

## Relative Brain Size, Stratification, and Social Structure in Anthropoids

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**ABSTRACT.** The relationships between relative brain size and both stratification and social structure were examined in a total of 82 species of anthropoids. The species were divided into a total of 42 congeneric groups which consisted of congeneric species with similar ecologies and social structures. The relative brain size (RBS) was calculated for each congeneric group in each superfamily, based on an allometric equation describing the relationship between brain weight and body weight for each superfamily. Among congeneric groups with a common category of diet, RBS was significantly greater for terrestrial groups than for arboreal groups, and for polygynous (i.e. multi-female) groups than for monogynous (single-female) groups. Furthermore, RBS was significantly and positively correlated with the size of the home range per individual for the Cercopithecoidea, and with troop size for frugivorous groups of the Ceboidea. The results obtained suggest that factors associated with terrestriality and polygyny have been involved in the increases in relative brain size of anthropoids.

**Key Words:** Relative brain size; Stratification; Social structure; Terrestriality; Polygyny (multi-female); Selection pressures; Anthropoids.

### INTRODUCTION

Primates, in particular anthropoids, have highly developed brains, and the size of the primate brain relative to body size is much larger for anthropoids than for most living mammals (JERISON, 1973; HOFMAN, 1982; MARTIN, 1983). Since it has been shown that strong selection pressures have favored the development of the brain during the evolution of anthropoids (JERISON, 1973; LANDE, 1979; MARTIN, 1983), it is possible that some ecological factors are associated with the development of the anthropoid brain. Consistent with this hypothesis, previous studies have demonstrated that differences in diet are closely associated with the relative sizes of the brain of anthropoids (CLUTTON-BROCK & HARVEY, 1980; MARTIN, 1983, 1984; HARVEY et al., 1987). Anthropoids reveal, in addition to differences in diet, differences of social structure and stratification. Since behavioral characteristics, such as social interactions and foraging strategies, differ with social structure and/or stratification, and since different behaviors may be associated with differentially developed brains, it seems likely that the relative size of the anthropoid brain may be related to such differences. Indeed, CLUTTON-BROCK and HARVEY (1980) reported that the relative sizes of the brain differed between monogamous and polygynous species of primates. However, since their study did not incorporate control for the effects of diet, it remains unclear whether or not this relationship secondarily reflected differences in diet. Furthermore, they did not separate primates into prosimians and anthropoids. It may be both relevant and important to distinguish between these distinct taxonomic groups, since (1) the function and structure of the brain, and in particular of the cerebral cortex, differ considerably between prosimians and

anthropoids (e.g. RADINSKY, 1975; ALLMAN, 1982; PRITZEL & MARKOWITSCH, 1982; KAAS, 1983, 1987; VAN ESSEN, 1985); and (2) recent studies have shown that ecological variables associated with cortical expansion differ between prosimians and anthropoids (SAWAGUCHI, 1988).

In the present study, the relationships between the relative sizes of the brain, stratification, and social structures were examined across congeneric groups of anthropoids which shared common categories of diet, based on recently accumulated data. This study represented an expansion and repetition of previous investigations by several authors (e.g. STEPHAN & ANDRY, 1969; JERISON, 1973; CLUTTON-BROCK & HARVEY, 1980; MACE et al., 1981; MARTIN, 1983; HARVEY et al., 1987). It was found that the relative sizes of the brain are closely associated with differences in social structure and stratification, when the effects of diet are controlled. Possible factors influencing the relative brain size of anthropoids are discussed.

## METHODS

Standard values for the body weights and brain weights of adult members of a total of 82 species of anthropoids (Ceboidea, Cercopithecoidea, and Hominoidea) were obtained from data provided by HARVEY and CLUTTON-BROCK (1985). When the body weights differed between females and males of a given species, the mean value was adopted. The stratification, diet, and social structures of these species were determined from studies cited in EISENBERG et al. (1972), CLUTTON-BROCK and HARVEY (1977, 1980), NAPIER and NAPIER (1985), and SMUTS et al. (1987). The various species were divided into two categories of stratification: (1) terrestrial species, whose habitats are open-country, the edge of forests, and/or the base of forests, although almost all of such species, as characterized by EISENBERG et al. (1972), are "semiterrestrial"; and (2) arboreal species, which are found in arboreal habitats in forests. This classification of the stratification was identical to that used by EISENBERG et al. (1972) and CLUTTON-BROCK and HARVEY (1977, 1980). The species were divided into four categories by diet: (1) frugivorous species, whose primary foods are fruits; (2) frugivorous-omnivorous species which eat fruits primarily, but also eat considerable amounts of other kinds of food, such as animals, seeds, and foliage; (3) folivorous species which eat primarily foliage; and (4) "grass/seed-eating" species which eat primarily seeds and grasses, as well as foliage and other kinds of food. The classification of diet was thus similar to that used by EISENBERG et al. (1972) and CLUTTON-BROCK and HARVEY (1977, 1980), although *Cercopithecus aethiops* and *Theropithecus gelada* were classified, according to NAPIER and NAPIER (1985), as "grass/seed-eating" species. In terms of social structure, the species were divided into five categories: (1) solitary species; (2) monogynous species (i.e. monogamous and presumed-polyandrous), whose troops include one adult female and one adult male (monogamous) or, presumably, a few adult males (presumed-polyandrous); (3) single-male polygynous species, whose troops include many adult females and one resident male; (4) multi-male polygynous species, whose troops include many adult females and more than one resident adult male; and (5) variable-male polygynous species, whose troops include many females and a variable number of adult males, from one to many. This classification was similar to that used by SMUTS et al. (1987). The term "polygynous" is synonymous with "multi-female," and an identical system of nomenclature has been used by several authors, for example, by CLUTTON-BROCK and HARVEY (1977, 1988) and by MARTIN and MAY (1981). Based on these classifications, the sampled species of anthropoids were grouped into a total of 42 "congeneric groups," which com-

prised groups of congeneric species sharing a common ecology and a common social structure: in the case of genera which consisted of species with the same ecology and social structure, the congeneric group was synonymous with the genus; in the case of genera which consisted of species with different ecologies and/or social structures, the species were grouped into different congeneric groups which consisted of congeneric species with a common ecology and a common social structure. A similar grouping of species into congeneric groups has been employed in previous studies, and it has been shown that analyses using such congeneric groups are useful for revealing relationships across species characterized by ecological and biological variables (e.g. home range size, population density, body weight, indices of sexual dimorphism etc.) (CLUTTON-BROCK & HARVEY, 1977, 1980; MACE et al., 1980, 1981). Throughout the present study, the analysis was performed at the level of the congeneric group. Table 1 shows the congeneric groups investigated in the present study.

For calculating the relative size of the brain for each congeneric group, the average values of the brain weight ( $E$ ) and body weight ( $P$ ) were calculated for the species in each congeneric group. As has been demonstrated previously (e.g. JERISON, 1973; MARTIN, 1983, 1984), the brain weight ( $E$ , in g) reveals an allometric relationship with body weight ( $P$ , in g) as follows:

$$E = k \times P^a,$$

where  $k$  and  $a$  are constants. Therefore,

$$\log E = \log k + a \times \log P \text{ (log } k, \text{ elevation; } a, \text{ slope)}.$$

The relative size of the brain for a given congeneric group can be extrapolated from the difference between the actual brain weight and brain weight expected from this allometric equation (cf. JERISON, 1973; MARTIN, 1983, 1984). It should be noted that the actual allometric relationship, that is, the slope and/or elevation of the allometric equation, differs considerably by taxa, and in particular by superfamily in the case of anthropoids (e.g. CLUTTON-BROCK & HARVEY, 1980; BAUCHOT, 1982; HOLLOWAY & POST, 1982; RADINSKY, 1982; MARTIN, 1983; see also below). Therefore, to control for phylogenetic affinity, the relative brain size (RBS) of each congeneric group was calculated for each superfamily as follows:

$$\text{Relative brain size (RBS) for congeneric group} = \log E - [(\text{elevation for superfamily}) + (\text{slope for superfamily}) \times \log P].$$

RBS is, thus, indicative of the size of the brain mass relative to the body size, being relatively independent of the phylogenetic affinity (see, for example, CLUTTON-BROCK & HARVEY, 1980; MACE et al., 1980). The allometric equation was evaluated by regression analysis for each superfamily. Although major-axis analysis was also carried out, the data obtained by such analysis are not described here in order to avoid redundancy, since the results of major-axis analysis were, just as in the study of CLUTTON-BROCK and HARVEY (1980), quite similar to those obtained by regression analysis. Table 2 lists the values for the elevation and slope of the allometric equation examined by regression analysis. From these values, the RBS of each congeneric group for each superfamily was calculated as follows:

$$\text{RBS for Ceboidea} = \log E - (-1.118 + 0.821 \times \log P),$$

$$\text{RBS for Cercopithecoidea} = \log E - (-0.092 + 0.525 \times \log P), \text{ and}$$

$$\text{RBS for Hominoidea} = \log E - (-0.052 + 0.552 \times \log P).$$

Furthermore, since two of the three families of the Ceboidea (i.e. the Callitrichidae and Callimiconidae) consist of small numbers of congeneric groups having almost the same ecolo-

**Table 1.** Congeneric groups and their ecology and social structures.

Congeneric group	Category <sup>1)</sup>	Species
Ceboidea		
Callimiconidae		
<i>Callimico</i>	A/FR/G	<i>Callimico goeldii</i> <i>Callimico torquatus</i>
Callitrichidae		
<i>Callithrix</i>	A/FR/G	<i>Callithrix jacchus</i>
<i>Leontopithecus</i>	A/FR/G	<i>Leontopithecus rosalia</i>
<i>Cebuella</i>	A/FR/G	<i>Cebuella pygmaea</i>
<i>Saguinus</i>	A/FR/G	<i>Saguinus oedipus</i> <i>Saguinus tamarin</i> <i>Saguinus fuscicollis</i> <i>Saguinus midas</i> <i>Saguinus geoffroyi</i>
Cebidae		
<i>Alouatta</i>	A/FO/V	<i>Alouatta seniculus</i> <i>Alouatta caraya</i> <i>Alouatta palliata</i>
<i>Ateles</i>	A/FR/M	<i>Ateles geoffroyi</i> <i>Ateles fusciceps</i> <i>Ateles belzebuth</i>
<i>Lagothrix</i>	A/FR/M	<i>Lagothrix lagotricha</i>
<i>Brachyteles</i>	A/FR/M	<i>Brachyteles arachnoides</i>
<i>Cebus</i>	A/FR/S	<i>Cebus capucinus</i>
<i>Cebus'</i>	A/FR/M	<i>Cebus albifrons</i> <i>Cebus apella</i>
<i>Cebus''</i>	A/FR/V	<i>Cebus nigrivittatus</i>
<i>Saimiri</i>	A/FR/M	<i>Saimiri sciureus</i> <i>Saimiri oerstedii</i>
<i>Chiropotes</i>	A/FR/M	<i>Chiropotes chiropotes</i>
<i>Aotus</i>	A/FR/G	<i>Aotus trivirgatus</i>
<i>Callicebus</i>	A/FR/G	<i>Callicebus moloch</i> <i>Callicebus torquatus</i>
<i>Pithecia</i>	A/FR/G	<i>Pithecia pithecia</i>
Cercopithecoidea		
Cercopithecidae		
<i>Macaca</i>	T/FR-OM/M	<i>Macaca mulatta</i> <i>Macaca sinica</i> <i>Macaca radiata</i> <i>Macaca sylvanus</i> <i>Macaca fuscata</i> <i>Macaca silenus</i> <i>Macaca niger</i> <i>Macaca speciosa</i>
<i>Macaca'</i>	T/FR-OM/V	<i>Macaca nemestrina</i>
<i>Macaca''</i>	A/FR-OM/M	<i>Macaca fascicularis</i>
<i>Cercocebus</i>	T/FR/M	<i>Cercocebus galeritus</i>
<i>Cercocebus'</i>	A/FR-OM/M	<i>Cercocebus albigena</i> <i>Cercocebus torquatus</i>
<i>Papio</i>	T/FR-OM/M	<i>Papio c. cynocephalus</i> <i>Papio c. anubis</i> <i>Papio c. papio</i> <i>Papio c. ursinus</i>
<i>Papio'</i>	T/FR/S	<i>Papio hamadryas</i>
<i>Mandrillus</i>	T/FR/S	<i>Mandrillus leucophaeus</i> <i>Mandrillus sphinx</i>
<i>Erythrocebus</i>	T/FR/S	<i>Erythrocebus patas</i>
<i>Cercopithecus</i>	T/GR-SE/M	<i>Cercopithecus aethiops</i>
<i>Cercopithecus'</i>	A/FR/S	<i>Cercopithecus cepus</i> <i>Cercopithecus lhoesti</i>

(continued)

Table 1. (continued)

Congeneric group	Category	Species
		<i>Cercopithecus mitis</i>
		<i>Cercopithecus mona</i>
		<i>Cercopithecus campbelli</i>
		<i>Cercopithecus pogonias</i>
		<i>Cercopithecus nictitans</i>
		<i>Cercopithecus ascanius</i>
<i>Cercopithecus</i> "	A/FR/G	<i>Cercopithecus neglectus</i>
<i>Miopithecus</i>	A/FR/M	<i>Miopithecus talapoin</i>
<i>Theropithecus</i>	T/GR-SE/S	<i>Theropithecus gelada</i>
Colobinae		
<i>Nasalis</i>	A/FO/V	<i>Nasalis larvatus</i>
<i>Colobus</i>	A/FO/V	<i>Colobus satanas</i>
		<i>Colobus verus</i>
		<i>Colobus badius</i>
		<i>Colobus angolensis</i>
		<i>Colobus polykomos</i>
<i>Colobus</i> '	A/FO/S	<i>Colobus guereza</i>
<i>Presbytis</i>	A/FO/S	<i>Presbytis cristatus</i>
		<i>Presbytis aygula</i>
		<i>Presbytis senex</i>
		<i>Presbytis johnii</i>
<i>Presbytis</i> '	A/FO/V	<i>Presbytis obscura</i>
<i>Presbytis</i> "	T/FO/V	<i>Presbytis melalophos</i>
		<i>Presbytis entellus</i>
Hominoidea		
Hylobatidae		
<i>Hylobates</i>	A/FR/G	<i>Hylobates lar</i>
		<i>Hylobates agilis</i>
		<i>Hylobates concolor</i>
		<i>Hylobates hoolock</i>
		<i>Hylobates klossii</i>
		<i>Hylobates moloch</i>
<i>Symphalangus</i>	A/FO/G	<i>Symphalangus syndactylus</i>
Pongidae		
<i>Pan</i>	T/FR/M	<i>Pan troglodytes</i>
<i>Gorilla</i>	T/FO/V	<i>Gorilla gorilla</i>
<i>Pongo</i>	A/FR/SOL	<i>Pongo pygmaeus</i>

1) Stratification/diet/social system: A: arboreal; T: terrestrial; FR: frugivorous; FR-OM: frugivorous-omnivorous; FO: folivorous; GR-SE: grass/seed-eating; G: monogynous; S: single-male polygynous; M: multi-male polygynous; V: variable-male polygynous; SOL: solitary.

gical and social characteristics (i.e. almost all of them were arboreal, monogynous, and frugivorous), and since the other family (i.e. the Cebidae) consists of a relatively large number of congeneric groups displaying show different social structures, RBS was calculated, for some analyses, for the congeneric groups of the Cebidae only, as follows:

$$\text{RBS for Cebidae} = \log E - (-0.570 + 0.669 \times \log P).$$

The differences in distribution of values of RBS across different ecological groups were examined by one-way analysis of variance. Moreover, the superfamilies used for investigating the relationship between RBS and different ecological groups were different, since different superfamilies include different ecological groups, and since RBS was calculated for each superfamily: for example, the relationship between RBS and stratification was examined only in the case of the Cercopithecoidea and Hominoidea, because these superfamilies include both terrestrial and arboreal groups, while the Ceboidea does not include any terrestrial

**Table 2.** Elevations, slopes, and correlation coefficients of correlations between log brain weight (g) and log body weight (g) (log brain weight = elevation + slope × log body weight) for each taxa of anthropoids.

Taxa	No. of congeneric groups	Elevation	Slope	$r^{1)}$	$t$ -value
Ceboidea	17	-1.118	0.821	0.958	12.927***
Cebidae	12	-0.570	0.669	0.883	5.960***
Cercopithecoidea	20	-0.092	0.525	0.892	8.379***
Hominoidea	5	-0.052	0.552	0.958	5.807*

1) Correlation coefficient. \* $p < 0.05$ ; \*\*\* $p < 0.001$  ( $t$ -test).

groups. The names of the superfamilies employed for each examination are not included in the text to avoid repetition, but they are given in the tables (i.e. Tables 3–5).

Ecological variables, namely, the troop sizes (TS) and sizes of the home range per individual (HRi, in ha), were obtained from studies cited by CLUTTON-BROCK and HARVEY (1977, 1980) and SMUTS et al. (1987) (see also, SAWAGUCHI, 1988). HRi has been shown to be closely related to the quality of habitat in the case of the Japanese macaques (TAKASAKI, 1981, 1984). Mean values for these variables were calculated for species which belonged to each congeneric group, and the values were normalized by logarithmic transformation. The correlations of RBS with these ecological variables were examined by regression analysis. Due to the nature of the study, the level of statistical significance was taken as 10% to permit detection of any tendencies or trends.

## RESULTS

Relative brain sizes (RBS) were calculated for a total of 42 congeneric groups of anthropoids, and the relationships between RBS and both social structure and stratification were examined among congeneric groups with a common category of diet. Since there were no

**Table 3.** Relative brain sizes (RBS) for groups with different categories of diet that share common social structures and/or stratification.

Groups <sup>1)</sup>	No. of congeneric groups	RBS (mean ± S.D.)		Examined superfamilies <sup>2)</sup>
“Frugivorous”/arboreal	23	0.016 ± 0.094		CEB + CER + HOM
Folivorous/arboreal	7	-0.128 ± 0.073		
		$F_{1,28} = 13.813$	***	
“Frugivorous”/terrestrial	7	0.077 ± 0.045		CER ± HOM
Folivorous/terrestrial	3	0.015 ± 0.069		
		$F_{1,9} = 2.93$	n.s.	
“Frugivorous”/polygynous	19	0.070 ± 0.082		CEB + CER + HOM
Folivorous/polygynous	9	-0.085 ± 0.103		
		$F_{1,26} = 18.432$	***	
“Frugivorous”/arboreal/polygynous	12	0.066 ± 0.099		CEB + CER + HOM
Folivorous/arboreal/polygynous	6	-0.135 ± 0.078		
		$F_{1,16} = 18.539$	***	
“Frugivorous”/terrestrial/polygynous	7	0.077 ± 0.045		CER + HOM
Folivorous/terrestrial/polygynous	3	0.015 ± 0.069		
		$F_{1,8} = 2.930$	n.s.	

1) “Frugivorous”: frugivorous plus frugivorous-omnivorous; polygynous: multi-male polygynous plus variable-male polygynous plus single-male polygynous. Differences between groups were tested by one-way analysis of variance (n.s.: not significant at 10% level; \*\*\* $p < 0.001$ ); 2) CEB: Ceboidea; CER: Cercopithecoidea; HOM: Hominoidea.

significant differences in RBS between frugivorous-omnivorous congeneric groups and frugivorous congeneric groups ( $F = 0.027$ ,  $df = 1, 9$ ,  $p > 0.2$ , n.s.), these groups were pooled together as "frugivorous" congeneric groups. A similar combination of frugivorous groups with frugivorous-omnivorous groups was made by CLUTTON-BROCK and HARVEY (1977, 1980). This classification did not influence the results in the present study; that is, the results of the analysis in which these groups were separated were exactly the same as those in the analysis in which data for these groups were pooled together. Furthermore, only two congeneric groups were "grass/seed-eating," so that these groups have been excluded from the analysis given below, although the RBS values for these groups were similar to those for folivorous groups ( $F = 0.376$ ,  $df = 1, 7$ ,  $p > 0.2$ , n.s.), and exactly the same results as those described below were obtained when these groups were combined with folivorous groups.

Consistent with previous studies (CLUTTON-BROCK & HARVEY, 1980; MARTIN, 1983, 1984; HARVEY et al., 1987), "frugivorous" congeneric groups (i.e. frugivorous-omnivorous groups plus frugivorous groups) yielded significantly larger values of RBS than did folivorous groups ( $F = 12.177$ ,  $df = 1, 38$ ,  $p < 0.01$ ). This finding held true when groups with common social structures and/or stratification were examined, although the differences in RBS between terrestrial/"frugivorous" and terrestrial/folivorous groups did not reach the level of statistical significance ( $p < 0.2$ , n.s.), as shown in Table 3 (in this examination, different subtypes of polygynous groups were pooled together, since there were no significant differences in RBS across these groups; see below). The differences in RBS were thus examined across "frugivorous" congeneric groups and across folivorous congeneric groups with different social structures and/or stratification.

#### SOCIAL STRUCTURE AND STRATIFICATION

In the case of "frugivorous" congeneric groups, the distribution of RBS values was significantly different across groups with different social structures, as demonstrated in Table 4. However, when only "frugivorous"/polygynous groups were considered, there were no significant differences in RBS between multi-male polygynous, variable-male polygynous, and single-male polygynous groups (Table 4). There were also no significant differences between folivorous/single-male polygynous and folivorous/variable-male polygynous groups (Table 4). In contrast, when monogynous groups, the majority of which are "frugivorous," were compared with polygynous groups, it was found that "frugivorous"/monogynous groups yielded significantly smaller RBS values than any of the three subtypes of "frugivorous"/polygynous groups ( $p < 0.01$ , in each case), as shown in Table 4. When the three subtypes of multi-male polygynous groups were combined into a single entity, as polygynous groups, the significance of the difference in RBS between "frugivorous"/polygynous groups and "frugivorous"/monogynous groups was less than 0.1% (Table 4). Furthermore, since the Ceboidea includes considerable numbers of both polygynous and monogynous groups, the difference in RBS between these two groups was examined for this superfamily. RBS was significantly larger for "frugivorous"/polygynous groups than for the "frugivorous"/monogynous groups ( $F = 9.936$ ,  $df = 1, 14$ ,  $p < 0.01$ ). Moreover, the Cebidae includes considerable numbers of both polygynous and monogynous groups. It was again found that the "frugivorous"/polygynous groups gave significantly larger values of RBS than did the "frugivorous"/monogynous groups ( $F = 14.655$ ,  $df = 1, 9$ ,  $p < 0.01$ ). Thus, RBS was significantly larger for polygynous congeneric groups than for monogynous groups, while RBS did

**Table 4.** Relative brain sizes (RBS) for groups with different social structures that share a common category of diet and/or stratification.

Groups <sup>1)</sup>	No. of congeneric groups	RBS (mean±S.D.)	Examined superfamilies <sup>2)</sup>
<b>"Frugivorous"</b>			
Multi-male polygynous	12	0.054±0.086	CEB±CER
Variable-male polygynous	2	0.131±0.132	
Single-male polygynous	4	0.069±0.051	
Monogynous	9	-0.049±0.043	
		$F_{3,23} = 5.664$	**
Multi-male polygynous	12	0.054±0.086	CEB+CER
Variable-male polygynous	2	0.131±0.132	
Single-male polygynous	4	0.069±0.051	
		$F_{2,15} = 0.726$	n.s.
Multi-male polygynous	13	0.061±0.086	CEB+CER+HOM
Monogynous	10	-0.043±0.045	
		$F_{1,21} = 11.910$	**
Variable-male polygynous	2	0.131±0.132	CEB+CER+HOM
Monogynous	9	-0.049±0.043	
		$F_{1,9} = 14.799$	**
Single-male polygynous	4	0.069±0.051	CEB+CER
Monogynous	9	-0.049±0.043	
		$F_{1,11} = 18.872$	**
Polygynous	19	0.070±0.082	CEB+CER+HOM
Monogynous	10	-0.043±0.045	
		$F_{1,27} = 16.033$	***
<b>"Frugivorous"/arboreal</b>			
Multi-male polygynous	9	0.046±0.096	CEB+CER
Variable-male polygynous	2	0.077±0.084	
Monogynous	9	-0.049±0.043	
		$F_{2,17} = 4.597$	*
Multi-male polygynous	9	0.046±0.096	CEB+CER
Single-male polygynous	2	0.077±0.084	
		$F_{1,9} = 0.162$	n.s.
Multi-male polygynous	9	0.046±0.096	CEB+CER
Monogynous	9	-0.049±0.043	
		$F_{1,16} = 7.384^*$	
Single-male polygynous	2	0.077±0.084	CEB+CER
Monogynous	9	-0.049±0.043	
		$F_{1,9} = 10.638$	*
Polygynous	12	0.066±0.099	CEB+CER
Monogynous	9	-0.049±0.043	
		$F_{1,19} = 10.433$	**
<b>"Frugivorous"/terrestrial</b>			
Multi-male polygynous	3	0.076±0.053	CER
Single-male polygynous	2	0.062±0.024	
		$F_{1,3} = 0.129$	n.s.
<b>Folivorous</b>			
Variable-male polygynous	4	-0.067±0.071	CER
Single-male polygynous	3	-0.050±0.109	
		$F_{1,5} = 0.064$	n.s.
<b>Folivorous/arboreal</b>			
Variable-male polygynous	3	-0.099±0.035	CER
Single-male polygynous	2	-0.112±0.011	
		$F_{1,3} = 0.233$	n.s.

1) "Frugivorous": frugivorous plus frugivorous-omnivorous; polygynous: multi-male polygynous plus variable-male polygynous plus single-male polygynous. Differences between groups were tested by one-way analysis of variance (n.s.: not significant at 10% level; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ). 2) CEB: Ceboidea; CER: Cercopithecoidea; HOM: Hominoidea.



not differ significantly between single-male polygynous, variable-male polygynous, and multi-male polygynous groups.

In relation to stratification, it was found that “frugivorous”/terrestrial congeneric groups yielded significantly larger values of RBS than did “frugivorous”/arboreal groups ( $p < 0.01$ ), as shown in Table 5. RBS was also larger for folivorous/terrestrial groups than for folivorous/arboreal groups ( $p < 0.01$ , Table 5). The Cercopithecoidea includes considerable numbers of terrestrial groups and arboreal groups. When only this superfamily was considered, RBS was again found to be significantly larger for the “frugivorous”/terrestrial groups than for the “frugivorous”/arboreal groups ( $F = 8.313$ ,  $df = 1, 9$ ,  $p < 0.05$ ), and for the folivorous/terrestrial groups than for the folivorous/arboreal groups ( $F = 47.656$ ,  $df = 1, 5$ ,  $p < 0.001$ ).

Thus, for congeneric groups sharing a common category of diet, RBS was related to differences in social structure and stratification. Since groups sharing a common category of diet and a common social structure may have different stratifications, and since groups sharing a common category of diet and common stratification may have different social structures, it may be necessary to separate the effects of stratification from those of social structure. As regards social structure, most of the groups which share a common category of diet and stratification but have different social structures are “frugivorous”/arboreal. Among these groups, the “frugivorous”/arboreal/polygynous groups had a significantly larger RBS than did the “frugivorous”/arboreal/monogynous groups ( $p < 0.01$ , Table 4). In terms of stratification, most of the groups which share a common category of diet and social structure but show differences in stratification are polygynous. RBS was significantly larger for the “frugivorous”/terrestrial/polygynous groups than for the “frugivorous”/arboreal/polygynous groups ( $p < 0.05$ , Table 5), and for the folivorous/terrestrial/polygynous

**Table 5.** Relative brain sizes (RBS) for groups with different stratification that share a common category of diet and/or social structures.

Groups <sup>1)</sup>	No. of congeneric groups	RBS (mean $\pm$ S.D.)	Examined superfamilies <sup>2)</sup>
“Frugivorous”			
Terrestrial	7	0.078 $\pm$ 0.043	CER+HOM
Arboreal	7	0.009 $\pm$ 0.025	
		$F_{1,12} = 13.591$	**
“Frugivorous”/polygynous			
Terrestrial	7	0.078 $\pm$ 0.043	CER+HOM
Arboreal	4	0.021 $\pm$ 0.024	
		$F_{1,9} = 5.831$	*
Folivorous			
Terrestrial	3	0.015 $\pm$ 0.069	CER+HOM
Arboreal	6	-0.102 $\pm$ 0.024	
		$F_{1,7} = 15.27$	**
Folivorous/polygynous			
Terrestrial	2	0.053 $\pm$ 0.031	CER
Arboreal	5	-0.105 $\pm$ 0.026	
		$F_{1,5} = 47.656$	***

1) “Frugivorous”: frugivorous plus frugivorous-omnivorous; polygynous: multi-male polygynous plus variable-male polygynous plus single-male polygynous. Differences between groups were tested by one-way analysis of variance (n.s.: not significant at 10% level; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ); 2) CER: Cercopithecoidea, HOM: Hominoidea.

groups than for the folivorous/arboreal/polygynous groups ( $p < 0.01$ , Table 5). These results indicate that a difference in either stratification or social structure is associated with a difference in RBS.

#### CORRELATIONS BETWEEN RBS AND ECOLOGICAL VARIABLES

Correlation coefficients and levels of significance of correlations between RBS and ecological variables, namely TS and HRi, are shown in Table 6. In the case of the Ceboidea, RBS was slightly correlated with TS ( $r = 0.50$ ,  $p < 0.1$ ), but was not correlated at all with HRi. When only "frugivorous" congeneric groups of the Ceboidea were examined, RBS was found to be significantly and positively correlated with TS ( $r = 0.53$ ,  $p < 0.05$ ). Furthermore, when only the Cebidae was examined, RBS was found to be significantly and positively correlated with TS ( $r = 0.65$ ,  $p < 0.05$ ), but not with HRi. A similar correlation between RBS and TS was also noted when only "frugivorous" groups of the Cebidae were considered ( $r = 0.69$ ,  $p < 0.05$ ). This finding may reflect the fact that the reported values of TS were significantly larger for polygynous groups than for monogynous groups ( $F = 23.509$ ,  $df = 1, 11$ ,  $p < 0.001$ ), and that, as described above, RBS was significantly larger for the polygynous groups than for the monogynous groups. Indeed, no significant correlations between RBS and TS were observed when "frugivorous"/polygynous groups and "frugivorous"/monogynous groups were considered separately ( $r = -0.06$ ,  $t = 0.1236$ ,  $n = 7$ ,  $df = 5$ ,  $p > 0.1$ , n.s., for "frugivorous"/polygynous groups; and  $r = -0.37$ ,  $t = 0.88$ ,  $n = 7$ ,  $df = 5$ ,  $p > 0.1$ , n.s., for "frugivorous"/monogynous groups).

In the case of the Cercopithecoidea, RBS was significantly and positively correlated with

**Table 6.** Correlation coefficients and significance levels of correlations between RBS and ecological variables for each taxa of anthropoids.

Taxa <sup>1)</sup>	No. of congeneric groups	$r^{2)}$	$t$ -value	
Troop size:				
Ceboidea	15	0.504	2.105	+
Ceboidea ("frugivorous")	14	0.533	2.181	*
Cebidae	11	0.654	2.594	*
Cebidae ("frugivorous")	10	0.690	2.698	*
Cercopithecoidea	18	0.283	1.183	n.s.
Cercopithecoidea ("frugivorous")	9	0.403	1.168	n.s.
Cercopithecoidea (folivorous)	7	0.084	0.187	n.s.
Hominoidea	5	0.588	1.258	n.s.
Hominoidea ("frugivorous")	3	0.968	3.855	n.s.
Home range size per individual:				
Ceboidea	15	0.051	0.183	n.s.
Ceboidea ("frugivorous")	14	0.077	0.268	n.s.
Cebidae	11	0.232	0.717	n.s.
Cebidae ("frugivorous")	10	0.201	0.580	n.s.
Cercopithecoidea	17	0.628	3.083	**
Cercopithecoidea ("frugivorous")	9	0.586	1.914	+
Cercopithecoidea (folivorous)	7	0.878	4.106	**
Hominoidea	5	0.076	0.133	n.s.
Hominoidea ("frugivorous")	3	-0.218	0.223	n.s.

1) "Frugivorous"; frugivorous plus frugivorous-omnivorous. The correlations were tested by regression analysis (n.s.: not significant at 10% level; \* $p < 0.1$ ; \* $p < 0.05$ ; \*\* $p < 0.01$ ); 2) correlation coefficients.

HRi ( $r = 0.63, p < 0.01$ ), but not with TS, as shown in Table 6. When only congeneric groups of the Cercopithecoidea which shared a common category of diet were considered, there was a tendency for RBS to be correlated with HRi ( $r = 0.59, p < 0.1$ ) in the case of the "frugivorous" groups, and RBS was significantly correlated with HRi ( $r = 0.88, p < 0.01$ ) in the case of the folivorous groups. The absence of any correlation between TS and RBS in the case of Cercopithecoidea may be due to the fact that, with one exception, all groups of the Cercopithecoidea are polygynous.

In the case of the Hominoidea, RBS was not significantly correlated with TS or HRi, although a high, positive correlation coefficient was observed for the relationship between RBS and TS in "frugivorous" groups of the Hominoidea ( $r = 0.97, p < 0.2, n.s.$ ), as shown in Table 6.

## DISCUSSION

The present data indicate that the relative brain size (RBS) of anthropoids is closely associated with differences in social structure and stratification. Since the present study was controlled for the effects of diet, these associations are not a result of any relationship between RBS and diet; a close relationship between RBS and diet has been demonstrated in previous studies on various mammals (EISENBERG & WILSON, 1978; CLUTTON-BROCK & HARVEY, 1980; MACE et al., 1980, 1981; HARVEY et al., 1987). In primates, it has been shown repeatedly that "frugivorous" (frugivorous-omnivorous plus frugivorous) species have relatively larger brains than folivorous species (CLUTTON-BROCK & HARVEY, 1980; MARTIN, 1983, 1984; HARVEY et al., 1987), and the present study confirmed this finding. As has been pointed out previously, this relationship might result from the fact that folivorous species have relatively larger digestive organs than "frugivorous" species (HLADIK, 1967; see also, CLUTTON-BROCK & HARVEY, 1980; MARTIN, 1983). This possibility can be excluded from any consideration of the present results, since the present study was controlled for the effects of diet. Furthermore, since RBS was calculated separately for each superfamily (and family in some cases), no influence of phylogenetic affinity contributed to the present results. Thus, the results obtained indicate that polygynous (multi-female) and terrestrial species have relatively larger brains than monogynous and arboreal species of anthropoids.

## SOCIAL STRUCTURE

RBS was significantly larger for polygynous (multi-female) congeneric groups than for monogynous groups, when the effects of diet were controlled. There were no significant differences in RBS between the subtypes of polygynous groups (i.e. multi-male polygynous, single-male polygynous, and variable-male polygynous groups). Furthermore, in the case of New World monkeys, which include considerable numbers both of monogynous and polygynous groups, RBS was significantly and positively correlated with troop size, and troop size was significantly larger for polygynous groups than for monogynous groups. Since there were no significant correlations between RBS and troop size across polygynous groups or across monogynous groups, it seems likely that differences of social structure, rather than of troop size, are more important in relation to differences of RBS, although it should be noted that different social structures are associated with different troop sizes (CROOK & GARTLAN, 1966; RICHARD, 1985). Thus, among anthropoids, the difference between polygyny and

monogyny appears to be closely associated with differences in RBS, and it is suggested that polygynous species tend to have larger, more highly developed brains than monogynous species.

As has been indicated previously, there are several differences in terms of ecological and social characteristics between polygynous and monogynous species of anthropoids. For example, the foods for polygynous species appear to be distributed more widely and to be harder to exploit than the foods for monogynous species (WRITE, 1986; WRANGHAM, 1987). Predation pressures appear to be stronger for polygynous species than for monogynous species (TERBORGH, 1986; WRANGHAM, 1987). However, the problems related to the ecological differences between polygynous and monogynous species still remain confusing, and the differences are not completely clear (cf. CHENEY & WRANGHAM, 1987; WRANGHAM, 1987). The most prominent differences between polygynous and monogynous species may be differences in their social and sexual interactions. Polygynous anthropoids develop social organizations and various social behaviors, such as dominance rank, affiliative behaviors, social cognition, and ostracism (CHENEY & SEYFARTH, 1985; CHENEY et al., 1986; LANCASTER, 1986; DE WAAL, 1987). It has been suggested that polygyny represents a more "advanced" society than monogyny (CROOK & GARTLAN, 1966; EISENBERG et al., 1972; WILSON, 1975; RICHARD, 1985), and the values of indices reflecting the complexity of social structure are much larger for polygynous species than for monogynous species of anthropoids (EISENBERG, 1981). Furthermore, it has been shown that intra-sexual competition for mating is more strenuous in polygynous species than in monogynous species (CLUTTON-BROCK & HARVEY, 1977; CLUTTON-BROCK et al., 1977; CLUTTON-BROCK, 1988). These findings suggest that differences in social and/or sexual interactions are associated with differences in the relative brain sizes of anthropoids.

#### STRATIFICATION

The terrestrial anthropoids yielded significantly larger RBS values than did the arboreal anthropoids examined, when the effects of diet were controlled. This result may be consistent with the finding in a recent study that cerebral indices for cortical expansion are larger for terrestrial species than for arboreal species of anthropoids (SAWAGUCHI, 1988), suggesting that terrestrial species tend to have larger and more developed brains than arboreal species.

The terrestrial habitats of anthropoids are characterized, in comparison with arboreal habitats, by their poorer quality and relatively severe conditions. Indeed, terrestrial monkeys have significantly larger HRi values than arboreal monkeys (SAWAGUCHI, 1988), and HRi is indicative of the quality of the habitat: larger values of HRi are correlated with poorer quality of habitat in the Japanese macaque (TAKASAKI, 1981, 1984). The present data indicated that RBS was closely and positively correlated with HRi in the Cercopithecoidea, and this finding may be consistent with the results of a previous study which demonstrated that cerebral indices for cortical expansion are closely and positively correlated with HRi in this superfamily (SAWAGUCHI, 1988). The absence of any correlations between RBS and HRi for the Ceboidea may reflect the fact that all species of the Ceboidea are arboreal. It is suggested, therefore, that the ecological factor associated with terrestrial habitats, that is, poor quality of the habitats, is also associated with an increase in the relative brain size among anthropoids.

## POSSIBLE SELECTION PRESSURES ON RELATIVE BRAIN SIZE

Strong, positive selection pressures have been shown to favor larger rather than smaller brains, such that the relative brain size of primates increased during their evolution (JERISON, 1973; LANDE, 1979; MARTIN, 1983). Although comparative investigations, like the present study, have problems in relation to the testing of causal relationships, such research is useful for the development of hypotheses concerning possible selection pressures involved in the evolution of phenotypic characters (ENDLER, 1986). Indeed, previous comparative studies have indicated that, given the close association between relative brain size and diet, ecological selection pressures associated with foraging strategies may have influenced the relative brain size of mammals, including anthropoids (EISENBERG & WILSON, 1978; CLUTTON-BROCK & HARVEY, 1980; MACE et al., 1980; GIBSON, 1986; KING, 1986; HARVEY et al., 1987). Similarly, the present findings enable us to suggest that ecological selection pressures associated with terrestriality, as well as selection pressures associated with polygyny, may have favored the increase in relative brain size of anthropoids.

For more than a century, there has been speculation that sexual selection may have been involved in the development of the brain of anthropoids (e.g. DARWIN, 1871; PARKER, 1987). However, little evidence has been obtained to support this hypothesis. Furthermore, it has been proposed, more recently, that "active" selection (associated with social interactions or social behaviors, such as social communication and ostracism), other than intra-sexual competition for mating or choice of mate, may have favored evolutionary changes in the morphological characters of primates (i.e. the "active" selection hypothesis; SAWAGUCHI & KUDO, 1987, submitted for publication). Since different social structures are associated with different sexual and social interactions (see earlier in this Discussion), the present findings tend to support these hypotheses, and they suggest that sexual selection and/or "active" selection, which arise from the sexual and/or social interactions associated with polygyny, may have favored the increase in relative brain size of anthropoids. This hypothesis remains to be confirmed.

## IMPLICATIONS FOR THE EVOLUTION OF THE HOMINID BRAIN

As is well established, the relative size of the brain has increased significantly during the course of hominid evolution (JERISON, 1973; HOFMAN, 1983; MARTIN, 1983). Since a large increase in relative brain size can hardly be explained without reference to selection pressures, several hypotheses have been put forward for the nature of the selection underlying the increase in relative brain size of hominids. These hypotheses can be broadly divided into three basic categories; (1) ecological selection hypotheses, emphasizing selection pressures associated with ecological factors such as foraging (e.g. DARWIN, 1871; WASHBURN & LANCASTER, 1968; GIBSON, 1986; KING, 1986); (2) sexual selection hypotheses, emphasizing sexual competition for mating and/or for other resources (e.g. DARWIN, 1871; PARKER, 1987); and (3) social or "active" selection hypotheses, emphasizing selection pressures associated with social interactions, including culture (e.g. DARWIN, 1871; HOLLOWAY, 1973; CASPARI, 1979; TOBIAS, 1981; SAWAGUCHI & KUDO, 1987, submitted for publication). Previous studies employing comparative, quantitative methods have predominantly demonstrated a close association between relative brain size and diet, rather than social or sexual factors (CLUTTON-

BROCK & HARVEY, 1980; MACE et al., 1980, 1981; MARTIN, 1983; HARVEY et al., 1987), and have thus exclusively supported ecological selection hypotheses, in particular the "foraging-strategy" hypothesis. The present findings suggest that, in addition to the diet factor, ecological factors associated with terrestriality, as well as social and sexual factors associated with polygyny, have also influenced the increase in relative brain size of anthropoids. It should be noted that early hominids were largely terrestrial and polygynous (e.g. MARTIN & MAY, 1981; FOLEY, 1987), and modern humans are largely polygynous (e.g. MURDOCK, 1949; FLINN & LOW, 1986). Thus, the present findings allow us to conjecture that multiple ecological, sexual, and social selection pressures associated with diet, terrestriality, and polygyny might have favored the increase in brain size throughout the course of hominid evolution. This inference may be consistent with the hypothesis that networks of multiple factors associated with foraging strategies, sexual relationships, and social interactions have been involved in the evolution of the brain and other phenotypic characters, such as bipedalism, of hominids (JOHANSON & EDEY, 1981; LOVEJOY, 1981).

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