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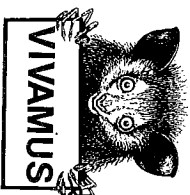
Positional Behavior in the Hominoidea

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Quantitative studies on the positional behavior of members of the Hominoidea are compared in order (1) to identify consistencies across the superfamily, (2) to contrast ape positional behavior with that of Old World monkeys (forest-living Papio anubis were chosen for study to reduce body size effects), and (3) to identify distinctive behaviors in each of the ape taxa. Differences in the way behaviors were sampled in the various studies necessitated considering posture and locomotion separately. Unimanual arm-hanging and vertical climbing were the most distinctive shared postural and locomotor modes among the apes (the gorilla excepted), constituting ≥5.0% and ≥4.9% of all behavior in each species. Arm-hanging and brachiation (sensu stricto) frequencies were the highest by far in hylobatids. Hand-foot hanging, bipedal posture, and clambering, an orthograde suspensory locomotion assisted by the hindlimbs, were more common in orangutans than in any other hominoid. Sitting and walking were observed in the highest frequencies in the African apes but were no more common than in the baboon. Relatively high frequencies of brachiation (sensu stricto) were reported for all apes except chimpanzees and gorillas. Brachiation and arm-hanging were kinematically different in apes and baboons, involving complete humeral abduction only in the former; whereas vertical climbing appeared to be kinematically similar in apes and baboons. It is concluded that the morphological specializations of the apes may be adaptations to (1) the unique physical demands of arm-hanging and (2) less kinematically distinct, but still quantitatively significant, frequencies of vertical climbing.

KEY WORDS: locomotion; posture; brachiation; climbing; arm-hanging.

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INTRODUCTION

It is presumed that some positional congruity among the apes accounts for the common occurrence among them of high intermembral indices, long, curved metacarpals and phalanges, mobile shoulders, mediolaterally reduced scapulae, cranially oriented glenoid fossae, anteroposteriorly flattened torsos with concomitantly long clavicles, strongly curved ribs resulting in more ventrally placed vertebral bodies, wide manubria of the sterna, reduced numbers of lumbar vertebrae, the lack of a tail (Keith, 1891, 1899, 1903, 1923; Schultz, 1930, 1936, 1953, 1956; Erikson, 1963; Roberts, 1974; Susman, 1979), distinctive pelvic floors (Keith, 1923), and a predominance of muscles that flex the elbow, extend the humerus, and raise the arm (Ashton and Oxnard, 1963, 1964a; Napier, 1963a; Oxnard, 1963, 1967; Ashton et al., 1965; Tuttle, 1969). It was realized early on that the important datum was not the behavior that most distinguishes a particular ape, but the behavior that is both common among apes and rare among other primates. Keith (1891, 1899, 1903, 1923, 1940, 1950) proposed that the important shared behavior was brachiation, and with modification and expansion (Gregory, 1916, 1928, 1934; Morton, 1922, 1926; Frey, 1923; Miller, 1932; Midlo, 1934; Washburn, 1950, 1963; Washburn and Avis, 1958; Washburn and Hamburg, 1965; Avis, 1962; Ripley, 1970; Ellefson, 1974; Rose, 1974, 1978; Mendel, 1976; Jenkins, 1981), the brachiation paradigm became so predominant that virtually every anatomical specialization of the apes was attributed to it (Napier, 1963a, b, 1967; Erickson, 1952, 1954, 1957, 1963; Ashton and Oxnard, 1963; Oxnard, 1963, 1967; Bishop, 1964; Benton, 1967, 1976; Jones, 1967; O'Connor, 1975, 1976; Napier, 1963a; Lewis, 1965, 1969, 1970, 1971a, b, 1972a, b, 1974).

Naturalistic study of ape behavior did not support the brachiation hypothesis. Gorillas (Schaller, 1963; Bingham, 1932; Donisthorpe, 1958; Schaller, 1963; Schaller and Emlen, 1963; Tuttle and Watts, 1985), chimpanzees (Nissen, 1931; Goodall, 1963; Kortlandt, 1962; Reynolds, 1965), and even orangutans (Carpenter, 1938; Schaller, 1961; Harrison, 1962) were observed to brachiate (sensu stricto)[2] little, although evidence from some chimpanzee researchers was equivocal (e.g., Reynolds and Reynolds, 1965; Goodall, 1968).

The brachiation hypothesis was salvaged by liberalizing the purview of brachiation. Humeral abduction and propulsion dominated by the forelimbs, whether in hand-over-hand suspensory locomotion or not, were perils.

[2]The 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). Ricochetal brachiation is used even more restrictively to mean only gibbon-like brachiation with a period of free flight.

Table I. Posture Compared in the Hominoidea

Species	Percentage of postural behavior								n	Reference
	Sit	Lie	Stand	Squat	Cling	Bipedal stand	Arm-hang	Hand-foot hang		
Hylobates agilis[a]	65.5	0.0	0.0	0.0	0.0	0.0	34.5	0.0	322 bouts	Gittins (1983)
Hylobates pileatus[b]	61.7	0.0	0.0	0.0	0.0	0.0	38.3	0.0	655 observations	Srikosamatara (1984)
Hylobates syndactylus[c]	38.3	0.0	0.0	0.0	0.0	0.0	61.7	0.0	1376 observations	Fleagle (1976b)
Hylobates syndactylus[d]	47.0	0.0	0.0	0.0	0.0	0.0	53.0	0.0	234 observations	Chivers (1972)
Pan paniscus[e]	90.0	3.0	2.0	0.0	0.0	0.0	5.0	0.0	132 observations	Kano and Malavwa (1984)
Pongo pygmaeus[f]	46.0	0.0	24.4	0.0	0.0	0.0	29.7	0.0	5836 bouts	Sugardjito and van Hoof (1986)
Pongo pygmaeus[g]	42.1	0.0	6.7	0.0	0.0	3.8	17.8	30.0	350 bouts	Cant (1987b)
Pongo pygmaeus[h]	49.0	0.0	1.0	0.0	0.0	2.0	12.0	36.0	1682 min	Cant (1987a)
Pan troglodytes[i]	80.0	5.0	15.0	0.0	0.0	0.0	0.0	0.0	186 hr	Sabater Pi (1979)
Pan troglodytes[j]	75.2	15.1	3.0	0.8	0.4	0.4	5.3	0.0	11848 observations	This study
Pan troglodytes[k]	80.9	3.4	1.3	1.9	0.3	0.3	12.1	0.0	2518 observations	This study
Gorilla gorilla[l]	60.3	1.3	2.7	35.4	0.0	0.2	0.0	0.0	2300 hr	Tuttle and Watts (1985)
Papio anubis[m]	75.3	4.0	19.7	0.2	0.3	0.1	0.2	0.0	1555 observations	This study
Papio anubis[n]	75.9	0.0	21.1	0.6	1.0	0.2	1.0	0.0	580 observations	This study

[a]Percentage of scan surveys, every 10 min.
[b]Percentage of scan surveys, every 5 min.
[c]Percentage of total positional behavior during feeding.
[d]Percentage of focal observations; instantaneous every 5 sec.
[e]Percentage of instantaneous surveys while feeding on fruit.
[f]Percentage of all bouts during travel and resting.
[g]Percentage of bouts while feeding on Ficus fruit.
[h]Percentage of time in each posture while feeding. Females only.
[i]Percentage of time in each posture.
[j]Percentage of instantaneous focal observations standardized for hour of day; adults only. Mahale and Gombe profiles averaged.
[k]Percentage of instantaneous focal observations while feeding on fruit. Standardized for hour of day; adults only. Mahale and Gombe profiles averaged.
[l]Percentage of time in each behavior; juveniles included.
[m]Percentage of instantaneous focal observations; all contexts.
[n]Percentage of instantaneous focal observations during feeding bouts.

Table II. Orangutan and Chimpanzee Posture Compared During Feeding in *Ficus* Trees[a]

Group	Posture						
	Sit	Bipedal stand	Stand	Arm-hang (AH)	AH supp	Hand-foot hang	Cling, squat
Mahale chimp (n = 436)	84.4	0.7	0.0	4.1	6.9	0.0	1.1
Gombe chimp (n = 76)	65.8	0.0	3.9	5.3	21.1	0.0	3.9
Orangutan (6.3 hr)	42.1	3.8	6.7	0.6	17.2	30.0	0.0

[a] Data for orangutans are midsex averages for two *Ficus* spp. trees from Cant (1987b). Data for chimpanzees are from feeding observations on all *Ficus* spp. except *Ficus urceolaris*.

ceived as the important kinematics of the brachiation hypothesis, and consequently the scope of the term brachiation was expanded to include any behavior for which these criteria applied, such as vertical climbing, hoisting, arm-swinging, and, at least tacitly, any humerus-abducted or forelimb-dominated behavior (Washburn, 1968, 1973; Morbeck, 1972). This generalization pooled very different positional modes and resulted in considerable confusion (as discussed by Tuttle, 1974; Andrews and Groves, 1976) without resolving the issue.

A more specific behavior than brachiation (*sensu lato*) seemed called for. Some features of the wrists of African apes were established to be adaptations to knuckle-walking (Tuttle, 1965, *et seq.*; Jenkins and Fleagle, 1975; Rodman, 1984; Grand, 1984). Such adaptation, however, may be limited to the wrist and manus,[3] since apes are no more walkers than other primates (Richard, 1970; Chivers, 1972; Rose, 1974, 1977, 1978; Mendel, 1976; Fleagle, 1976a; Mittermeier and Fleagle, 1976; Morbeck, 1977a, b; Mittermeier, 1978; Sabater Pi, 1979; Fleagle and Mittermeier, 1980; Susman et al., 1980; Sugardjito, 1982; Gittins, 1983; Crompton, 1984; Garber, 1984; Crompton and Andau, 1986; Cant, 1986) (Tables I–III), leaving most ape specializations unexplained. Subsequently, quadrumanous (or cautious) climbing was hypothesized to be the positional behavior responsible for "brachiating" characters (Kortlandt, 1974; Tuttle, 1975; Fleagle, 1976b; Mendel, 1976; Stern et al., 1977; Fleagle et al., 1981; Tuttle et al., 1979; Cartmill and Milton, 1977). Quadrumanous climbing, however, encompasses, among other behaviors, both suspensory locomotion (Fleagle,

[3] The hypothesis that the olecranon fossa in African ape humeri is formed to "lock" the elbow during knuckling behavior (McHenry, 1975) was disputed by Feldesman (1982). In any case, it is the greater body size of the apes, not knuckling, that makes close packing advantageous.

Table III. Locomotion Compared in the Hominoidea

Species	Percentage of locomotor behavior									n	Reference
	Walk	Climb	Leap/hop	Run	Bipedal walk	Brachiate	Clamber	Other susp.	Transfer		
Hylobates agilis[a]	3.5	6.3	23.9	0.0	0.0	66.3	0.0	0.0	0.0	255 observations	Gittins (1983)
Hylobates lar[b]	0.0	34.1	9.5	0.0	5.2	51.2	0.0	0.0	0.0	211 bouts	Fleagle (1980)
Hylobates pileatus[c]	0.0	6.0	8.7	0.0	0.9	84.4	0.0	0.0	0.0	218 observations	Srikosamatara (1984)
Hylobates synd.[d]	0.0	10.0	0.0	0.0	11.0	80.0	0.0	0.0	0.0	208 observations	Chivers (1972)
Hylobates synd.[e]	0.0	54.3	3.2	0.0	4.6	37.9	0.0	0.0	0.0	1206 bouts	Fleagle (1976b)
Pan paniscus[f]	34.0	20.0	18.0	0.0	8.0	20.0	0.0	0.0	0.0	131 bouts	Susman et al. (1980)
Pan paniscus[g]	31.0	31.0	10.0	0.0	6.0	21.0	0.0	0.0	0.0	1722 bouts	Susman (1984)
Pongo pygmaeus[h]	13.0	10.0	0.0	0.0	0.0	21.0	41.0	0.0	15.0	219 hr	Sugardjito (1982)
Pongo pygmaeus[i]	10.8	9.8	0.0	0.0	0.0	19.8	43.0	0.0	16.8	10601 bouts	Sugardjito and van Hooff (1986)
Pongo pygmaeus[j]	12.0	31.3	0.0	0.0	0.0	10.6	39.4	1.2	5.6	4360 min	Cant (1987a)
Pan troglodytes[k]	92.1	4.9	0.1	1.3	0.4	0.5	0.3	0.0	0.3	2239 observations	This study
Pan troglodytes[l]	36.4	48.9	0.4	0.3	6.7	5.3	2.3	0.6	2.4	223 observations	This study
Papio anubis[m]	97.0	0.7	0.5	1.6	0.0	0.0	0.0	0.0	0.0	497 observations	This study
Papio anubis[n]	64.2	21.3	10.4	4.1	0.0	0.0	0.0	0.0	0.0	26 observations	This study

[a] Percentage of 10 min scan surveys.
[b] Percentage of bouts, continuous focal observation.
[c] Percentage of 5-min scan surveys.
[d] Percentage of focal observations; instantaneous every 5 sec.
[e] Percentage of bouts, continuous focal observation; feeding and travel bouts pooled.
[f] Figures represent percentage bouts during arboreal feeding.
[g] Figures represent percentage of observed bouts, mostly during feeding.
[h] Percentage of observed bouts during travel.
[i] Percentage of observed bouts during travel.
[j] Proportions of travel distance during feeding and travel. Females only.
[k] Percentage of locomotion in all contexts. Standardized for hour of day; Gombe and Mahale data pooled.
[l] Percentage of arboreal locomotion in all contexts; Gombe and Mahale data pooled. Too few observations to standardize.
[m] Percentage of locomotion in all contexts; Standardized for hour of day; adults only.
[n] Percentage of arboreal locomotion in all contexts; adults only. Too few observations to standardize.

1976b, Fig. 2) and quadrupedal walking on slightly inclined boughs (Fleagle, 1976b, Fig. 3) and suffers from many of the same drawbacks as the term brachiation (Cant, 1986).

Emphasis was placed on two specific kinds of climbing: large-diameter WBS (weight-bearing structure) vertical climbing, wherein long arms were hypothesized as functioning to "reach around" trees (Kortlandt, 1968, 1974; Cartmill, 1974; Jungers, 1976; Mendel, 1976; Stern et al., 1977; Fleagle et al., 1981; Jungers and Stern, 1980, 1981, 1984; Jungers et al., 1982; Jungers and Susman, 1984), and vertical climbing (Stern et al., 1977, 1980a, b; Fleagle et al., 1981).

Despite this emphasis on climbing, there remained evidence that suspensory behaviors also were important. The remarkable energetic economy of arm-hanging indicated possible skeletal and ligamentous adaptation to it in apes (Tuttle and Basmajian, 1974a, b, c, 1977, 1978a, b; Tuttle et al., 1983), whereas muscular specializations showed evidence of adaptation for brachiation (sensu stricto) (Tuttle and Basmajian, 1977; Preuschoft and Demes, 1984; Hollihn, 1984).

There is now considerably more quantitative information on the locomotion and posture of the apes (Chivers, 1972; Fleagle, 1976b; Gittins, 1983; Srikosamatara, 1984; Sabater Pi, 1979; Susman et al., 1980; Sugardjito, 1982; Susman, 1984; Kano and Mulavwa, 1984; Tuttle and Watts, 1985; Sugardjito and van Hoof, 1986; Cant, 1987a, b; Hunt 1989a, b, in press-a) than when the most recent interpretive comparative review was presented [Fleagle, 1976b; Tuttle (1986) presented quantitative data but did not attempt this kind of systematic interpretation]. Here the positional behavior of chimpanzees[4] is presented in such a way that it can be used as a standard of comparison for the other Hominoidea, and ape dyads are compared to baboons to identify positional specializations. Forest living baboons were chosen for study, because of all Old World monkeys at Gombe and Mahale, they are the closest in body weight to apes, and body weight is presumed to be an important variable in WBS size and positional behavioral choice.

Such an approach relies on the assumption that the positional behavior of contemporary hominoids is reflected in their anatomy, i.e., that morphology tracks positional behavior on a relatively short evolutionary time scale. It seems plausible, given the anatomical convergences of the atelines, alouattines, and apes (Erikson, 1963) and the concomitant similarity of their positional behaviors (Richard, 1970; Mendel, 1976; Mittermeier, 1978; Schön Ybarra and Schön, 1987; Cant, 1986) (Tables I-III), that such is the case and, therefore, that a close examination of ape positional

[4]Throughout this paper "bonobo" refers to Pan paniscus and "chimpanzee" denotes Pan troglodytes.

behavior will yield some insight into which behaviors have selected for "ape" anatomical specializations.

METHODS

Study Sites

Data on chimpanzees are derived from a year-long study at the Mahale Mountains and Gombe Stream National Parks, Tanzania. Details of the habitats of the Mahale M group and the Gombe Kasekela community ranges are reviewed elsewhere (Hunt, 1989b). Mahale was slightly wetter than Gombe [mean rainfall, 1870 mm, versus 1495 mm at Gombe (McGrew et al., 1981)]. The vegetation in the Mahale M group range was "predominantly forested vegetation (i.e., vine tangle and closed forest)," whereas the habitat at Gombe was thicket woodland with less vine tangle and forest and more open woodland (Collins and McGrew, 1988, p. 564). At both sites there was little primary forest left (Nishida, 1968; Clutton-Brock and Gillett, 1979; Goodall, 1986), though both showed clear signs of recovery (Collins and McGrew, 1988).

Individuals Studied

Details of the study populations are presented by Hunt (1989). Of the most common male focal targets, all were between 16 and 34 years of age. One was ranked alpha, one was of medium and stable rank, one was of low, stable rank, one was of high but falling rank, and the final one was of low but rising rank. Of the most common female targets, all were healthy, aged 16 to 39, one with a 2- to 3-year-old infant, one with a 4- to 5-year-old infant, one with 1-year-old infant which died halfway through the study, and a sexually cycling female. As nearly as possible, identical methods of data collection were employed for baboons. Only healthy, prime adults were observed. The home range of the troop studied was considerably smaller than the chimpanzee Kasekela community range and located near its center.

Data Collected

Data were collected on focal individuals with instantaneous sampling. At precise 2-min intervals as many positional variables as could be discerned from a total of 25 were recorded. If, at the precise 2-min point,

the animal could not be observed, no data were collected. Data recorded in feeding camp (Goodall, 1986), in staff camp (Goodall, 1986), or while the animals were mobile-provisioned (Nishida, 1979) were not used in the analysis presented below. Chimpanzees were observed for 571 hr at Mahale and 130 hr at Gombe, for a total of 16303 instantaneous 2-min focal observations. Baboons at Gombe were observed for 83 hr, and 2087 observations were recorded.

RESULTS

Chimpanzee Study

Results of my chimpanzee study are presented in more detail elsewhere (Hunt, 1989b, in press-a,b). The selective forces acting on chimpanzee anatomy were assessed by examining the frequency, the presumed physical stress, and the distinctiveness of positional modes in chimpanzees. Physical stress was crudely estimated by assigning posture low stress and locomotion either high or medium stress, according to whether the mode involved rapid and/or vertical acceleration or not. Distinctiveness was assessed by comparing positional mode frequencies in chimpanzees and baboons; modes much more common in chimpanzees were hypothesized to be more selectively important than modes with similar frequencies in the two species. Results are reviewed in Tables I and III. Brachiation (sensu stricto) constituted less than 0.1% of all positional behaviors in chimpanzees and was therefore presumed to exert a relatively minor selective pressure on chimpanzee morphology. Knuckle-walking was clearly an extremely important part of the chimpanzee positional repertoire (15.7% of all behavior), but chimpanzee walking differed from that of other quadrupeds primarily in the use of the manus and wrist, leaving other chimpanzee specializations unexplained. Quadrumanous climbing was separated into vertical climbing, large diameter WBS vertical climbing, walking, arm-swinging, transferring (=bridging in this study), clambering, and scrambling. Of these modes, only vertical climbing was significantly more common in chimpanzees than in baboons [Fisher's exact test, $p < .05$, df $= 1$ (Hunt, in press-a)], though the frequency was rather low in both species (0.9 vs 0.5%). Large-diameter WBS vertical climbing (i.e., extended-arm climbing) was held to be an unlikely behavior to explain chimpanzee anatomical specializations because during vertical climbing chimpanzees and baboons did not differ significantly in choice of weight-bearing stratum (WBS) diameters, nor did kinematics appear to differ in the two species.

It was concluded that arm-hanging and, perhaps to a lesser extent, vertical climbing are likely to be the behaviors that have selected for distinctive chimpanzee morphology. Although evidence indicating selective pressure for adaptations to vertical climbing were higher in chimpanzees than baboons, they are perhaps not as great as that for arm-hanging for three reasons. First, arm-hanging had a higher frequency than vertical climbing (4.4 vs 0.9%). Second, the difference in frequency between chimpanzee and baboon behavior was greater for arm-hanging than for vertical climbing, indicating that it was a more distinctive behavior. Third, vertical climbing was kinematically similar in baboons and chimpanzees, whereas arm-hanging was distinctive. Balanced against these three factors is the fact that climbing is likely to exert greater stresses on the musculoskeletal system than arm-hanging is and therefore is likely to require greater morphological adaptations.

Comparative Quantitative Data

Different data collection protocols make comparisons between positional behavior studies of apes problematic. Two previous studies utilized instantaneous scan sampling: the first with 10-min intervals, the second with 5-min intervals (Gittins, 1983; Srikosamatara, 1984). Kano and Malawwa (1984) observed only feeding individuals, utilizing "random sampling." Presumably, their figures reflect the percentage of positional bouts. Chivers (1972) used instantaneous focal sampling every 5 sec; values are presented for frequency of positional types, or as percentages of the total number of observations, and the sample values represent the percentage of time spent in each positional mode. Sugardjito and van Hooff (1986) used continuous sampling. Fleagle (1976b, 1980) observed posture during feeding using instantaneous 2-min focal sampling. Continuous observation of focal individuals was the method used to quantify locomotion during both feeding and travel (figures are percentage of all posture and percentage of locomotor bouts, respectively). Cant (1987a, b) presented posture as the percentage of time spent in each mode (using continuous focal observation) and locomotion as the proportion of the distance traveled. Other studies reviewed here used continuous focal observation (Susman et al., 1980; Susman, 1984; Sugardjito, 1982; Sugardjito and van Hooff, 1986). To compound difficulties further, some studied presented locomotion only during feeding bouts (Susman et al., 1980, Susman, 1984), others during travel and feeding (Fleagle, 1976b, 1980; Cant, 1987a), and still others only during travel (Sugardjito, 1982; Sugardjito and van Hooff, 1986).

Positional mode categories vary between studies. When positional mode descriptions were presented, such information was used to recalculate positional profiles so that positional mode categories conformed to those presented by Hunt (1989b, in press-a). The "stand" mode includes both tripedal and quadrupedal standing. Arm-hang includes all humerus-abducted suspensory postures wherein half or more of the body weight is suspended from an arm. Brachiation is restricted to hand-over-hand suspensory locomotion, with or without a period of free flight. Clamber is a suspensory locomotion assisted by the feet (Cant, 1987a). The climb mode has been applied loosely in general but was confined to vertical climbing for original chimpanzee and baboon observations were pooled and a single positional profile was calculated. Where possible, data on juveniles were omitted and midsex averages were calculated.

To allow comparison with other studies, chimpanzee data are presented in four formats: restricted to fig feeding bouts, restricted to feeding bouts, restricted to arboreal observations, and unrestricted (i.e., all contexts). Without such stratification there is no way of knowing whether context introduces significant biases. By conforming chimpanzee contexts to those of other ape studies, chimpanzee data can serve as a common point of comparison. Accordingly, appropriately restricted chimpanzee data are compared to those of each of the other apes in turn, and the behaviors that commonly distinguish each ape dyad from baboons are noted.

DISCUSSION

Postural Comparisons

Cant (1987b) renewed some of the functional aspects of the brachiation hypothesis (Avis, 1962) by substituting suspensory posture (which might be considered brachiation *sensu lato*) for brachiation (*sensu stricto*). His Prediction 2 (Cant, 1987b) was that the frequency of suspensory behavior should increase with increasing body size. Although orangutans did not fit this model [perhaps because of social rank and/or sex effects (Hunt, 1989b)], it is worth noting that the prediction is confirmed in hylobatids (Table 1). *H. agilis* [body weight, 5.7–6.0 kg (Harvey *et al.*, 1986)] arm-hung 34.5% of the time, compared to 61.7 and 51.5% in two studies of *H. syndactylus* [body weight, 10.6–10.9 kg (Harvey *et al.*, 1986)]. However, the trend does not hold in a comparison between chimpanzees and gibbons. Even during feeding, arm-hanging constituted only 12.1% of all posture in chimpanzees (Table I). Compared to baboons, the most striking feature of

hylobatid posture is the high percentage of arm-hanging —35% or more in all studies, versus only 1% even during feeding for the baboon. Other studies of baboon positional behavior (Rose, 1974, 1977) report virtually no arm-hanging. Moreover, baboons, unlike apes, did not fully abduct their humeri during arm-hanging (personal observation). Hylobatids were reported only to sit and to arm-hang, and since hylobatids spent less time sitting than baboons, arm-hanging is demonstrably the postural mode specialization of the hylobatids. Therefore, arm-hanging is the postural specialization that hylobatids share with chimpanzees (Hunt, in press-a).

Bonobo postural frequencies were reported for feeding individuals (Kano and Mulavwa, 1984). Of the studies reviewed here, this one had the smallest number of observations (132 surveys), and the figures should be considered with caution. Of four modes reported, sitting constituted 90% of all posture, considerably more than the 75–80% in chimpanzees. Arm-hanging was the second most common feeding posture in bonobos, constituting 5.0% of all behavior, which is considerably less than the 12.1% for feeding *Pan troglodytes*. Other values are quite similar. Compared to baboons, bonobos vary in the same direction as chimpanzees in having higher frequencies of sitting and arm-hanging and much lower frequencies of standing.

Table II compares posture in orangutans and chimpanzees with observations limited to those while feeding on figs (Cant, 1987b). Although positional behaviors were described as kinematically similar in two species (Cant, 1987a, b; Hunt, 1989b, in press-a), the frequencies of various behaviors were quite different. Suspensory behavior was common in both species, but the most common type of suspensory behavior was common in orangutans diverged from that of chimpanzees. Chimpanzees arm-hung unimanually (i.e., without support from any other body part) more often than orangutans did, perhaps because the denser canopy of the orangutan habitat may have offered an increased opportunity for utilizing foot support. Cant (1987a, b) described a hand-foot hang mode in orangutans, in which the body was suspended by a hand and the ipsilateral foot with the shoulders oriented vertically. This type of hanging was seen 30% of the time in orangutans, but among chimpanzees it was so rare that it was not a postural category in this study. When suspended from two contact points, equal in height, by a hand and foot, chimpanzees oriented their shoulders horizontally, so that the body was suspended like a hammock. Next to sitting, the hand-foot hang was the most common posture in orangutans, followed by arm-hanging. Orangutans diverged sharply from chimpanzees in their low frequency of lying and sitting (Tables I and II). Orangutans used bipedal posture more often than chimpanzees did, though the difference was not great (3.8 vs < 1%).

There is substantial consistency between the Cant postural data (1987b) and those presented by Sugardjito and van Hooff (1986), despite the fact that the former were taken only during feeding bouts and the latter during travel and pausing (presumably this means any posture not in the context of a feeding bout). In chimpanzees, arm-hanging was most common in feeding contexts (Hunt, 1989a, b, in press-a) (Table II). Likewise, suspensory behaviors were more common in Cant's study than in that of Sugardjito and van Hooff. Standing was more common in chimpanzees in nonfeeding than in feeding contexts; orangutans displayed a similar trend.

Although not as predominant as in hylobatids, the frequency of arm-hanging was highest in orangutans of all the great apes (Table 1). Compared to baboons the low frequency of sitting and the high frequencies of bipedal standing and arm-hanging distinguish orangutans, but the difference in the frequencies of the hand-foot hang is by far the greatest (30+ vs 0.0%). Comparing chimpanzees and orangutans to baboons, all in feeding contexts, arm-hanging is the posture that most distinguishes the chimp-orang dyad; the frequency was 11% greater in the apes.

Mountain gorillas have a positional profile distinctly unlike that of the other apes, reflecting their terrestrial adaptation (Tuttle and Watts, 1985). Here it is assumed that either the nature of the Virunga habitat and/or the recent phyletic body size increase accounts for the lack of arboreal behavior in mountain gorillas. If it is shown to be otherwise, the conclusions of this paper are incorrect, since gorillas exhibit much of the morphology that distinguishes apes from monkeys. Anecdotal (Yerkes and Yerkes, 1929; Dixon, 1981) and anatomical (Schultz, 1934, 1969) evidence suggest that the positional behavior of lowland gorillas diverges in the direction of the other apes.

The proportion of sitting was 60% in mountain gorillas versus 75.2% in chimpanzees. Squatting was common among mountain gorillas (Tuttle and Watts, 1985), but Watts' squatting mode was more equivalent to the sit category in chimpanzees than the squat mode (personal communication). If squatting and sitting observations are pooled, the two make up nearly 83% of all feeding behavior in chimpanzees, versus >95% in mountain gorillas. Arboreal postures such as arm-hanging constituted most of the remainder of chimpanzee positional profile, whereas arm-hanging was not observed in gorillas. Compared to baboons, gorillas squatted more often and stood less often.

Sabater Pi (1979) noted only three postural modes in common chimpanzees. Sitting was seen in approximately the same proportion as in this study, whereas standing was much more common among Rio Muni chimpanzees than in Tanzanian chimpanzees. Arm-hanging was not observed in Rio Muni chimpanzees.

Postural Summary

Compared to baboons, arm-hanging is the postural specialization common to all ape dyads. If study protocol differences are ignored and a simplistic quantitative comparison is made, sitting emerges as the most common posture in the apes, ranging from 38.3% in one study of *Hylobates syndactylus* to 90% in bonobos (the latter value derived from only 132 observations); sitting is not, however, particularly distinctive of the apes since its frequency is 75% in baboons. With the exception of mountain gorillas (Tuttle and Watts, 1985) and one chimpanzee study (Sabater Pi, 1979), all ape studies report a frequency of arm-hanging that is at least 5% greater than that seen in baboons. No other posture is so uniformly distinctive, and only sitting is seen in more consistently high frequencies among apes.

Locomotor Comparisons

Quadrupedal walking was observed at a frequency of 0.0% in four of five hylobatid studies, whereas quadrupedal walking constituted 92% of all locomotion in common chimpanzees and 97% in baboons (Table III). Even in arboreal contexts quadrupedal walking constituted 36.4% of all locomotion in chimpanzees and 64% in baboons. The frequency of vertical climbing among hylobatids ranged from 6 to 54% in five studies. Although the two highest figures were those from studies that used a very broad definition of climbing (Fleagle, 1976b, 1980), other studies reported figures of 6.0, 6.3, and 10.0%, frequencies higher than those of both chimpanzees (4.9%) and baboons (0.7%). Both apes climbed >4% more often than baboons. Leaping, including dramatic dropping and hopping, ranged from 0 to 23.9% in hylobatid studies (Table III), most values being considerably higher than those reported here for baboons. Leaping constituted less than 1% of all locomotion in chimpanzees. Most studies reported considerably higher frequencies of bipedal walking in hylobatids than in chimpanzees (0.0 to 11.0% in hylobatids, 0.4% in chimpanzees), whereas in baboons the frequency of bipedal walking was 0.0%. Brachiation constituted 38-84% of gibbon locomotion, compared to 0.5% in chimpanzees and 0.0% in baboons. Brachiation is clearly a much more common behavior in gibbons and siamang than in chimpanzees, but perhaps even the 0.5% in chimpanzees is significant compared to 0.0% in baboons. Running, clambering, transferring, and nonbrachiating suspensory behaviors were uniformly rare in chimpanzees, hylobatids, and baboons. Among all of these behaviors, climbing was observed at the highest frequencies in both chimpanzees and hylobatids: it was reported at 5% or more in all studies of both species.

No other locomotor mode is represented in all studies in both hylobatids and chimpanzees at a frequency higher than 1%.

Susman and colleagues (1980; Susman, 1984) were unable to provide quantitative positional profiles for terrestrial behavior in bonobos, though they reported that, like chimpanzees, when bonobos traveled on the ground they knuckle-walked (Hunt, in press-a). Accordingly, locomotor frequencies for bonobos are compared to chimpanzee and baboon observations restricted to arboreal contexts (Table III).

In arboreal contexts roughly 31% of all bonobo positional behavior was quadrupedalism, a figure virtually identical to that of common chimpanzees if quadrupedal palmar walking and knuckle-walking are combined (Table III). Chimpanzees and bonobos walk arboreally approximately half as often as baboons do and, therefore, cannot be said to be specially adapted to quadrupedal walking. Leaping and diving together accounted for 10% of locomotion in bonobos, a figure comparable to that for baboons (Table III); these behaviors were rare in chimpanzees ($<0.1\%$).

Compared to baboons, bonobos and chimpanzees displayed high frequencies of climbing, a behavior over twice as common in chimpanzees as in baboons (49 vs 21%), and assuming that Susman's expanded data set (Susman, 1984) is the more accurate one, notably more common in bonobos than in baboons (31 vs 21%). Climbing was more common in chimpanzees than bonobos (49 vs 31%), whereas, arm-swinging (=brachiation) made up 20% of bonobo arboreal behavior, compared to only 5.3% in chimpanzees. It was not seen at all in baboons.

Differences in climbing and brachiating in chimpanzees and bonobos may be related to their respective habitats. First, because Gombe and Mahale were rather open [compared to Lomako (Collins and McGrew, 1988; Susman et al., 1980)], tree crowns seldom interdigitated consistently enough to present long-distance travel routes. Consequently, there may have been fewer opportunities to travel in the canopy at Mahale and Gombe than at Lomako and, therefore, less call for brachiation. Second, a higher canopy at Lomako (Collins and McGrew, 1988; Susman et al, 1980) may have made it relatively more expensive to travel on the ground than in the trees, regardless whether similar travel routes were available. The relative cost of traveling between feeding sites on the ground must be greater the higher the canopy (assuming that resources are found higher in the canopy as well), since a higher canopy necessitates a greater climbing distance both during descent and reascension. Individuals might minimize climbing by traveling solely in the canopy. Such a line of reasoning would predict that the arboreal locomotion most commonly used for traveling between adjacent feeding sites would be more common in bonobos than in common chimpanzees, whereas climbing and knuckle-walking would be more common in

chimpanzees. Perhaps brachiation is one component of arboreal travel for bonobos, as it is for Hylobates syndactylus (Fleagle, 1976b).

Both chimpanzees and bonobos are distinctive in their use of bipedal walking. This positional mode is common in both apes (>5% of arboreal locomotion) and rare in baboons (0.0%). However, the most distinctive aspect of chimpanzee and bonobo locomotion was their common high frequency of climbing; climbing was at least 10% higher in the Pan dyad than in baboons. Brachiation (=arm-swinging) and bipedalism were both 5% more common in the Pan dyad than in baboons. Proportionally (ie., Pan spp. frequency divided by baboon frequency), brachiation and bipedalism were very distinctive (>5/0%), whereas climbing was somewhat less distinctive (>31/21%). Other locomotor modes were less common in apes than in baboons or were not observed at high frequencies in either ape species. Given differences in data collection methods and the small sample sizes, it is not possible to state that one of these three locomotor modes—climbing, brachiation, or bipedalism—distinguishes the locomotor behavior of the chimpanzee-bonobo dyad from that of baboons better than the other two. All three are likely to be important.

The locomotion of orangutans, as described by MacKinnon (1974) and Cant (1987a), is broadly similar to that of chimpanzees (Table III), but unlike chimpanzees, orangutans were almost exclusively arboreal (MacKinnon, 1974; Cant, 1987a). Observations were not limited to those in trees, consequently, the low frequency of orangutan terrestriality is likely to reflect a true difference between species. Therefore, comparisons of chimpanzees and orangutans are made on values that include arboreal and terrestrial contexts for chimpanzees. Climbing is described as an important part of orangutan behavior. Unlike chimpanzees, orangutans use a pulse climb (bear climb, in MacKinnon's terminology) that was seen in baboons but not in chimpanzees. MacKinnon's (1974) illustration of climbing appears to show a forelimb kinematic similar to that of chimpanzees, involving protraction of the humerus, not abduction. Cant (1987a) states that vertical climbing on larger WBS (i.e., >20 cm) is rare in orangutans. Arboreal behaviors are much more common in orangutans than in chimpanzees (Table III), but the proportion of knuckle-walking is the most profound difference between them. Orangutans do not knuckle-walk (Tuttle, 1967, 1969, 1975; MacKinnon, 1974), and MacKinnon (1974, p. 11) describes their terrestrial locomotion as clumsy. Climbing (10 to 31%, compared to 5%) and brachiation (10.6 to 21.0%, vs 0.5%) are considerably more common in orangutans than in chimpanzees. Climbing represents 5% or more of locomotor behavior in both apes and <1% in the baboons and is therefore the behavior that most clearly distinguishes the chimpanzee-orangutan dyad from

the baboon. No other locomotor behavior frequency is both high in the chimp–orang dyad and low in baboons.

Observations on locomotion in mountain gorillas (Tuttle and Watts, 1985) were collected as m/km covered by each locomotion and are not directly comparable to others presented here. However, it is clear that mountain gorillas are primarily terrestrial knuckle-walkers. This mode comprised 940.2 m/km locomoted. In chimpanzees, over 98% of all terrestrial locomotion was knuckle-walking. Arboreal behavior was extremely rare in gorillas, but of the arboreal locomotor modes observed, climbing was most common, constituting 2.56 m/km. Given the high values for walking in baboons, climbing may be the most distinctive shared behavior in the gorilla–chimpanzee dyad.

Locomotor Summary

In context-specific comparisons of all locomotor behaviors, climbing distinguished the hylobatid–chimpanzee dyad from baboons. Climbing, bipedal walking, and brachiation distinguished bonobos and chimpanzees from baboons. Climbing was the shared mode that best distinguished the orangutan–chimpanzee dyad from baboons. Quantitative comparisons that do not take context into account reveal the same trend. Climbing was seen at a frequency of 5% or more (the 5% being in the chimpanzees) in all apes except mountain gorillas. Brachiation was the next most distinctive locomotor behavior in apes, but it represented only 0.5% of all locomotion in chimpanzees and thus is unlikely to have exerted a significant selective pressure on at least chimpanzee anatomy.

CONCLUSIONS

Hylobatids and orangutans exhibited the highest levels of suspensory behavior and the lowest levels of terrestrial quadrupedalism, the mountain gorilla showed the converse, and bonobos and chimpanzees are intermediate. The behaviors of the great apes in arboreal contexts are somewhat similar, but the difference in the proportion of time spent in the trees varies dramatically from 100% in gibbons to nearly 100% in the orangutan to 50–60% in common chimpanzees[5] to 5% in gorillas, with bonobos presumably intermediate between orangutans and common chimpanzees (Tuttle, 1986).

[5] The figures were 60.7% for Mahale chimpanzees (n = 11896) and 47.2% for Gombe chimpanzees (n = 3056).

Among postures, arm-hanging was clearly the most distinctive shared mode among the apes (the mountain gorilla excepted), constituting 5% or more in each. However, individual species showed evidence of specialization. Arm-hanging was that specialization in hylobatids; they displayed by far the highest arm-hanging frequency of any ape. Bipedal posture and a unique hand-foot hang were more common in orangutans than in any other ape. Compared to orangutans and hylobatids, African apes were distinctive for their high frequency of sitting.

Locomotor specializations were apparent as well. As might be expected, brachiation was the predominant locomotor mode among hylobatids. Among orangutans clambering, brachiation and an orthograde suspensory locomotion assisted by the feet (clambering) were the most common locomotor modes. Knuckle-walking was characteristic of African apes, but walking, even arboreal walking, was uncommon in other apes. No ape had a frequency of walking as great as that of baboons. Of locomotor modes, only climbing was represented in significant frequencies among each of the apes, constituting 5% or more in each of the apes (gorilla excepted). No other locomotor mode exhibited such consistently high frequencies in apes nor was so different in comparison to baboons.

However, climbing is a term that may span a variety of behaviors. In chimpanzees and orangutans it referred to vertical climbing, but in other studies it included walking on slightly inclined boughs and suspensory behaviors that are kinematically more similar to walking and brachiation, respectively, than to vertical climbing. The frequencies of climbing in studies of hylobatids and bonobos were so high that it seems likely that vertical climbing is found at high frequencies as well. Nevertheless, the importance of vertical climbing as an evolutionary determinant of ape morphology is diminished by its kinematic similarity in chimpanzees and baboons, indicating that it may require fewer and less profound anatomical modifications than behaviors that are kinematically dissimilar. It remains to be seen how kinematically distinctive vertical climbing is in the orangutan and the gibbon. But arm-hanging involves a degree of humeral abduction in apes far greater than that observed in baboons, indicating that detectable modifications of the shoulder should accompany an arm-hanging adaptation.

Hunt (1989a, b, in press-b) has argued that, in chimpanzees, an abductible humerus, a broad thorax, a cone-shaped torso, and an elliptical (i.e., "narrow") scapula are a coadapted functional complex that reduces energy expenditure and fatigue during arm-hanging. The predominance of muscles that retract the humerus and flex the elbow, such as latissimus dorsi, sterno-costal pectoralis major, biceps brachii, brachialis, and brachioradialis, was hypothesized to be an adaptation to vertical climbing. A large ulnar excursion of the manus, long fingers, a short torso, an iliac origin of the latissimus

dorsi, and large muscles for arm-raising (i.e., deltoid, clavicular pectoralis major, teres minor, and cranial trapezius) were hypothesized to be adaptations to both behaviors. Given the evidence that vertical climbing and arm-hanging are the distinctive, shared positional behaviors among all apes, adaptations to these behaviors are likely to account for some of the shared, derived characters common in the hominoids (Keith, 1891, 1899, 1903, 1923; Schultz, 1930, 1936, 1953, 1956; Erikson, 1963; Susman, 1979; Ashton and Oxnard, 1963, 1964a; Napier, 1963a; Oxnard, 1963, 1967; Ashton et al., 1965; Tuttle, 1969).

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Seed-Eating by Red Leaf Monkeys (*Presbytis rubicunda*) in Dipterocarp Forest of Northern Borneo

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Data are presented on the feeding behavior of Presbytis rubicunda at Sepilok, north Borneo. Emphasis is given to describing the fruit-eating behavior of this small colobine monkey, which specializes in eating seeds from large, dull-colored, and fleshless fruits. The seed predation is conspicuously different from the seed dispersal effected by sympatric monogastric primates and is characteristic of colobine frugivory at other forest sites. Most seed-eating occurred during the period of maximum fruit production and fewer small-seeded, animal-dispersed fruits were eaten at other times.

KEY WORDS: Presbytis rubicunda; fruit structure; seed predation; fruiting synchrony.

INTRODUCTION

The colobine monkeys of Asia, despite being diverse in size, structure and taxonomic relationships, are linked by two characteristics of the subfamily Colobinae: a reduced thumb and an enlarged and sacculated forestomach (Napier, 1985). The forestomach contains a suspension of bacteria that breaks down foodstuffs through anaerobic fermentation (Bauchop and Martucci, 1968; Kay *et al.,* 1976). This can allow the digestion of plant cell wall molecules, such as cellulose, and much has been made of the potential for colobine monkeys to exploit foliage as a food source.

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