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Body Size Effects on Vertical Climbing Among Chimpanzees

Kevin D. Hunt[1]

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I analyzed observations from a yearlong study of the positional behavior of Pan troglodytes *at the Mahale Mountains National Park to determine whether there are detectable differences in behavior between large and small individuals. Analysis was complicated by a weak correlation between body size and social rank. To factor out rank effects, I performed two types of analyses, depending on the type of data: (1) multiple regressions or (2) comparisons of similarly ranked animals of different body size. With social rank effects accounted for, larger males fed lower in the canopy, fed on the ground more often, fed preferentially among food tree species with smaller adult heights, and climbed significantly less often than smaller males did. Contrary to expectation, large males utilized smaller weight-bearing structures than small males did. These results suggest that large males minimized climbing versus optimizing support diameters, perhaps because vertical climbing is disproportionally expensive for larger animals. The large body weight of chimpanzees compared with other primates suggests that minimizing altitude changes, and therefore vertical climbing, is an important consideration in budgeting daily energy expenditures.*

KEY WORDS: allometry; body weight; Taylor/Caldwell/Rowntree rule; positional behavior.

INTRODUCTION

Body weight imposes constraints on primate positional behavior, especially locomotion, most particularly ascents and descents (Taylor *et al.*, 1972; Cartmill, 1974; Grand, 1972, 1984; Cant, 1992). Via its effect on po-

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sitional capabilities, size determines an animal's habitat choice and positional repertoire and, through these, its diet. Several studies showed that when two primate species differ chiefly in body size, the smaller of the dyad commonly leaps more often during ascents than the large one does, which usually prefers to ascend trees by less physically demanding vertical climbing (Cartmill, 1974; Cartmill and Milton, 1977; Rollinson, 1975; Rollinson and Martin, 1981; Fleagle and Mittermeier, 1980; Crompton, 1984; cf. Taylor *et al.*, 1972).

Because animals of very different body weights can be compared interspecifically, such comparisons are particularly valuable for establishing positional contrasts. The disadvantage of interspecific comparisons is that they are often difficult to interpret because positional differences may be due to factors other than body size, such as anatomy, diet, predation pressure, and group size (Rudran, 1978a, b; Struhsaker, 1978). Perhaps this is why, among apes, differences in frequencies of suspensory behavior and vertical climbing do not clearly follow theoretical expectations based on body weight (Hunt, 1989, 1991). For example, the frequency of leaping is greater in the larger bonobo than in some hylobatids (Hunt, 1991). Other interspecific comparisons among anatomically similar species that feed in the same trees, often for days at a time, yield differences in diet and preference in weight-bearing structural size or canopy level or both that have not been explained satisfactorily (Chivers, 1973; Dunbar and Dunbar, 1974; Moreno-Black and Maples, 1977; Mittermeier and van Roosmalen, 1981; Hladik and Hladik, 1972; Hladik, 1979; Sussman, 1974; Gautier-Hion, 1978; Rodman, 1978; Terborgh, 1983).

Body size has particularly important implications for vertical climbing. Dangers from falls are greater for larger animals, making feeding sites in the upper canopy riskier. Due to metabolic changes with body weight, climbing is energetically relatively more expensive for larger animals (Taylor *et al.*, 1972; Cartmill, 1972, 1974; Cartmill and Milton, 1977). Moreover, because of the square-cube law, bone, muscles, and ligaments, the strength of which depend on their cross-sectional area, must be disproportionally large in larger animals to allow the same locomotor competence. In other words, an isometrically scaled, larger animal cannot function in the same way as its smaller isomorph. Such limitations are particularly significant during stressful or fatiguing locomotor activities such as leaping and vertical climbing. Square-cube and metabolic effects together suggest that among animals with essentially similar anatomies, larger individuals should ascend less often. This might be called the Taylor/Caldwell/Rowntree (TCR) rule (Taylor *et al.*, 1972). The TCR rule is especially significant for the apes since they are not only the largest living primates but also the largest ar-

boreal animals. Accordingly, many allometri
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competence with larger body size (Jungers
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boreal animals. Accordingly, many allometric differences between apes and monkeys have been attributed to adaptations to retain vertical climbing competence with larger body size (Jungers, 1984, 1985, Jungers and Susman, 1984; Shea, 1984).

Given the potential biases of interspecific positional comparisons, the most convincing tests of allometric effects on leaping and climbing have been made within species (Cant, 1987; Doran, 1993). Intraspecific tests can demonstrate body size effects more clearly because there are fewer anatomical and dietary differences than occur between species. Still, other variables that influence positional behavior may confound intraspecific body size comparisons. For example, among highly social animals, dominance rank may be a more significant determinant of feeding rates (Janson, 1985) and positional behavior (Hunt, 1992a) than body size is. If body size is correlated with social rank — however weakly — comparisons between larger and small individuals may unintentionally reflect differences in social rank. When social rank effects and body size effects are contrary, as they can be in chimpanzees, spurious indications of body size effects are possible. For example, among chimpanzees, high-ranking animals prefer larger branches, while large individuals prefer smaller branches. A simple comparison of large and small males indicated that large males prefer larger branches, but multiple regression and like-rank comparisons showed the opposite (Hunt, 1992a). Such contrary effects demand that special care be taken when making positional behavior comparisons between groups that have different social ranks, such as males versus females, juveniles versus adults, and, in some cases, large versus small males.

In a previous analysis, I examined body weight effects via multiple regression, which factored out social rank. Contrary to expectation, larger males positioned themselves on smaller weight-bearing structures (WBS) than smaller males did (Hunt, 1992a). Classic predictions such as "large individuals prefer larger branches" may fail in this case because larger males have other competing positional demands — perhaps pressures to minimize vertical climbing — that are more important than branch stability.

Because *Pan troglodytes* spend half of their time in the trees and half on the ground, they have the opportunity to adjust their arboreal activities in response to individual body weight and are, therefore, a particularly informative animal on which to test the TCR rule. I employ two methods of analysis to determine the influence of body size on vertical climbing in chimpanzees: multiple regression on positional variables that includes body weight and social rank data and like-rank comparisons of large and small chimpanzees.

STUDY SITE AND METHODS

I observed chimpanzees for 571 h at the Mahale Mountains National Park, Tanzania, from September 1986 to August 1987. Details of the study site and data collection protocol are available elsewhere (Nishida, 1968; Hunt, 1989, 1991). Data collection consisted of instantaneous survey sampling (= time-point sampling) on focal individuals (Altmann, 1974). I examined 6600 2-min instantaneous observations from 67 separate focal follows for this study. I limited analysis to males because social rank and body size rank could not be determined accurately for the less social, shyer females. I recorded 25 positional behavior variables every 2 min, including the number and sex of adult individuals ≤10 m from the target. I estimated height in canopy for the target subject to the nearest meter by locating its elevation in relation to a tree trunk and counting meters up from the ground using the trunk as a reference. I practiced height estimation using a clinometer to establish reference heights.

I observed all focal individuals both in groups and alone in the course of study. I did not attempt to observe the same individual 2 days in a row in order to avoid potential bias associated with the collection of temporarily abundant fruit. Of 67 chimpanzee follows analyzed here, no individual was followed on 2 consecutive days. I sampled behavior from a representative proportion of large vs. small and high-ranking vs. low-ranking individuals (Table I). Possible biases due to following like-sized animals during months when a particular fruit with unique characteristics was available are probably small. Only 1 month appears to be skewed toward one body size; the February sample included only small animals. It might be argued that if a fruit were available that could be harvested only high in the canopy, small animals may appear to harvest fruits at high elevations due to sampling bias. Since animals of varying body sizes were sampled most months, such a bias is probably remote. In fact, results below depict a trend that is opposite to that which a bias like that in February would produce.

I located target subjects as early in the day as possible and followed them for as long as possible. I made all decisions to cease taking data at least an hour in advance, and took no other data in the same day. I recorded no data in feeding camp, in staff camp (Goodall, 1986), or while the animals were being mobile-provisioned (Nishida, 1979). Of the most common subjects, 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 a fifth was of low but rising rank. I ranked body size (= body weight) by noting which of two animals appeared larger whenever they were near one another. Sitting height proved especially helpful since it was not affected by hair erection. Uehara and Nishida (1987) weighed the two individuals

Table I. Dominance Rank, Body Size Rank, and Hours of Observation by Month

			Dominance rank by month											
	Age	Size rank	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
NTologi	31	1	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
Observations[a]				5(2)	15(3)		4(1)		8(1)	22(4)	4(1)	15(2)	6(2)	
KagImimi	42	2	**2**	**2**	**2**	**2**	**2**	—	—	—	—	—	—	—
Observations				4(2)		8(1)								
KalunDE	23	3	**6**	**6**	**6**	**6**	**5**	**4**	**4**	**4**	**3**	**2**	**2**	**2**
Observations			6(1)				3(1)					2(1)	4(1)	
KasangaZi	24	4	**9**	**9**	**9**	**9**	**9**	**8**	**5**	**5**	**4**	**3**	**3**	**3**
Observations									11(2)	5(1)	7(1)	11(2)	26(4)	
Shike (SU)	31	5	**8**	**8**	**8**	**8**	**7**	**6**	**7**	**7**	**7**	**5**	**4**	**4**
Observations														4(1)
BAkali	32	6	**4**	**4**	**4**	**4**	**4**	**3**	**2**	**2**	**2**	**5**	**5**	**5**

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Observations[a]				5(2)	15(3)		4(1)		8(1)	22(4)	4(1)	15(2)	6(2)	
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Shike (SU)	31	5	8	8	8	8	7	6	7	7	7	5	4	4
Observations														4(1)
BAkali	32	6	4	4	4	4	4	3	2	2	2	5	5	5
Observations			3(1)		4(1)			4(1)				5(1)		
LukaJa	21	7	3	3	3	3	3	2	3	3	5	7	7	7
Observations				2(1)	4(2)		6(1)		8(3)					
MUsa	29	8	7	7	7	7	8	7	8	8	8	8	8	8
Observations				3(1)	5(2)		1(1)		10(2)	14(2)			4(1)	
LUbulungu	29	9	5	5	5	5	6	5	6	6	6	6	6	6
Observations				14(4)	4(1)	9(2)	2(1)	5(1)			9(2)	6(1)	4(1)	

[a] Hours of observation, with number of days of observation in parentheses. Does not include ad hoc observations, observations while animals were provisioned (or for 1 h afterward), observations in feeding camp or staff camp, or follows lasting <1 h.

judged smallest, and their results confirm my rankings. I assigned the largest individual a rank of 1, which results in rather counterintuitive positive versus negative correlations.

I used three criteria to establish dominance rank. An individual that pant-grunted consistently to another is considered subordinate (following Goodall, 1986). At Gombe, pant-grunting is unidirectional; that is, 99% of the time only one animal pant-grunts (Bygott, 1979). Certain individuals were rarely together, so the pant-grunting criterion could not be used. In some instances, one individual intensely monitored the movements of another and coordinated his movements to avoid the first. Such monitoring is similar to a supplant; the avoiding animal is subordinate. An individual that consistently fled after another's display is subordinate. Between two animals that are close in rank, the one that displayed often in front of the other without reciprocal action is dominant. Occasionally an individual of lower rank displayed with impunity near a higher-ranking animal, but these were cases in which the relative status of each individual seemed to be well established and their relationship friendly. Fear grins were rarely exhibited by adults and so did not suggest dominance rank.

Frequencies presented here are the proportions of all 2-min samples. For statistical tests I pooled sequential observations wherein positional behavior mode did not change. The effect of pooling is to create rather artificial positional bouts, under the assumption that they are independent, but two sequential observations of the same positional mode are less so. For regression analysis I assumed that each positional bout (not each instantaneous observation) was independent. This statistical treatment is not ideal, since two bouts by the same individual are treated as just as independent as two bouts by different individuals are. This assumption is valid because there were frequent rank changes (Table I) that probably overwhelmed individual bias, i.e., most individuals assumed a number of ranks in the course of study.

I assumed that positional mode preferences are expressed most strongly during feeding, when competition is high and when acrobatic arboreal behavior is often necessary. Most analyses are on feeding animals. Feeding-tree size limits the number of individuals that can feed together, the height that can be climbed, and the size of available WBS. For some analyses I employed only food trees with heights >15 m.

RESULTS

Canopy height was no different for large and small males when they fed among smaller trees (adult height, ≤15 m). This was the case regardless of whether individuals were solitary or in gro
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allowed comparisons of large males with a
1747; body size ranks, 3 and 4) to small ma
5.15 ($n = 1629$; body size ranks, 7 and 9).

Large males fed from small trees (≤15
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$= 9.69$, df $= 1$, $p = 0.002$, $n = 166, 61$),
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feeding. Large males (matched for social ra
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RESULTS

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of whether individuals were solitary or in groups, presumably because small trees offered little chance for an individual to limit ascents: They must either climb or not climb the tree. When solitary males fed in trees >15 m, partial correlations considering social rank, body size, and canopy height show that larger individuals tended to be lower in the canopy than smaller males ($r = 0.30, p < 0.0002$). One might expect that such differences would be even more pronounced when individuals fed in groups, but there are no significant results among group males. It is not clear why this is so, but previous results (Hunt, 1992a) show that rather complicated relationships between positional variables can obscure important trends. It may be that males congregate in groups to feed only when no individual suffers increased feeding costs, that there is some social exchange that high-ranking males trade for feeding efficiency, or that the relationship between canopy height and body size is nonlinear and therefore nonsignificant in multiple regression analysis.

Other variables showed similar results regardless of whether males fed in groups or solitarily, so analyses included both cases. Multiple regressions were not possible for these variables, so I compared groups of large and small males with similar social ranks. I performed matching by systematically eliminating specific individuals from large-male and small-male groups until the average social rank was nearly equal. The best permutation allowed comparisons of large males with a mean social rank of 4.55 ($n = 1747$; body size ranks, 3 and 4) to small males with a mean social rank of 5.15 ($n = 1629$; body size ranks, 7 and 9).

Large males fed from small trees (≤ 15 m tall) more often than smaller males did (Fig. 1; comparison matched for social rank; 39.9 vs 18.0%, $\chi^2 = 9.69$, df $= 1$, $p = 0.002$, $n = 166, 61$), though there is no significant difference in tree size between large and small males when they were not feeding. Large males (matched for social rank) spent a greater proportion of time on the ground whether feeding (46.0 vs 29.4%, $\chi^2 = 7.16$, df $= 1$, $p = 0.007$, $n = 161, 102$) or not feeding (73.0 vs 66.1%, $\chi^2 = 4.0$, df $= 1$, $p = 0.05$, $n = 509, 499$; see Fig. 2). Large males also climbed significantly less frequently than smaller males did, when matched for social rank (0.8 vs 3.2%, $\chi^2 = 6.65$, df $= 1$, $p = 0.01$, $n = 494, 476$).

DISCUSSION AND CONCLUSION

Although vertical climbing has been both predicted and demonstrated to be more frequent in the larger of a dyad of some anatomically similar species (Cartmill, 1974; Cartmill and Milton, 1977; Rollinson, 1975; Rollinson and Martin, 1981; Fleagle and Mittermeier, 1980; Crompton, 1984),

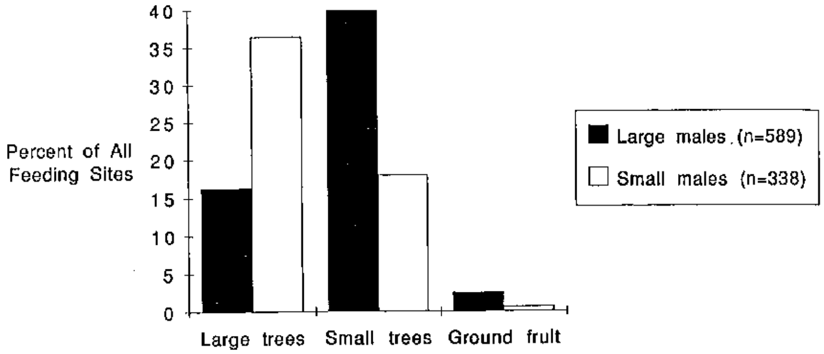

Fig. 1. Feeding site choice in males matched for social rank. Large males fed significantly more often among small trees and on the ground. Sample sizes are the number of 2-min instantaneous observations; *n*'s are lower for statistical analysis because sequential observations wherein positional behavior mode did not change were pooled to assure independence of data points.

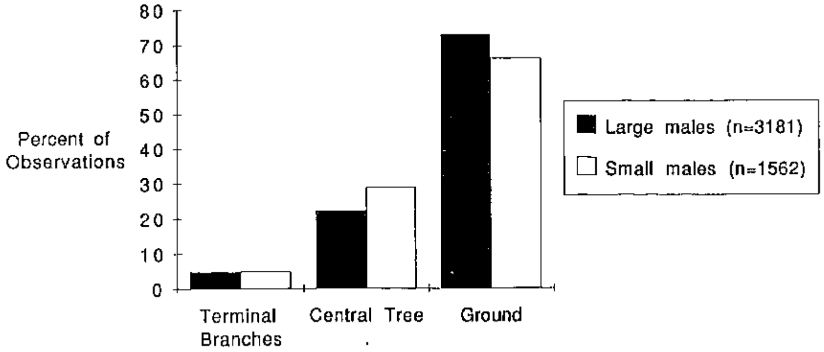

Fig. 2. Canopy location compared in males matched for social rank. Although the percentage of time in the terminal branches was similar in large and small males, large males spent considerably more time on the ground compared to small males. Results are similar during feeding. Sample sizes are the number of 2-min instantaneous observations; *n*'s are lower for statistical analysis because sequential observations wherein positional behavior mode did not change were pooled to assure independence of data points.

this is so only because vertical climbing increased at the expense of leaping ascents. Since chimpanzees virtually never ascend by leaping, the expectation for chimpanzees, and perhaps for other large primates, should be that the larger animal will climb vertically less often. With the effects of social rank accounted for by multiple regression, large chimpanzee males, at least

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climbing to the absolute minimum, that is, t
Accordingly, such a choice may be due as
as to locomotor competence in the trees.

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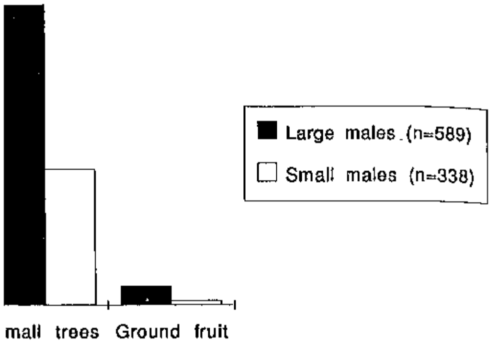
script. John G. H. Cant commented extens
stages of preparation. John Warner of the Un
Laboratory provided critical statistical advice.
from the Margaret Wray French Fund, Sigm



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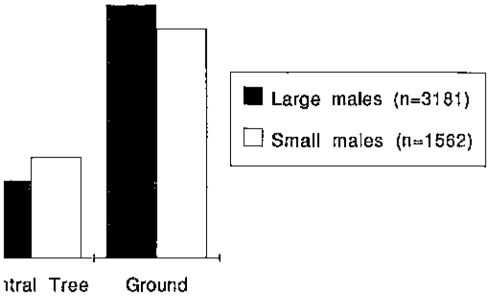

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of 2-min instantaneous observations; *n*'s are lower for
bservations wherein positional behavior mode did not
dence of data points.

climbing increased at the expense of leaping
ually never ascend by leaping, the expecta-
aps for other large primates, should be that
rtically less often. With the effects of social
regression, large chimpanzee males, at least

when solitary, fed lower in the forest canopy. This means that less ascension was necessary to reach the feeding sites that large males frequented. In comparisons matched for social rank, large males were on the ground more often, utilized smaller species of trees, and climbed significantly less frequently than small males did. It appears that chimpanzees conform to the TCR rule, i.e., larger individuals ascend less often than smaller individuals.

Although ascent frequencies conform to body size expectations, other aspects of positional behavior do not. In a previous analysis (Hunt, 1992a) I observed that large males utilize smaller branches than small males do (social rank effects factored out through multiple regression). This is contrary to the expectation that, all other things being equal, large animals prefer larger branches because they are more stable, fail less often, and are easier to grip. The most obvious explanation for this difference is that all other things are not equal. That is, there are advantages to small branches that negate their disadvantages. By utilizing shorter trees, climbing frequencies may be reduced even though the individual must bear the cost of locomotion and posture among the necessarily smaller WBS that are found among trees with adult heights ≤15 m. Large males may choose to bear whatever costs (if any) accompany the utilization of smaller-statured species of food trees in order to minimize climbing. Whereas branch stability is an important consideration in choosing a feeding site (Hunt, 1992c), larger individuals may obtain a better net energy return by minimizing climbing rather than optimizing branch diameters. Very small trees offer the further advantage that some food may be gathered from the ground, by either reaching up into the tree or pulling the tree over.

Since *Pan troglodytes* are relatively large animals, the TCR rule suggests that they more than most other primates are selected to minimize elevation changes in the course of their daily activities. At its extreme, the TCR rule predicts that very large animals are under pressure to reduce climbing to the absolute minimum, that is, to become terrestrial full-time. Accordingly, such a choice may be due as much to energetic constraints as to locomotor competence in the trees.

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