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Neocortex size and group size in primates: a test of the hypothesis

In this paper, the analysis of the factors influencing the evolution of neocortex size in primates given in Dunbar (1992) is extended in three specific ways. (1) An independent test is undertaken of the hypothesis that group size is a function of relative neocortex size in primates by using estimates of neocortex size to predict group size for those species that were not involved in the original analysis. The results confirm the results of the earlier analysis. (2) A more satisfactory test is attempted of the alternative hypothesis that species which differ in the degree of extractive foraging also differ in relative neocortex size. This particular version of the hypothesis is rejected. (3) These results are used to identify the "cognitive" group size for those species of baboons that live in multi-layered social systems.

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Introduction

Using data on neocortex volume given by Stephan *et al.* (1981), Sawaguchi & Kudo (1990), Dunbar (1992) and Barton & Purvis (in press) have shown that mating system and/or mean group size are a function of relative neocortex volume in primates. This relationship suggests that the size of the neocortex imposes some kind of constraint on the number of social relationships that an individual animal can keep track of within its social group. Dunbar (1992) interpreted this relationship in terms of the Social (or Machiavellian) Intelligence Hypothesis (Byrne & Whiten, 1988) which suggests that primates' unusually large brains are a consequence of the need to process more complex information about social relationships in the kinds of social groups that uniquely characterize primates. Some evidence to support this comes from Byrne's (1993) recent demonstration that the relative frequency of tactical deception in primates also correlates with neocortex size. However, it is clear that the number of relationships that have to be managed at any one time will also be an important component of the information-processing problem, so that group size itself might be expected to correlate with neocortex size, in addition to more qualitative aspects of the relationships themselves.

In this paper, an independent test of the relationship between neocortex size and group size reported in Dunbar (1992) is undertaken by using neocortex size to predict group sizes for species not included in Stephan *et al.*'s (1981) original analyses. Although data on brain parts are still not available for these species, it is nonetheless possible to test the hypothesis providing neocortex size can be estimated from some other variable which is available. Cranial capacity is widely available for most primate species (see Harvey *et al.*, 1987), and, since Aiello & Dunbar (1993) have shown that neocortex ratio is a direct function of cranial volume in the anthropoid primates, this is used to determine neocortex volume.

In a previous paper (Dunbar, 1992), a number of alternative hypotheses were tested that might explain taxonomic differences in neocortex size. Although these analyses were able to discredit most of the conventional ecological hypotheses, it proved difficult to derive an adequate test of the extractive foraging hypothesis (Parker & Gibson, 1977; Gibson, 1986). In essence, the extractive foraging hypothesis argues that sensorimotor skills are a function of the kinds of manipulative actions that animals engage in when harvesting their food, and that this will be reflected in some way in the relative size of the brain or its parts. In this paper, the hypothesis is more directly tested with specific respect to neocortex size.

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Finally, while the original analyses tended to view primate groups as simple phenomena that can be easily quantified in a rather straightforward way, there are a number of primate species for which this is less than obvious. Those species with fission-fusion social systems provide a problem in that it is not clear which of their several grouping levels is the appropriate one to compare with neocortex size. Fortunately, only the chimpanzee was included in Stephan's original analyses of brain composition, and in their case the appropriate group size seems quite uncontroversially to be the community rather than the foraging party (given the definition of a group as a set of individuals who see each other sufficiently often to have detailed social knowledge about each other's relationships). In an attempt to identify this "cognitive group" in some of the other fission-fusion species, I use estimated neocortex sizes to predict the cognitive group sizes for several species of baboons and their allies and then try to identify which of the several grouping levels that characterize these species' social systems is closest to that predicted.

Methods

In order to test the relationship between group size and neocortex size, it is first necessary to determine relative neocortex size in those species for which brain part volumes were not determined by Stephan *et al.* (1981). Dunbar (1992) found that neocortex ratio (defined as the ratio of neocortex volume to the volume of the rest of the brain) gave the best fit to the data on group size and we therefore need to be able to estimate this variable. Aiello & Dunbar (1993) have shown that, for Anthropoid primates, neocortex ratio is a simple allometric function of cranial capacity, with the following reduced major axis regression equation:

$$\log_{10}(C_R) = -0{\cdot}618 + 0{\cdot}200 \log_{10}(B) \tag{1}$$

($r^2 = 0{\cdot}857$, $P < 0{\cdot}001$, $N = 26$ Anthropoid genera), where C_R is the neocortex ratio (defined as above) and B is the total brain volume (in mm^3). Total brain volume can be determined from cranial capacity using the following allometric equation given by Aiello & Dunbar (1993), based on data given by Stephan *et al.* (1981) and Martin (1989):

$$\log_{10}(B) = 3{\cdot}015 + 0{\cdot}986 \log_{10}(C) \tag{2}$$

($r^2 = 0{\cdot}995$, $P < 0{\cdot}001$, $N = 36$ genera including *Homo*), where C is the internal cranial capacity (measured in cm^3).

Harvey *et al.* (1987) provide data on brain weights that were derived from cranial capacity, so that these need first to be converted back to cranial capacity using the following allometric equation given by Martin (1989):

$$\log_{10}(C) = -0{\cdot}025 + 1{\cdot}018 \log_{10}(W) \tag{3}$$

($r^2 = 0{\cdot}996$), where W is the brain weight (in grams).

With neocortex ratio determined by Equation (1), mean group size can be predicted using the following equation from Dunbar (1992):

$$\log_{10}(N) = 0{\cdot}093 + 3{\cdot}389 \log_{10}(C_R) \tag{4}$$

($r^2 = 0{\cdot}764$, $P < 0{\cdot}001$, $N = 35$ genera), where N is the mean group size. However, it should be noted that there do appear to be grade differences among the primate taxa in this relationship. Dunbar (1993) found that prosimians, simians and hominoids lie on regression lines of similar slope but different intercept. The RMA regression line for New and Old World monkeys is:

$$\log_{10}(N) = -0{\cdot}221 + 4{\cdot}135 \log_{10}(C_R) \tag{5}$$

($r^2=0{\cdot}53$, $P<0{\cdot}001$, $N=23$ genera). Since setting a regression line through data sets that involve different grades inevitably results in a line of lower or higher slope, both relationships are used in the present analysis.

I use Equations (1)–(5) to predict group sizes for those species that were not included in Stephen *et al.*'s (1981) sample for which brain weights are given by Harvey *et al.* (1987). Group sizes predicted by equations (4) and (5) are then compared with the observed mean group size determined from the relevant chapters in Smuts *et al.* (1987). For these purposes, only those species are included for which estimates of group size are available for at least two groups. Studies which provide census data for only a single study group tend to select groups of untypical size (see for example Sharman & Dunbar, 1982).

Because the sample size is limited to species from a small number of genera, the method of independent contrasts recommended by Harvey & Pagel (1991) is used to compare variables at the species level. In this way, all the data can be used without the relationships being confounded by phylogeny. The values for neocortex ratio and observed group size were plotted onto a standard phylogeny for the species involved (with relationships between the species of the genus *Macaca* following Delson, 1980); all branch nodes are bifurcating except one (for three pairs of macaque species). Values for higher nodes were calculated as the average of the values at the immediately lower pair, following Harvey & Pagel (1991). Note that higher nodes do not reconstruct the ancestral condition; rather, they partition the variance in the end-points among the higher taxonomic levels (M. Pagel, pers. comm.).

As specific hypotheses are being tested, one-tailed tests are used unless otherwise stated.

Results

Testing the basic hypothesis

Table 1 gives data on brain weight neocortex ratio, the group sizes predicted by Equations (4) and (5) and observed mean group size for all species for which these variables could be determined. In general, the observed group sizes are close to the predicted values, irrespective of which equation is used to predict group size. For the 14 species in Table 1, there are 12 independent contrasts (five at species level and seven at higher nodes). Figure 1 plots the contrasts in observed group size against the contrasts in estimated neocortex ratio. With Spearman $r_S=0{\cdot}708$ ($N=12$, $P\approx 0{\cdot}01$), it is clear that, even though the fit leaves something to be desired, the estimated neocortex ratio does predict observed mean group size in these species.

The relatively poor fit compared to the original analysis given in Dunbar (1992) can probably be attributed to the fact that errors are being successively compounded as initial values for brain weight are interpolated through a series of equations, each of which has an associated error. The compounded errors resulting from interpolating successively through Equations (1) to (5) would yield a value of $r^2=0{\cdot}857 \times 0{\cdot}995 \times 0{\cdot}996 \times 0{\cdot}530=0{\cdot}450$ if Equation (5) is used to predict group size. The actual fit for the data points in Figure 1 is a respectably close $r^2=0{\cdot}402$.

Testing the extractive foraging hypothesis

Gibson (1986) distinguished between four different categories of extractive foraging. Table 2 lists the species she suggested might be included in each category. If the extractive foraging

Table 1 Data on brain size and group size for species not included in Stephan *et al.*'s (1981) original study

Taxon	Brain wt (g)[a]	C_R[b]	$N_{pred(4)}$[c]	$N_{pred(5)}$[d]	Observed N[e]
Brachyteles	120·1	2·498	27·6	26·5	21·0
Cacajao	73·3	2·262	6·0	4·2	5·0
Macaca sinica	69·9	2·241	19·1	16·9	24·8
M. fasicularis	69·2	2·236	18·9	16·8	28·0
M. mulatta	95·1	2·383	23·5	21·8	40·8
M. silenus	85·0	2·330	21·8	19·9	21·0
M. nemestrina	106·0	2·436	25·3	23·9	34·2
M. radiata	76·8	2·283	20·3	18·3	30·8
M. sylvanus	93·2	2·374	23·2	21·5	18·3
C. aethiops	59·8	2·171	17·1	14·8	19·5
P. entellus	135·2	2·558	29·9	29·2	33·0
P. obscura	67·6	2·226	18·7	16·4	10·3
P. melalophos	80·0	2·302	20·9	18·9	12·8
Colobus guereza	82·3	2·315	21·3	19·3	8·6

[a] From Harvey *et al.* (1987).
[b] Neocortex ratio (neocortex volume to volume of rest of brain) estimated from brain weight using Equations (1)–(3).
[c] Mean group size predicted from neocortex ratio by Equation (4).
[d] Mean group size predicted from neocortex ratio by Equation (5).
[e] Observed mean group size, calculated from data in Smuts *et al.* (1987).

Table 2 Gibson's (1986) classification of extractive foragers

	Extractive foragers		Non-extractive foragers
Skilled	Unskilled	Specialized	
Homo	*Pongo*	*Gorilla*	*Hylobates*
Pan	*Papio*	*Callithrix*	*Cercopithecus*
Cebus	*Macaca*		*Miopithecus*
Daubentonia	*Lagothrix*		*Erythrocebus*
	Saimiri		*Cercocebus*
			Procolobus
			Presbytis
			Nasalis
			Pygathrix
			Alouatta
			Pithecia
			Saguinus
			Cebuella
			Tarsier
			All other Prosimii

hypothesis is in any way related to neocortex size, then there ought to be significant differences in neocortex size between these categories of species; alternatively, skilled extractors should have larger neocortices than species in the other categories.

Figure 2 suggests that, for those species for which exact brain part volumes are given by Stephan *et al.* (1981), there are significant differences between the categories (Kruskal–Wallis ANOVA: $\chi^2=8{\cdot}956$, df=3, $P<0{\cdot}05$). The differences are even more pronounced if only Anthropoids are considered ($\chi^2=14{\cdot}342$, df=3, $P<0{\cdot}01$). Comparisons of means suggests that

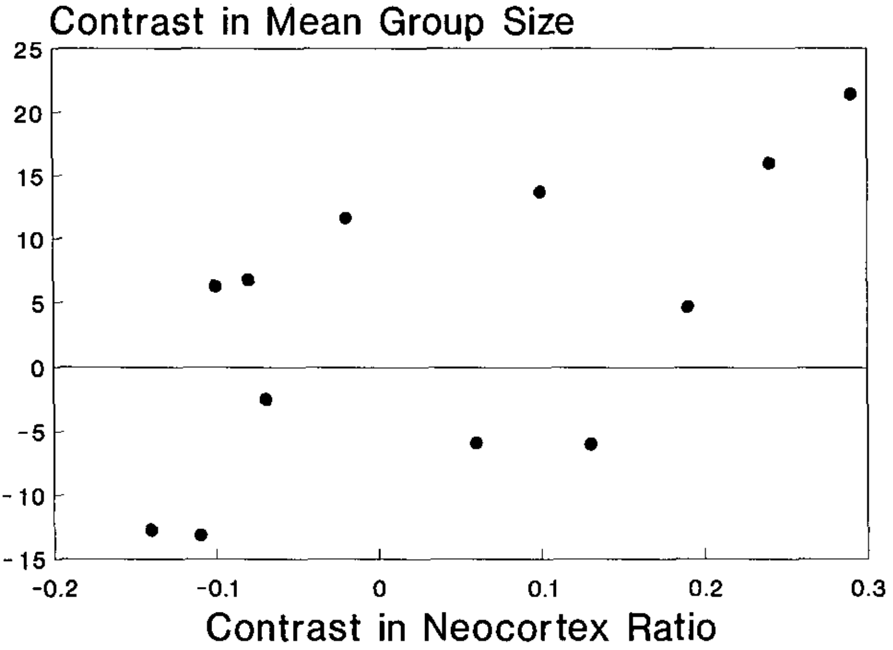

Figure 1. Contrast in observed mean group size plotted against contrast in predicted neocortex ratio. For each variable, the plotted value is the difference between two taxa at a given node, when these values are mapped onto a phylogenetic tree for the species concerned (see Harvey & Page, 1991). All higher nodes except one are dyadic; the exception is three pairs of *Macaca* species, for which the average of all three possible pairwise combinations was determined. There are five comparisons between pairs of species, two between pairs of species dyads within the same genus, three between generic means from the same subfamily, and two (colobines *vs.* cercopithecines, catarrhines *vs.* platyrrhines) at higher nodes.

it is largely the difference between skilled extractors and the other categories that is responsible for the significance of this result (Anthropoids only: skilled *vs.* unskilled, $z=1{\cdot}965$, $P=0{\cdot}05$; skilled *vs.* non-extractors, $z=2{\cdot}323$, $P=0{\cdot}020$; unskilled *vs.* non-extractors, $z=1{\cdot}391$, $P=0{\cdot}165$; all tests two-tailed). However, this seems to be largely a consequence of the fact that *Homo* and *Pan* dominate the skilled extractor category, possibly creating a phylogenetic artefact. Relative to either total brain size or body size, *Cebus* does not have an exceptionally large neocortex by simian standards; nor does *Daubentonia* have a larger neocortex than other prosimians (none of whom are extractive foragers).

An alternative possibility is that while neocortex ratio is primarily correlated with group size, the residuals from the regression line (i.e. the excess neocortex volume over and above that accounted for by group size) is a function of foraging regime. Figure 3 plots the residuals for neocortex ratio regressed on group size for the four grades of foraging style. Although skilled extractors seem to have larger residuals than unskilled extractors, it is clear that, taken as a whole, there are no significant differences between extractive and non-extractive foragers, either within the Prosimians or within the Anthropoids.

These results suggest that, at least as far as the neocortex is concerned, the extractive foraging hypothesis is largely a reflection of the cognitive and behavioural capacities of the hominoids. This conclusion is supported by the fact that if *Homo* and *Pan* are excluded, there are no longer any significant differences among the Anthropoids (*Cebus* included in unskilled extractors: Kruskal-Wallis ANOVA, $\chi^2=2{\cdot}422$, df$=2$, $P>0{\cdot}30$).

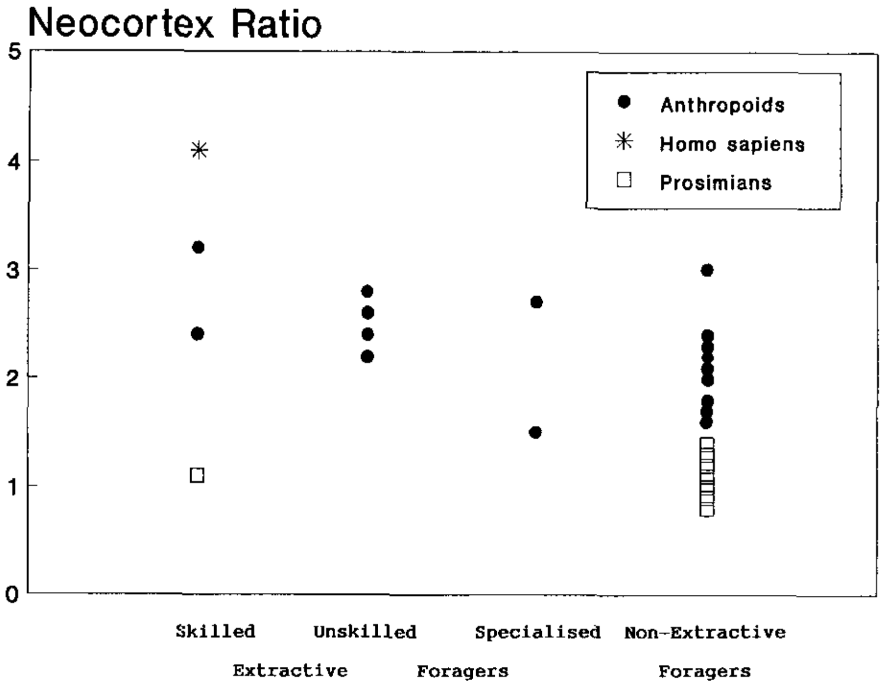

Figure 2. Neocortex ratios for species listed by Gibson (1986) as representing her four types of extractive foraging regime. Source: data given in Dunbar (1992, Table 1).

Group size in baboons

Four species of baboons (the gelada and hamadryas and the drill and mandrill) were not included in the above analyses because it is not clear which of several possible groupings that characterize their complex fission-fusion social systems is the appropriate one to consider for this analysis. The relevant data for these four species are given in Table 3.

For the drill and the mandrill, the group sizes predicted from relative neocortex size are 32·3 and 33·4, respectively. Although none of the studies that have been carried out on these species (Gartlan, 1970; Jouventin, 1975; Hoshino *et al.*, 1984) were able to provide accurate censuses, all nonetheless agreed that both species possess a fission-fusion type of social system in which smaller more cohesive groups coalesce into larger more unstable groups. Mean group sizes for the smaller group type were 16·6 ($N=9$ independent groups with a single adult male: Gartlan, 1970), 26·0 ($N=23$ subgroups: Jouventin, 1975) and 52·0 ($N=4$ groups: Hoshino *et al.*, 1984). While it it not clear just what the status of these groupings are [Hoshino *et al.* (1984) note that their groups sometimes split into subgroups], they are of about the right magnitude to constitute the species' cognitive grouping. Certainly, the instability of the larger groupings (whose size can range up to 250 animals) would make these an unlikely candidate.

In the case of the hamadryas, the predicted group size of 30·5 seems to correspond most closely to the size of the patrilineal clans (essentially brotherhoods that exchange females among themselves: see Sigg *et al.*, 1982; Colmenares, 1992). Censuses of three clans in one wild band over a 6-year period yield a mean size of 21·6 animals (range 10–36: Sigg *et al.*, 1982). In contrast, mean band size at 63·1 (range 55–70, $N=11$ half-yearly censuses: Sigg *et al.*, 1982) and mean troop size at 121 (Kummer, 1968) are clearly too large, while mean harem (i.e. one

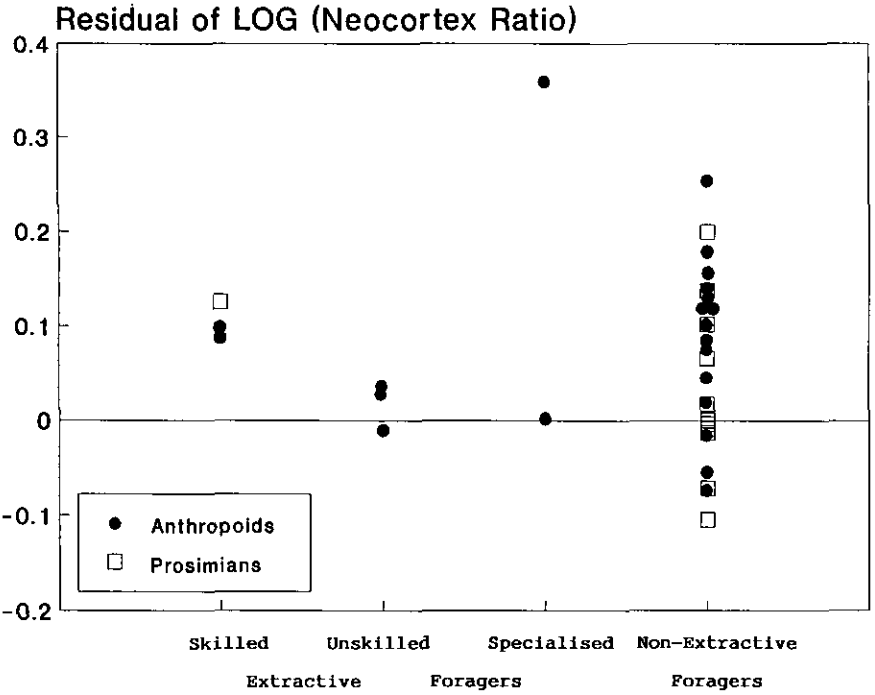

Figure 3. Residuals of Log_{10} neocortex ratio regressed against Log_{10} group size for the four types of extractive foraging regime. The plotted value is the observed neocortex ratio minus that predicted by group size, for logged data. Source: as for Figure 2.

Table 3 Data on brain size and group size for fission-fusion baboon species

Taxon	Brain wt (g)[a]	C_R[b]	$N_{pred(5)}$[c]	Observed group sizes
Theropithecus	131·9	2·545	28·6	13·0, 29·5, 99·7, 363·7[d]
P. hamadryas	142·5	2·584	30·5	7·8, 21·6, 63·1, 121[e]
M. sphinx	159·4	2·643	33·4	39·3, 119·2[f]
M. leucophaeus	152·7	2·621	32·3	16·6, 87·8[g]

[a] From Harvey *et al.* (1987)

[b] Neocortex ratio (neocortex volume to volume to rest of brain) estimated from brain weight using Equations (1)–(3).

[c] Mean group size predicted from neocortex ratio using Equation (5).

[d] Mean sizes for reproductive units, teams, bands and communities, respectively (except for teams, average of three population means in each case), based on data given by Dunbar & Dunbar (1975), Kawai (1979), Dunbar (1984), Ohsawa & Dunbar (1984); data for team sizes are given in Table 4.

[e] Mean sizes for reproductive units, clans, bands and troops, respectively, based on data given by Sigg *et al.* (1982) for units and clans and Kummer (1968) for bands and troops.

[f] Mean sizes for subgroups and aggregations, based on data given by Jouventin (1975) and Hoshino *et al.* (1984).

[g] Mean size for single male and multimale groups for counts classed as "reliable" by Gartlan (1970).

male group) size at 7·8 (range 2–23, N=82 units censused at half-yearly intervals; Sigg *et al.*, 1982) is too small.

In the case of the gelada, all the conventional groupings are either too small (one male units with mean size 13·0, N=3 population means) or too large (bands at mean size 99·7, communities at mean size 363·7: N=3 communities in each case). (A community is defined as

Table 4 **Size and composition of teams in two populations of gelada baboons**

Population	Band	Units in team[a]	Unit sizes	Total
Bole	ST	A+F	22+ 8	30
	Bonfeter	M+O	21+11	32
	Kusai	I+K	17+12	29
Sankaber	Main	H17+H22	18+11	29
	Abyss	H39+H51	10+16	26
	Main	N12+N17	18+14	32
	Main	N14+N27	11+11	22
	Main	N13+N16	16+20	36
	Main	N7 +N21	21+ 8	28
	E2	N38+N9	11+16	27

[a] For Bole, teams defined by similarity of ranging areas (see Dunbar & Dunbar, 1975, Figure 45); for Sankaber, teams defined as units that were recorded as each other's nearest neighbours on at least 10% of samples (N=12–17 three nearest neighbour samples for H-prefix units; 100 nearest neighbours for N-prefix units: unpublished data).

the set of bands that forage together in the same herd on at least 15% of days: see Kawai *et al.*, 1983, Figure 1; at Gich, the only community that was completely censused included three bands totalling 478 animals, at Sankaber again three bands totalling 487, and at Bole two bands totalling 126).

A more plausible suggestion is that, for the gelada, the cognitive grouping corresponds to a "team", a set of two (occasionally three) reproductive units that seem to have a particularly close affiliation with each other (see Kawai *et al.*, 1983). Teams at Bole averaged 30·3 animals and those at Sankaber 28·6 (see Table 4). Teams appear to be the product of the recent fission of a large unit; it seems that the residual relationships between individual members of the two daughter units result in the two units continuing to forage near each other (and even occasionally interact) for some time after the fission itself has occurred (see Kawai *et al.*, 1983).

Discussion

These results confirm, at least as far as anthropoids are concerned, the earlier finding that relative neocortex size correlates with group size in primates. This finding thus seems to be quite robust. Note that the evolutionary argument (as expressed in most versions of the Social Intelligence Hypothesis) implies that the need to increase group size (presumably driven by some ecological selection pressure) acted as the selection pressure to evolve large neocortices. To test this hypothesis, the logic of the argument is reversed (and hence group size is plotted against neocortex ratio) because, from an individual animal's perspective at any given moment in time, neocortex size acts as a constraint on the size of group it can sustain. Animals who need to increase group size will, over the evolutionary long-term, only be able to do so providing they also increase neocortex size.

In addition, Aiello & Dunbar's (1993) claim that neocortex ratio can be predicted from cranial volume gains support, although it is clear that the number of interpolations involved greatly reduces the accuracy of any predictions that can be made. Nonetheless, this is a valuable result because it suggests that we can estimate neocortex ratios (and so predict group sizes) for extinct species as well as extant ones.

A more precise test of the extractive foraging hypothesis suggests that this hypothesis cannot explain the evolution of neocortex size in primates in general. Gibson (1986) noted that *Cebus* and *Daubentonia*, among other skilled extractive foragers, had larger Progression Indices for neocortex size than non-extractive foragers. This appears to conflict with the present findings which suggest that both these taxa have only a moderate neocortex ratio. Stephan *et al.*'s (1981) Progression Index was a measure of brain (part) size relative to that for a basal insectivore of the same body mass. However, brain size seems to be evolutionarily more conservative than body mass (see Willner, 1989; Deacon, 1990; Dunbar, 1992); as a result, body size can change without corresponding changes in brain size taking place. The result is large-bodied species with relatively small brains (e.g. *Papio*) and small-bodied species with relatively large brains (e.g. the Callitrichidae). Stephan's index may thus reflect changes in body mass rather than changes in brain size, and this seems to be the reason why *Cebus* and *Daubentonia* have large neocortex Progression Indices but only moderate neocortex ratios.

This does not, however, mean that the extractive foraging hypothesis is necessarily wrong. It may still be relevant to specific species (e.g. *Cebus* and *Homo*). One possibility is that extractive foraging skills evolved in a window of opportunity provided by the evolution of larger brains that was consequent on the need to evolve larger groups. Any observed relationship between brain size and an extractive foraging lifestyle would thus be a consequence (rather than a cause) of enlarged brain size.

It is worth pointing out in conclusion that this analysis focuses on one specific form of grouping pattern, namely the "cognitive group" (i.e. that which is held together by direct social knowledge of the other group members). This does not specify the particular kind of group involved; nor does it identify the selection pressure that has given rise to it. This much should be clear from the fact that the "cognitive group" does not correspond to the same grouping level within the social system of fission-fusion species. In these cases, the different types of group appear to subserve different functions within the animals' social and ecological worlds (see Dunbar, 1989). What it does perhaps suggest is that this form of grouping has been under sufficiently intense selection pressure in a given species to warrant the evolution of specific neural machinery to enable it to be held together through time and space. Identifying the function that such groups subserve may then allow us to evaluate the relative importance of the different selection pressures influencing social evolution.

The finding that, in the gelada, the "cognitive" group size corresponds to teams provides a possible explanation for the relative instability of the large scale groupings characteristic of this species (i.e. bands and herds). One reason why the bands lack the cohesion of more conventional *Papio* baboon troops may be that they far exceed the size which gelada (with their relatively small neocortices) are capable of integrating. That hamadryas bands are more stable than those of the gelada might be due either to the fact that they are smaller or to the fact that they are ecologically constrained into remaining together (e.g. by the lack of safe refuges), or both. More detailed information on the dynamics of the various group types in these species would clearly be enlightening.

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