PRIMATES, 33(3): 347–357, July 1992

Social Rank and Body Size as Determinants of Positional Behavior in *Pan troglodytes*

KEVIN D. HUNT
Indiana University

ABSTRACT. A yearlong study of the positional behavior of *Pan troglodytes* at the Mahale Mountains National Park yielded 571 hr of observation. CANT (1987) articulated four predictions concerning the relationship between body weight/branch diameter and positional behavior based on the classic suspensory-ape paradigm. He noted that only two were supported by orangutan data. Three of these four hypothesis were not supported by chimpanzee data, as follows: there was no significant difference between the three largest males and the four smallest males in (1) branch diameters (5.8 cm vs 5.2 cm) nor (2) in the percentage of arm-hanging (13.6% vs 12.1%); and (3) large males did not arm-hang significantly more often than small males in any of three support diameter categories. The fourth hypothesis, that arm-hanging should be more common among smaller branches, was supported: arm-hanging as a percentage of all posture rose from 2.5% to 8.3% to 24% as stratum size decreased from >10 cm to <3 cm. The possibility that the first three hypotheses failed because of confounding effects of a correlation between body size and social rank was examined. Multiple regressions were done on 6600 2-min instantaneous observations on focal individuals. With social rank effects factored out, larger individuals preferentially utilized smaller, rather than larger supports. When positional mode frequencies were compared between large and small males matched for social rank, large males exhibited a lower frequency of arm-hanging than small males. An unexpected result was that social rank more consistently predicted branch diameter choice than body size. The most profound trend was for high ranking males to use larger supports, even though they spent more time in the terminal branches. These results suggest that (1) suspensory behavior is functionally related to small branch diameters; (2) chimpanzees do not prefer smaller branches, rather they are forced into them by food choice limitations; and (3) social rank more profoundly affects chimpanzee behavior than body weight.

Key Words: Group effects; Feeding behavior; Arm-hanging; Positional behavior.

INTRODUCTION

Body weight imposes constraints on diet (BELL, 1971; JARMAN, 1974; KAY, 1975; GAULIN & KONNER, 1977; GAULIN, 1979) and canopy mobility (GRAND, 1972, 1984) and is therefore an important determinant of habitat usage and positional behavior. Some allometry among primates may be attributed to maintaining similar function with a larger body size (WASHBURN, 1957; NAPIER, 1963a, b, 1967; BIEGERT & MAURER, 1972; CARTMILL, 1974; ANDREWS & GROVES, 1976; JUNGERS, 1984, 1985; SHEA, 1984; JUNGERS & SUSMAN, 1984). Body weight is particularly significant among the great apes since they are both the largest living primates and the largest arboreal animals. Accordingly, ape suspensory behavior and its associated anatomy have been hypothesized to be adaptations to their weight (e.g. KEITH, 1891, 1923; MILLER, 1932; NAPIER, 1963a, b, 1967; LEWIS, 1970, 1971a, b, 1972; RIPLEY, 1970, 1976, 1979; ROSE, 1974; CARTMILL, 1974; CARTMILL & MILTON, 1977; ROLLINSON & MARTIN, 1981; HUNT, 1991a). ROSE (1974) showed that among monkeys the heavier the primate in relation to the diameter of its typical WBS, the more likely the

species was to engage in suspensory behavior. Perhaps the linchpin of the suspensory hypothesis was AVIS' (1962) demonstration that compared to monkeys, apes preferred thin (and therefore unstable) weight-bearing structures (**WBS**), and that their locomotion on these structures was suspensory. Although quantitative data on wild primates suggest that suspensory posture rather than suspensory locomotion is more characteristic of apes (HUNT, 1991a), this does not dramatically alter the suspensory hypothesis.

The implications of body size for ape posture were articulated rather precisely by CANT (1987). He presented four predictions proceeding from the hypothesis that suspensory posture is an adaptation to relatively large body weight, some of which were borne out in an examination of male-female differences in orangutans, and some of which were not. The predictions were: (1) larger animals will use larger WBS (borne out); (2) suspension should increase with increasing body size (not borne out); (3) if WBS diameter is held constant, suspension should increase with body weight (not borne out); and (4) if body weight is held constant, the frequency of suspension should increase among smaller WBS (borne out).

Here CANT's predictions concerning WBS diameter use will be examined for chimpanzees (*Pan troglodytes schweinfurthii*) and the complicating factor of social rank will be considered.

STUDY SITE AND METHODS

Five hundred seventy-one hr of observations were made on chimpanzees at the Mahale Mountains National Park, Tanzania from September 1986 to August 1987. Details of the study site and data collection protocol are given elsewhere (NISHIDA, 1968; HUNT, 1989, 1991b). Data collection consisted of instantaneous survey sampling on focal individuals (ALTMANN, 1974). Twelve thousand eight hundred and thirty-eight 2-min instantaneous (i.e. time-point) observations were made, 6,600 of which were on males examined in this study (social rank and body size rank could not be determined accurately for females). Twenty-five positional behavior variables were recorded every 2 min, including the number of adult individuals within 10 m of the target. When possible the identity of nearby individuals was determined, and at least sex was nearly always observed. All focal individuals were observed both in groups and alone in the course of study. Observations in the artificial provisioning areas or when the animals were mobile-provisioned were excluded.

WBS diameter was estimated visually and recorded as a continuous variable from 1 cm to >80 cm. Interwoven, matted "tangles" of branches presented a special difficulty. Because tangles were actually concave, they were more stable than even the largest branches, yet constituent diameters were typically small. To overcome this difficulty WBS diameters were categorized (1=0−1 cm, 2=>1 to 2 cm, 3=>2−4 cm, 4=>4−6 cm, 5=>6−8, 6=>8−10, 7=>10−20, 8=>20−30, 9=>30−40, 10=>40−50, 11=>50−60, 12=>60−70, 13=>70−80, 14=tangle) and regressions were done using category numbers rather than diameters. Note that categories were constituted so that there was in effect a crude logging of WBS diameters.

Table 1 lists individuals on which observations used here were made. With the exception of one older, high ranking individual (*KagImimi*, 42), all were of prime or middle estimated age (21−32). Of the most common targets, 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 final was of low but rising rank.

Body size (=estimated weight) rank was determined by noting relative proportions whenever two individuals were near one another, and collating these observations. Note

Table 1. Focal individuals and their estimated ages.[1)]

Individual	Age[2)]	Number of surveys
NTologi	31	1808
KagamIni	42	316
KalunDE	23	283
BAkali	32	298
KasangaZi	24	1464
LUbulungu	29	1231
MUsa	29	814
LukaJa	21	398

1) Individuals are identified by names; two letter abbreviations for individuals used by many previous workers are in bold face; 2) Age estimates are only approximate.

that the largest individual is given a rank of 1, resulting in rather counter-intuitive positive versus negative correlations. The two individuals judged smallest at Mahale were weighed (UEHARA & NISHIDA, 1987).

Social dominance hierarchy at initial observation had been established by Mr. K. MASUI (Wildlife Research Officer, Ministry of Natural Resources and Tourism, affiliated with the Mahale Mountains Wildlife Research Centre) (pers. comm.). This hierarchy was used with only one modification from September 1986 to December 31, 1986 (***KalunDE*** was ranked higher than ***MUsa***). Consultation among on-site chimpanzee researchers (KDH, R. OLOMI & MASUI) produced a new dominance hierarchy on January 16, 1987 that persisted until March, after which rank was assessed monthly by the author. Among chimpanzees the most reliable measure of dominance relationship is pant-grunting (99% consistent; BYGOTT, 1979; GOODALL, 1986) and this criterion was used in most cases. In cases where individuals could not be ranked by pant-grunting observations, two methods were used. If one animal consistently avoided another the avoider was deemed subordinate. If two animals were close in rank and one was seen to display often in front of the other, yet the converse was not seen, the individual that displayed was assumed to be dominant. If an individual consistently fled during or after display by another, the retreating animal was assumed to be subordinate.

Instantaneous observations are not ideal for statistical testing since sequential observations may be dependent. To reduce dependence sequential observations wherein positional behavior mode did not change were pooled and other variables such as WBS diameter were averaged across the pooled observations to create rather artificial bouts (see HUNT, 1989, 1991b for more discussion of this method). For regression analysis each bout is assumed to be independent. Such statistical treatment is not ideal, since two bouts by the same individual are treated as just as independent as two bouts by different individuals. Such an assumption is argued to be valid because there are frequent rank changes (see Table 2) that probably overwhelm individual bias (i.e. most individuals assumed a number of ranks in the course of study).

For some analyses males were segregated into three categories: high ranking (ranks 1, 2, and 3), middle ranking (ranks 4 and 5), and low ranking males (ranks 6–9). Similarly, males were grouped into three body size categories, large (three largest males), medium (size ranks 4 and 5), and small (size ranks 6–9). Note that in comparisons between "large" and "small" males ranks 1, 2, and 3 are compared to ranks 6, 7, 8, and 9 and medium sized individuals are not considered. Body size comparisons follow the same procedure.

Some analyses involved comparisons of large and small males that were matched for social rank. Matching was done by systematically eliminating specific individuals from large

Table 2. Dominance rank among Mahale males.[1) 2)]

	Age	Size rank	Dominance rank by month											
			Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
NTologi	31	1	1	*1*	*1*	1	*1*	1	*1*	*1*	1	*1*	*1*	1
KagImimi[3)]	42	2	2	*2*	2	*2*	2	—	—	—	—	—	—	—
LukaJa	21	7	3	*3*	*3*	*3*	*3*	2	*3*	3	5	7	7	7
BAkali	32	6	*4*	4	*4*	*4*	4	*3*	2	2	2	*5*	5	5
LUbulungu	29	9	5	*5*	*5*	*5*	*6*	*5*	6	6	*6*	*6*	*6*	6
KalunDE	23	3	*6*	6	6	6	*5*	4	4	4	3	*2*	*2*	2
MUsa	29	8	7	*7*	*7*	7	*8*	7	*8*	*8*	8	8	*8*	8
Shike (SU)	16	5	8	8	8	8	7	6	7	7	7	5	4	4
KasangaZi	24	4	9	9	9	9	9	8	*5*	*5*	*4*	*3*	*3*	3

1) Age and body size rank are given as well in columns 2 and 3. Rank by month is given in the row headed by the individual's name. Italicized numbers in matrix indicate months in which data used in this analysis were collected; 2) Individuals are identified by name; two letter abbreviations for individuals used by many previous workers are in bold face; 3) After being sighted January 16, 1987, *KagImimi*, a past prime male (estimated age: 42), had not been sighted again as of March 1989 (H. TAKASAKI, pers. comm.) and is presumed to have died.

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 were 3 and 4) to small males with a mean social rank of 5.15 (N=1629, body size ranks 7 and 9).

Feeding tree size limits both the number of individuals that can feed together and the size of available WBS. For some analyses food trees were divided into two groups, those with adult heights estimated at $\leq$15 m and those with heights of >15 m.

It was assumed that preferences were expressed most strongly during feeding, when competition is high and when acrobatic arboreal behavior is often necessary. Analysis was limited to feeding animals except where noted.

RESULTS

Of CANT's (1987) four predictions, 1, 2, and 3 were not borne out by data from chimpanzees. (1) There was no significant difference between the three largest males and the four smallest males in WBS diameters (Mann-Whitney U test, U=42,808, large male N=334, small male N=270, P=0.26, see Table 3). (2) The percentage of arm-hanging* was not significantly greater among larger vs smaller males (13.6% vs 12.1%, N=358,306, χ^2=0.29, P=0.59). (3) When WBS diameters were divided into three size groups, <3 cm, 3–10 cm, and >10 cm, large males did not arm-hang significantly more often among WBS <3 cm (χ^2=0.05, P=0.83), among WBS 3 cm–10 cm (χ^2=1.6, P=0.21) nor among WBS>10 cm (χ^2=0.49, P=0.48; see Table 4). Prediction 4 was borne out: arm-hanging as a percentage of all posture rose from 2.5% to 8.3% to 24% as stratum size decreased from >10 cm to 3–10 cm to <3 cm. Arm-hanging was significantly more common among WBS <3 cm than among WBS $\geq$3 cm–10cm (χ^2=57.25, P<0.0001, $d.f.$=1, N=1820) and among $\geq$3–10 cm WBS compared to >10 cm (χ^2=15.79, P<0.0001, $d.f.$=1, N=1183).

Such testing, however, may be less legitimate for highly social chimpanzees than for

*Arm-hanging is defined here as unimanual suspension with the humerus abducted and more than half of the body weight suspended from a single manus.

largely solitary orangutans. By some measures body weight is significantly correlated with social rank among Mahale chimpanzees. Although mean rank over 12 months for 9 Mahale males was non-significantly correlated with body size rank (rank correlation, $\varrho = .583$, $P = 0.10$), highest attained rank for the 12 month study period was significantly correlated with body size rank (ϱ corrected for ties = .731, $P = 0.04$). If social rank has more profound effects on positional behavior than body size, comparisons of large and small individuals may be an indirect measure of social rank effects rather than gauging body size effects.

To factor out social rank effects on WBS diameter selection, multiple regressions were done for 6600 observations of adult males. This analysis allows body size effects and rank effects to be considered separately. WBS diameter was a dependent variable, and body size rank and dominance rank were independent variables.

Preliminary analyses revealed that the presence of other males had effects on WBS diameter choice. Accordingly, analyses were done separately on "solitary" males, that is, individuals that were more than 10 m from any other male, and "group" males, or males that had one or more male companions within 10 m. Females did not significantly change WBS diameter choice of males as determined by a comparison of two sets of analyses. First, the number males within 10 m was held at 0, and the number of females allowed to vary. Second, the number of females was held at 0 and males were allowed to vary. Although levels of significance varied, the presence of females did not change values of the regressions markedly, whereas the results varied dramatically in the presence of males. It was concluded that the presence of females affected WBS diameter choice of males little.

WBS Diameter Choice

Solitary Males

Although simple comparisons revealed a (non-significant) trend for larger males to use larger branches (see Table 3), as predicted by the suspensory hypothesis, multiple regression revealed that the relationship was actually the opposite. Partial correlation between body size rank and WBS diameter, with the effects of social rank factored out, showed that large

Table 3. Mean substrate size by body size in feeding males (all foods).[1)]

	Solitary[2)]			Group[3)]		
Body size	Mean	*N*	s.d.	Mean	*N*	s.d.
Big	6.6	146	5.9	5.2	185	3.0
Small	5.5	124	3.6	4.9	117	3.0

1) Data on tangles not included; 2) no males within 10 m of target; 3) target within 10 m of at least one male.

Table 4. Frequency of arm-hanging compared in large and small males in 3 WBS diameter categories.

Branch diameter	Body size	*N*	Percentage of arm-hanging	χ^2	*P*-value
< 3 cm	Large	118	22.8	0.1	$P = 0.83$
	Small	106	25.5		
3 – 10 cm	Large	148	9.5	1.6	$P = 0.21$
	Small	119	5.0		
> 10 cm	Large	85	3.5	0.5	$P = 0.49$
	Small	63	1.6		

Table 5. Mean substrate size by rank in feeding males.

	Solitary			Group		
Rank	Mean	N	s.d.	Mean	N	s.d.
High	6.7	148	5.9	5.2	183	3.0
Low	4.8	101	3.1	3.9	61	1.5

animals fed preferentially on small WBS (partial correlation=.27, $N=143$, $P<0.001$). Because size of the feeding tree may influence both the number of competitors and the size of available WBS diameters, observations were divided into those made on animals feeding in large trees (>15 m in height) versus small trees (≤15 m). There was no significant partial correlation between WBS diameter category and rank among small trees. Partial correlation between body size and WBS diameter was greater for solitary males feeding in large trees ($\varrho=.40$, $P<0.0004$, $N=67$, $R^2=.2$; i.e. size and rank together accounted for 20% of the variation in WBS diameter).

In contrast, simple comparisons between high ranking and low ranking males (Table 5) are paralleled in partial correlations between rank and WBS diameter category (i.e. with the effects of body size factored out; $\varrho=-.29$, $P<0.0005$, $N=143$); higher ranking males used larger substrates when feeding. The partial correlation between social rank and WBS diameter was even greater when only larger trees were considered ($\varrho=-.44$, $P<0.002$, $N=67$).

Simple comparisons between large and small males contradict results from multiple regressions (which factor out social rank effects), whereas simple comparisons of high and low ranking males parallel multiple regression results. Body size effects, it appears, are not great enough to bias social rank effects, whereas the effect social rank effects completely disguise body size effects. This suggests that social rank is more important for determining behavior than body size, and therefore that simple comparisons between high and low ranking males are legitimate, whereas simple comparisons between large and small males are not.

Group Males

Multiple regressions on group feeding males revealed no significant partial correlations between rank and WBS diameter nor between body size and WBS diameter. This result was true whether the type of food being eaten was controlled for or not, or whether the size of the fruiting tree was taken into consideration or not. This result contradicts the intuitive prediction that rank effects will be more obvious among group males than among solitary males. The distribution of WBS diameters in high and low ranking males were examined (Figs. 1a & 1b). Note that among solitary males the curves are similar in shape, even though high ranking males to used larger diameter WBS (Fig. 1a). Such is not true for group male data (Fig. 1b). When in groups low ranking males severely restricted their use of WBS diameters to the middle of the distribution, whereas high ranking males displayed a distribution very similar to that when they were solitary. It appears that even though there is no mean difference in WBS diameter use for males in groups, there was still an important social rank effect. High ranking males utilized feeding sites in all WBS diameter categories, whereas low ranking males limited use to a small range of diameters.

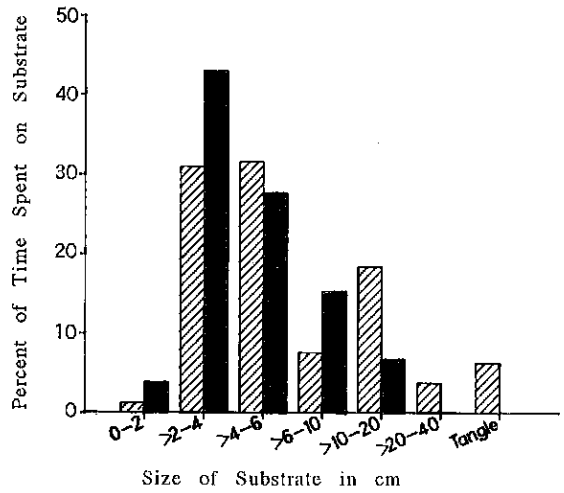

Fig. 1a. Comparison of substrate diameter differences between high and low ranking peripheral feeding males. $N=158$ for high ranking males, 105 for low ranking males. Note that the distribution of substrate diameter usage is very similar for high and low ranking males when they are solitary. ▨: High rank; ■: row rank.

Terminal Branch Use and its Effects

Although high ranking males fed among the terminal branches (within 1 m of the "edge") more often than low ranking males ($\chi^2=5.99$, $P=0.01$, $d.f.=1$, $N=704$), they

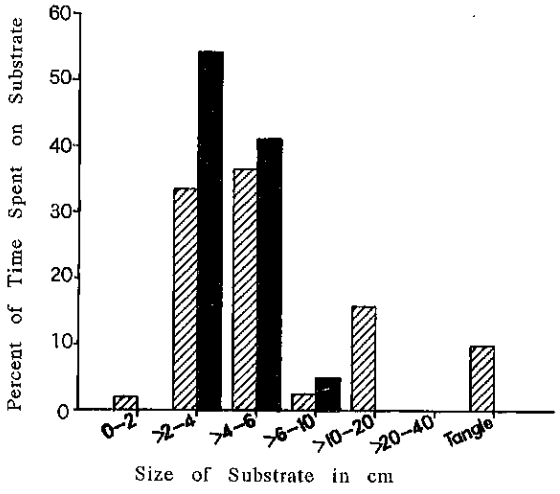

Fig. 1b. Comparison of substrate diameter differences between high and low ranking group feeding males. $N=203$ for high ranking males, 61 for low ranking males. Note that in groups the low ranking males use a restricted range of substrate diameters, while high ranking males show the same distribution as when solitary. ▨: High rank; ■: row rank.

Table 6. WBS diameter high ranking and low ranking males compared for while feeding in terminal branches.

	Solitary (% time on each size)					Group (% time on each size)				
Rank	*N*	≦4 cm	>4, ≤6 cm	>6 cm	Tangle	*N*	≦4 cm	>4, ≤6 cm	>6 cm	Tangle
High	36	55.6	13.9	11.1	19.4	60	48.4	18.3	0.0	33.3
Low	44	79.6	20.5	0.0	0.0	25	68.0	32.0	0.0	0.0

monopolized the most stable feeding sites in the tree periphery. In observations limited to individuals feeding among the terminal branches, high ranking solitary males utilized larger WBS (i.e. >6 cm, $\chi^2 = 5.15$, $P < 0.023$, $d.f. = 1$, see Table 6) and tangles ($\chi^2 = 9.38$, $P < 0.002$, $d.f. = 1$) more often than low ranking males. In groups, males feeding among terminal branches utilized tangles more often ($\chi^2 = 10.90$, $P = 0.001$, $d.f. = 1$). No such differences were found between large and small males whether solitary or in groups.

ARM-HANGING FREQUENCY ADJUSTED FOR SOCIAL RANK

In a comparison of large (size ranks 3 and 4) and small (size ranks 7 and 9) feeding males matched for social rank, large males did not arm-hang significantly more often than small males (8.0% vs 12.8%, $\chi^2 = 0.57$, $d.f. = 1$, $P = 0.45$, $N = 84$, 61); indeed, the non-significant trend was the opposite. Although there were too few observations to expect significant results by branch size categories, in each category smaller males had higher frequencies of arm-hanging, contrary to the suspensory hypothesis predictions.

DISCUSSION

Of CANT's four predictions, only prediction 4 was strongly supported by data on chimpanzees; the frequency of arm-hanging increases among smaller branches. This suggests that as previously hypothesized arm-hanging is a behavioral response to large body weight to branch diameter ratios such as are encountered most often during feeding. With varying levels of statistical significance, trends opposite of those predicted by the suspensory hypothesis were observed for other tests. Rather than disproving the hypothesis that a large body size to WBS diameter ratio tends to elicit suspensory behavior, these observations demonstrate a complex interrelationship between social rank, body size, nearness of competitors, and WBS diameter that confounds simple comparisons between large and small individuals.

The consistency of social rank effects suggests that they may be more profound than body size effects. Although simple comparisons indicate that larger males used larger WBS (Table 3), more reliable partial correlations demonstrate the opposite, that large males utilized smaller diameter WBS. Simple comparisons of high to low ranking male WBS diameters show that higher ranking males used larger WBS (Table 5), a trend supported by multiple regressions that removed body size effects.

Although results varied between group and solitary observations, higher ranking males always monopolized the largest WBS and tangles (see Figs. 1a & 1b), suggesting that stability is an important factor in feeding site selection, perhaps because stable sites allow two-handed harvesting and/or require less muscular effort to maintain balance. The presence of rank effects among solitary males suggests that high ranking males may be able to

monopolize not only preferred feeding sites within trees, but also that they may monopolize trees that have preferred feeding sites in them.

CONCLUSION

Contrary social rank and body size effects demand that special care be taken in making positional behavior comparisons between groups that have different social ranks, such as males and females, juveniles and adults, and in some cases large and small males.

High ranking males monopolized stable feeding sites, and low ranking males utilized less stable feeding sites, even when high ranking males were not nearby.

Of the predictions of the classic suspensory hypothesis, only the prediction that arm-hanging is associated with feeding among smaller branches is clearly supported. Some classic predictions falsely appeared to be borne out only because of the correlation between social rank and body size. Contrary to suspensory hypothesis predictions, larger males preferred smaller WBS. Classic predictions may fail because larger males have other competing positional demands that are more important than branch stability, perhaps limitations imposed by more energy consuming locomotor demands.

Acknowledgements. Comments by C. LORING BRACE, COLIN A. CHAPMAN, FRANK B. LIVINGSTONE, and DAVID P. WATTS were of great benefit in composing this manuscript. JOHN WARNER of the University of Michigan Statistical Laboratory provided critical statistical advice. Dr. JANE GOODALL, Prof. KENJI KAWANAKA, and Prof. TOSHISADA NISHIDA exhibited unusual generosity in embracing this project at their field sites. I am grateful to EDEUS MASSAWE, the staff of the MMWRC, the staff of the Gombe Stream Research Center, the Tanzania Scientific Research Council, the Serengeti Wildlife Research Institute, Prof. KARIM HIRJI and the Socialist Republic of Tanzania for their hospitality during my field work. RICHARD W. WRANGHAM provided crucial criticism of this research, further funding and other vital support. Research was aided by grants from the Margaret Wray French Fund, Sigma Xi, the Leakey Foundation, the University of Michigan Museum of Anthropology, Rackham Graduate School (U.M.), N.S.F. grant BNS-86-09869 and a Harvard University Postdoctoral Fellowship.

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—— Received *June 11, 1991*; Accepted *February 8, 1992*

Author's Name and Present Address: KEVIN D. HUNT, *Department of Anthropology, Indiana University, Bloomington, Indiana 47405, U. S. A.*