach, side, or some part of the forelimbs may have been in contact with the supporting stratum. This mode is made up mostly of a torso-orthograde posture similar to that of a person sitting in a chair.

iii. *Cling*: this posture was observed on vertical or subvertical strata. One or two hands grasped the WBS, the elbow(s) was (were) flexed, the humerus was adducted and the torso was held at or near an orthograde orientation. The feet may or may not have grasped the substratum, but supported a proportional part of the body weight. The ischia bore none of the body weight. Rarely, two separate horizontal branches were used in clinging, or the hands grasped a horizontal branch while the feet contacted a vertical support.

iv. *Stand*: posture on 3 or 4 limbs on a relatively horizontal supporting stratum. The elbow and knee were typically extended and the trunk was close to horizontal (pronograde). Crouch was rare (<1% of all behavior) and was subsumed under standing; in this behavior the individual stood quadrupedally on a relatively flat stratum with the elbows flexed. Rarely the knees also were slightly flexed.

v. *Bipedal stand*: posture on the two hindlimbs with no significant support from any other body part. The torso was typically held at a 45° angle, and was rarely completely orthograde.

vi. *Arm-hang*: unimanual suspension with no other part of the body contacting a WBS. The humerus was abducted and the elbow was complete extended. The trunk was orthograde.

vii. *Arm-hang with support* (AHsupp): hanging with what was judged to be approximately half of the body weight suspended from one forelimb and the other half supported by some combination of the ischia, feet (with hindlimbs flexed), side, back or (rarely) the elbow of the contralateral arm. Rarely one arm was observed to be completely abducted whereas the other forelimb was used in a manner similar to that seen in clinging, that is, with the humerus adducted and the forearm flexed. In these rare cases whether the animal was scored as arm-hanging or clinging depended upon which arm appeared to be bearing the most weight. The humerus was less often completely abducted in this type of posture than in unimanual

arm-hanging. Arm-hang/stand was a rare posture and was subsumed under this mode. It is a combination of suspension by the arm(s), with the humerus completely abducted, and bipedal standing, with the knee and hip extended and weight borne equally by the forelimb(s) and the feet. The trunk was almost always orthograde. The hand-foot hang typical in orangutans (trunk horizontal; Cant, 1987a,b) was rare in chimpanzees and was subsumed under this mode.

viii. *Lie*: reclining on a relatively horizontal WBS with the body weight borne by the back, side, or stomach. Occasionally the animal grasped a supporting WBS, but it was judged that the limb involved bore little more than its own weight. Often, however, when lying on a side individuals supported the upper body by an elbow resting on the lower stratum, usually the ground.

ix. *Squat*: the body weight was borne by the feet, with both the hip and the knee strongly flexed. The arms bore less than a proportional amount or none of the body weight. The trunk was vertical.

x. *Quadrupedal knuckle-walk*: locomotion characterized by the common primate diagonal couplet (Hildebrand, 1967; Larson and Stern, 1987). Forelimbs contacted the WBS via the knuckles and the feet either rested on the volar skin or grasped a WBS. Crutching (a rare behavior constituting <0.1% of all locomotion) was also included in this mode. This was a terrestrial knuckling locomotion where the adducted forelimbs moved forward in concert, the elbow completely or almost completely extended. After planting the forelimbs the body and the hindlimbs are swung through the arms. Crutching was seen almost exclusively in the descent of extremely steep hills.

xi. *Climb*: ascending and descending locomotion on WBS at greater than a 45° angle. This mode refers to vertical climbing only. The kinematics of the mode described here are depicted in Fleagle et al. (1981, Fig. 5). Of the modes Fleagle (1976b) included in quadrumanous climbing, only that depicted in Figure 4 falls into this category. Other behaviors that might be labeled quadrumanous climbing were categorized as walking (Fleagle, 1976b, Fig. 3), suspensory locomotion (other than brachiation, e.g., amoebic locomotion; Fleagle, 1976b, Fig. 2), arm-swinging, transferring, clambering (sensu Cant, 1987a), and scrambling. In the most common type of vertical climbing a hindlimb

and its contralateral forelimb provided propulsion. The arms helped to elevate the body by the retraction of the humerus and flexion of forearm. This flexion is noted in calling this mode of locomotion flexed-arm climbing. In flexed-arm climbing the elbow rarely rose more than approximately 10 cm above the shoulder, and the humerus was typically protracted, (i.e., overhead anterior reach, Larson and Stern, 1986) in the process of reaching upward, not abducted. The torso was held nearly parallel to the WBS being climbed. When descending there was more abduction of the arm than was common in ascension. A variation on flexed-arm climbing was observed on horizontal WBS, or tangles of small twigs. This type of climbing was very similar to the movement of a person climbing a ladder. It was similar to flexed-arm climbing and the two modes were pooled for this analysis. On large WBS (> 20 cm) a different type of climbing was observed. The elbow was extended and the WBS was gripped by the entire volar surface of the hand, including palm and fingers, and the retraction of the arm appeared to provide very little of the force needed to elevate the body. Instead, retraction of the humerus and extension of the hindlimbs provided most of the propulsive power. This mode of climbing is considered in more detail above, where it is analyzed separately from other types of climbing. For most analyses, however, it was pooled with other climbing behaviors. Two other extremely rare behaviors kinematically similar to hand-over-hand climbing were included in this mode; namely, "pull-up" (hauling or hoisting) and "pulse climbing" or bear climbing (MacKinnon, 1974; this mode was observed only in baboons in this study). In a pull-up a branch, usually horizontal, was grasped by both hands in an arm-hanging posture and the body was lifted by retraction of the humerus and flexion of the forearm. In pulse climbing the forelimbs grasped the WBS and the hindlimbs were gathered underneath the body by flexure of the knee, hip, and spine, the legs and back were extended pushing the body upward, while the forelimbs simultaneously and in unison reached upward to grasp a higher handhold. This motion has a pulsing appearance as the animal ascends the vertical or subvertical WBS. Pooled also with climbing is a rare mode (< 0.1% of all behavior) labeled firepole slide, wherein a vertical WBS, usually very large, was grasped by circum-

ducting it with the arms and legs, after which the animal allowed its body to descend by sliding. Sometimes the arms regulated the velocity of the descent with a hand-over-hand movement.

xii. *Quadrupedal palm-walk*: locomotion similar to knuckle-walking, except that the forelimbs contacted the WBS by the volar surface. This behavior was similar to Fleagle (1976b, Fig. 3). Chimpanzees supinated and partly dorsiflexed the wrist so that a larger portion of the volar area contacted the WBS. Occasionally the thumb was recruited to produce a power grip. The term *scrambling* was used to describe nonsuspensory quadrupedal progression without a regular gait and with grasping cheirideal contact. This type of locomotion was seen on small and/or extremely irregular WBS, especially in the terminal branches of trees. Progression was primarily horizontal. The torso was typically held fairly pronograde, unlike the largely suspensory *clambering* mode common in orangutans, in which the torso was held vertical and progression was assisted by the hindlimbs (Cant, 1987a,b). Scrambling was rare in chimpanzees and the mode was subsumed under palm-walking.

xiii. *Bipedal walk*: only the hindlimbs were used in locomotion. In most cases bipedalism was characterized by hip and knee flexion but still involving a stride of perhaps 0.25 m. Although bipedal running was seen rather often during adult male social display, it was never sampled.

xiv. *Run*: the hand and wrist bore weight in a knuckled orientation, while the volar surface of the foot contacted the WBS. A period of free flight was observed.

xv. *Brachiate*: hand-over-hand orthograde suspensory locomotion was virtually no contribution by the hindlimbs in support or locomotion. In chimpanzees this behavior was typically slow and without a period of free flight. The swing phase ended with both arms contacting the superstratum approximately a meter apart briefly after which the trailing grip was released and a pendulum-like swing began. In almost all cases the humerus was completely abducted and the elbow was completely extended. When the term brachiation is used, only this hand-over-hand suspensory locomotion is meant.

xvi. *Leap*: the flexed hindlimbs and spine were forcefully extended to propel the animal into a period of free flight. Hop described a bipedal progression where both feet

pushed off roughly simultaneously followed by a period of free flight; it was rare and was subsumed under leaping. Included in this mode is a rare (i.e., < 0.1% of all behavior) "dropping" locomotion where the animal leapt with little force, or dropped, and caught itself on a lower stratum with the forelimbs, after which a period of suspensory locomotion or posture was commonly seen. The suspensory aspect of the behavior was recorded as such and included in the next category.

xvii. *"Other suspensory locomotion"* was used as a catch-all suspensory category that included a number of kinematically similar locomotor modes in which there was full humeral abduction, but which could not be called brachiation (*sensu stricto*). This mode is pooled with brachiation in Table 1 under the label "miscellaneous suspensory behavior." Among these behaviors were arm-swinging, transferring, "riding," and "amoebic" locomotion (*sensu Kortlandt, 1974*). Arm-swinging is used to denote a mode in which both hands release a WBS at the same time after briefly swinging under it. Often both grasp another WBS nearly simultaneously as well. In chimpanzees a typical bout began with the elbows extended, the arms adducted, and the hands near the hips bearing most of the weight on a single hori-

zontal WBS. From this pose the torso descended, remaining orthograde, so that the individual swung under the branch that had been near the waist. Transferring most often began with arm-hanging, followed by a lunge to grasp an adjacent small branch. The branch was pulled toward the animal with a hand-over-foot motion, and weight was gradually transferred to the new WBS. Unlike brachiation this locomotion was irregular; it often involved support or partial suspension from the hindlimbs. "Riding," a behavior similar to tree swaying, was subsumed under this category as well. In this mode of locomotion a vertical, small-diameter tree was grasped in a clinging posture and a violent movement was used to overbalance it. The weight of the animal's body pulled the tree from a vertical orientation toward horizontal. As the tree approached horizontal a suspensory posture resulted, after or during which the grip with the hindlimb was released and the feet contacted some lower WBS, usually the ground. "Amoebic" locomotion, also included in the "misc. susp." category, was a suspensory movement among very small WBS whereby changing contact points and shifting weight effected a slow movement without a distinct locomotor bout. This behavior is perhaps analogous to Cartmill and Milton's (1977) cautious climbing.