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Received 3 March 1989
Revision received 18 October 1991 and accepted 2 December 1991

Keywords: behavioural ecology, grooming, brain size, body size, social intellect.

Neocortex size as a constraint on group size in primates

Two general kinds of theory (one ecological and one social) have been advanced to explain the fact that primates have larger brains and greater congnitive abilities than other animals. Data on neocortex volume, group size and a number of behavioural ecology variables are used to test between the various theories. Group size is found to be a function of relative neocortical volume, but the ecological variables are not. This is interpreted as evidence in favour of the social intellect theory and against the ecological theories. It is suggested that the number of neocortical neurons limits the organism's information-processing capacity and that this then limits the number of relationships that an individual can monitor simultaneously. When a group's size exceeds this limit, it becomes unstable and begins to fragment. This then places an upper limit on the size of groups which any given species can maintain as cohesive social units through time. The data suggest that the information overload occurs in terms of the structure of relationships within tightly bonded grooming cliques rather than in terms of the total number of dyads within the group as a whole that an individual has to monitor. It thus appears that, among primates, large groups are created by welding together sets of smaller grooming cliques. One implication of these results is that, since the actual group size will be determined by the ecological characteristics of the habitat in any given case, species will only be able to invade habitats that require larger groups than their current limit if they evolve larger neocortices.

Journal of Human Evolution (1992) **20,** 469–493

Introduction

Primates, as a group, are characterised by having unusually large brains for their body size (Jerison 1973). Implicitly or explicitly, it has usually been assumed that large relative brain size correlates with these animals' greater cognitive ability. Three general kinds of hypotheses have been suggested to explain the evolution of large brain size within the primates. One group of explanations emphasises the ecological function of cognitive skills, especially in large ecologically flexible species like primates (Clutton-Brock & Harvey, 1980; Gibson, 1986; Milton, 1988). The second emphasises the uniquely complex nature of primate social life, arguing for a mainly social function to intellect (Jolly, 1969; Humphrey, 1976; Kummer, 1982; Byrne & Whiten, 1988). The third type of explanation argues that neonatal brain size is constrained by maternal metabolic rates; species therefore have large brains only when maternal nutrition is on a high enough plane to allow the mother to divert spare energy into the foetus (e.g., Martin, 1981, 1984; see also Hofman, 1983*a*,*b*; Armstrong, 1985).

The third type of explanation need not concern us here for two quite different reasons. In the first place, this kind of explanation offers a purely developmental account; it essentially states that there is a limit (imposed by maternal nutrition) beyond which foetal brain size cannot grow. But it offers no explanation of any kind as to why the brain should always grow to this limit. Given that the brain is the most expensive organ of the body to maintain (it consumes approximately 20% of the body's total energy output in humans, while accounting for only 2% of adult body weight), it is evolutionarily implausible to suggest that organisms will develop large brains merely because they can do so. Natural selection rarely leads to the evolution of characters that are wholly functionless simply because they are possible. Hence, even if it were true that energetic considerations constrain brain size, a proper functional

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explanation must still be given to explain why brains grow to the size they do. Thus, at best, this argument only provides a *necessary* condition for the evolution of large brains; it does not provide a *sufficient* reason as to why organisms should be prepared to devote so much energy to a single organ. The second reason why we can ignore this explanation is that its validity has been questioned (see Pagel & Harvey, 1988; Harvey & Pagel, 1991; Deacon, 1990*a*). Pagel & Harvey (1988) have shown that brain size correlates with gestation length among mammals as a whole. They argue that brain size is determined largely by the length of the period available for maternal investment and not by the mother's nutritional status.

So far, evidence in support of the "social intellect" (or "Macchiavellian Intelligence"; Byrne & Whiten, 1988) hypothesis has been, at best, circumstantial. No direct quantitative tests have been possible, largely because the hypothesis itself is phrased somewhat vaguely. We neither know precisely what is meant by "social intelligence" nor how to measure it.

In contrast, quantitative evidence has been adduced in a number of cases to support the rival hypothesis that primate intellectual abilities are essentially ecological in origin. There are, in fact, three quite distinct versions of the ecological theory. (1) Clutton-Brock & Harvey (1980) demonstrated that, among primates, frugivores have significantly larger brains relative to body weight than folivores and interpreted this as indicating that greater cognitive skills are required to monitor such ephemeral resources as fruiting trees. [Milton (1988) developed a similar argument from a detailed comparison of the behavioural ecology and cognitive skills of two South American monkeys (the folivorous howler monkey, *Alouatta*, and the frugivorous spider monkey, *Ateles*).] (2) In addition, they were also able to show that relative brain size correlated with mean home range size, as might be expected if larger brains were required to accommodate mental maps for larger areas. Mace & Harvey (1983) found much the same relationship between brain size and ecology in rodents. Finally, (3) Gibson (1986, 1990; Parker & Gibson, 1977) has used experimental data from *Cebus* monkeys to argue that the key to primate brain evolution lies in the cognitive demands of "extractive foraging" (the exploitation of food items that are embedded in a matrix from which the edible components have to be removed).

One of the problems with all the analyses to date is that the tests of the main candidate hypotheses have invariably been "one-sided"; none of them unequivocally excludes the possibility that the alternative theory might in fact be true. The results obtained by Clutton-Brock & Harvey (1980), for instance, are confounded by the fact that both diet and range size correlate closely with group size (see, for example, Dunbar, 1988). Indeed, Clutton-Brock & Harvey (1980) themselves found a significant difference in brain size between monogamous and polygamous species (a difference that partly reflects group size).

In this paper, I try to test directly between the main hypotheses by using comparative data to search for the behavioural indices that correlate best with relative brain size. Deacon (1990*a*) has drawn attention to an important distinction between selection processes and the processes governing ontogeny that are often confused in such analyses. However, it is important to appreciate that how we interpret the causal arrows in these cases depends on the timescale. In ontogenetic terms, the size of the brain may impose a constraint on the size of the social group. But, in evolutionary terms, the causal arrow is reversed; selection pressures favouring the evolution of bigger groups force the evolution of larger brains in order to make this possible. Here, brain size is assumed to act as a constraint on some aspect of the animals' behaviour. Consequently, although in evolutionary terms a behavioural requirement is the functional cause of changes in brain size, the hypotheses are tested by regressing the behavioural variable onto brain size, because, in proximate terms, the behaviour of contemporary populations is constrained by current brain size. This is a crucial distinction and it has frequently been conflated in the literature.

Selection of variables

From the animal's point of view, the problem is essentially an information processing one: the more information that an animal needs to be able to store and manipulate about its social or ecological environment, the larger the computer it needs. Hence, we need to identify the key factor that is most likely to create an information overload for the animal under each of the main hypotheses.

From the social knowledge point of view, there would seem to be three primary candidates. One is the sheer number of individuals that an animal has to know and maintain relationships with. If the cohesion of a group through time depends on the strength of each animal's relationships with all the other members of its group, then the information load will be directly related to group size; group size should therefore be a linear function of brain size. An alternative possibility would recognise the fact that an animal has to keep track not just of its own relationships with every other member of the group, but also all the third party relationships between every possible pair of dyads. In this case, the information load will be a power function of group size (see Whiten & Byrne, 1988), and group size should therefore be a logarithmic function of brain size. The third possibility is that the problem may lie with the nature of the relationships themselves rather than their absolute number. One way in which this might be important is if the group's cohesion through time depends on the intensity of the relationships within small cliques (or sub-sets of interacting animals), with the cliques themselves being linked by a limited number of relationships in a hierarchically structured pattern (see, for example, Sade, 1972; Kawai *et al.*, 1983; Dunbar, 1989). In this case, the quality of the relationships between individuals may be a function of their ability to exploit certain forms of social knowledge. Group size might then be either a linear or a power function of brain size, but, in either case, the size of interacting cliques will be a logarithmic function of brain size.

Most primates live in groups that are usually cohesive both spatially and temporally. However, the social systems of some species are sufficiently complex to raise doubts about which level of grouping is the most appropriate for analyses of this kind (see Dunbar, 1988, 1989). In the present context, my interest is in the number of individuals that an individual animal knows and interacts regularly with (see also Dunbar, 1991). For those species like the chimpanzee and the spider monkey which have so-called "fission-fusion" societies, this level of grouping is identified as the set of individuals from which the unstable foraging parties are derived. For the chimpanzee, this is clearly the community (Wrangham, 1986); for the spider monkey (*Ateles* spp.), it is the group as defined by Robinson & Janson (1987).

The ecological hypotheses can also be interpreted in one of three ways. Firstly, frugivores need proportionately larger brains in order to be able to monitor the availability of their dispersed, often ephemeral, food supply (Clutton-Brock & Harvey, 1980). Consequently, we would predict a correlation between relative brain size and the dietary importance of fruit. The proportion of the diet accounted for by fruits is used here as the most appropriate index.

The second possibility is that the information overload is created by the sheer size of the mental map that the animal has both to hold in its head and to manipulate cognitively in order to navigate its way from one food source or refuge to another. That primates (and other animals) do have mental maps (or at least spatial cognition) of this kind is now fairly certain (see, for example, Sigg & Stolba, 1981; Boesch & Boesch, 1984; Olton, 1985). In this case, we would expect a correlation between brain size and the size of the ranging area, although the relationship might well be an allometric one. Alternatively, the information overload might be related to some more immediate aspect of navigation (for example, due to the animal using short-term inertial navigation rather than a large-scale mental map to find its way about). In this case, we might expect a correlation between brain size and day journey length.

The third version of the ecological hypothesis concerns "extractive foraging". This is the most difficult of the hypotheses to test. Extractive foraging, as conceived by Gibson (1986) for example, seems to be primarily concerned with the removal of food items from an embedded matrix. The primary source of any information overload would seem to lie in the need to learn high-level cognitive rules that can be applied in a wide range of circumstances to different kinds of embedded resources. There is some uncertainty as to just what constitutes an embedded resource in this sense, however. Cracking open nuts to extract the contents and fishing for termites both seem to count as examples of extractive foraging, but picking fig fruits or insects from an open tree branch do not. Hunting (but not scavenging?) might also count as extractive foraging in the sense that the prey animal has to be tracked down and caught. Unfortunately, few studies have differentiated primate diets in this kind of quantitative detail. Moreover, Parker & Gibson (1977) base most of their argument on evidence from a single taxon (*Cebus* spp.) that happens both to have a large brain and engage in extractive foraging; they then extend the argument to chimpanzees and humans largely by analogy. The only way of testing this hypothesis at present is to ask whether species that have been classed as extractive foragers have larger brains than other primates. Among the species available in my sample, humans, chimpanzees, baboons, capuchins, the aye-aye and (less certainly) marmosets (but not tamarins) have been designated as extractive foragers. Humans, chimps and capuchins are taken to be extractive foragers because these are the taxa that Gibson specifically identifies. Baboons are considered to be extractive foragers because they are the only other taxon to hunt and also they commonly eat roots and grass corms dug up from the ground. The aye-ayes are counted because of the way they use their long index finger to extract insects from hiding places under tree bark and the contents from eggshells. Marmosets might be another candidate taxon because of their use of incisors to gouge trees in order to obtain sap, but tamarins would be excluded because they do not feed in this way (see Sussman & Kinzey, 1984).

Finally, we need an appropriate measure of brain size. Previous analyses have tended to use whole brain size (or alternatively, cranial capacity). Clutton-Brock & Harvey (1980), for example, found that relative brain size (i.e., brain size adjusted for body weight) correlates positively with home range size in most (but not all) primate families, and that monogamous primates have relatively smaller brain sizes than polygamous primates when body weight is taken into account (see also Mace & Harvey, 1983). Subsequently, Sawaguchi (1990) demonstrated that relative brain size correlates significantly with group size in the ceboid platyrrhines, but with range size in the cercopithecoid catarrhines. He was also able to show that terrestrial primates had larger brain sizes than arboreal species when diet was held constant.

However, both neurological and evolutionary considerations suggest that total brain size may not be the most appropriate measure of cognitive capacity for the purposes of testing specific functional hypotheses. There is growing evidence, for example, to suggest that the hippocampus is specifically concerned with the analysis and/or storage of spatial information (O'Keefe & Nadel, 1978; Krebs *et al.* 1989). Although there is evidence to suggest that some midbrain structures are implicated in social skills (e.g., certain thalamic nuclei; Armstrong *et al.*, 1987), the evolutionary changes that have occurred in primate brains mainly involve the forebrain (Stephan, 1972; Passingham, 1973; see also MacLean, 1982). This strongly suggests that, as far as the present set of hypotheses are concerned, we should be looking in the cortical areas. Indeed, there is some evidence to suggest that at least some cortical structures are essential to social life (Myers *et al.*, 1973; Kling, 1986), though the precise functional interpretation of ablation experiments of the kind carried out in these studies remains debatable.

In terms of primate brain evolution, it is the neocortex that accounts for most of the differences between living taxa (see Stephan, 1972; Passingham, 1973, 1982). Hence, if our concern is mainly with the factors that have promoted the increase in the overall size of primate brains, it would be logical to focus on that part of the brain that has largely been responsible for the change in size. In addition, given that, in crude terms, the neocortex is the "thinking" part of the brain, it seems most plausible to use neocortical volume as the main index of cognitive capacity.

Sawaguchi (1988) has recently demonstrated that a number of indices of relative cortex size [including Jerison's (1973) "extra cortical neurons" index, N_c, and Hofman's (1982) "extra cortical volume" index, V_e] correlate best with group size in the prosimians, with absolute range size in platyrrhines and with relative range size (taking group size into account) in catarrhines. He argued that this reflected the influence of different selection pressures acting on cortex size in these three taxonomic groups. However, these results might also be explained by differences in body size between these taxonomic groups. Removing the scaling effects of body size on range size is likely to leave group size (which correlates with range size in all these taxa) as the main correlate of neocortex size. Some evidence to support this is given by Sawaguchi & Kudo (1990) who found that relative neocortex size (i.e., discounting body weight) discriminates between solitary and social prosimians, and between monogamous and polygamous ceboids and hominoids.

Therefore, neocortex volume will be considered as the main anatomical index of cognitive capacity.

Methods

Table 1 gives data on all the variables for the 38 genera used in this analysis. Data on neocortex and total brain volume derive from Stephan *et al.* (1981). Data on group size and the three ecological indices (percentage of the diet devoted to fruit, size of ranging area and length of day journey) were obtained from the information collated in relevant chapters in Smuts *et al.* (1987), with supplementary data from Clutton-Brock & Harvey (1977), Richard (1985) and Dunbar (in press). Body weight data are those given by Stephan *et al.* (1981): these authors scaled their estimates of brain size to a particular average body weight for each taxon examined. Although the estimates of body weight given by Stephan *et al.* (1981) do not differ markedly from those given in more recent compilations (e.g., Harvey *et al.*, 1987; Willner, 1989), it seems preferable to maintain consistency here by using Stephan *et al.*'s figures.

In most cases, data on brain size are available for only a single representative species in each genus (exceptions are the prosimian genera *Cheirogaleus*, *Lemur* and *Galago*, and the anthropoid genus *Cercopithecus*). In order to maintain comparability, the demographic and

Table 1 Data for main variables (generic means)

Genus	Body mass^1 (kg)	Brain: Part volumes^2 (mm^3): N	Brain: Part volumes^2 (mm^3): H	Brain: Total	Brain: C^3_R	Brain: N^4_C	Mean group size^5: Total	Mean group size^5: Females	Fruit in diet (%)	Range area^6 (ha)	Day journey^6 (m)
Cheirogaleus	0·31	1040	1539	4667	0·80	—	1	1	—	4	—
Microcebus	0·05	740	552	1680	0·79	—	1	1	—	1	—
Lepilemur	0·92	3282	2467	7175	0·84	—	1	1	0	0·2	—
Lemur^7	2·20	13,750	7897	25,910	1·23	—	9·5	—	25	0·9	680
Avahi	1·07	4628	3172	9461	0·96	—	2	1	0	—	—
Propithecus	3480	13,170	8155	25,194	1·1	—	5	1	46	5·3	850
Indri	6250	20,114	10,735	36,285	1·24	—	4·3	1	25	17·9	—
Daubentonia	2800	22,127	12,414	42,611	1·08	—	1	1	—	—	—
Loris	322	3524	1719	6269	1·28	—	1	1	—	—	—
Nycticebus	800	6192	3260	11,755	1·11	—	1	1	50	—	—
Perodictus	1150	6683	3794	13,212	1·02	—	1	1	65	24·5	—
Galago^7	372	2810	1866	5794	0·94	—	1	1	17	9·3	—
Tarsier	125	1768	1135	3393	1·09	—	1	1	0	1·3	—
Callithrix	280	4371	1924	7241	1·52	—	8·5	2·5	—	1·2	704
Cebuella	140	2535	1203	4302	1·43	—	6·0	1·0	0	0·3	—
Saguinus	380	5894	2484	9537	1·62	0·26	5·2	2·4	60	39·8	1413
Callimico	480	6476	2779	10,510	1·61	—	7·3	1	—	45	2000
Aotus	830	9950	3657	16,195	1·59	—	3·8	1	45·5	10	710
Callicebus	900	11,163	4314	17,944	1·65	0·37	3·3	1	57·3	4·1	520
Pithecia	1500	21,028	947	32,867	1·78	—	3·6	1	82	7	—
Alouatta	6400	31,660	11,622	49,009	1·82	0·82	8·2	3·6	37	28·6	43,611
Ateles	8000	70,856	21,088	101,034	2·35	1·46	17	9·8	82	7·2	2525

Lagothrix	5200	65,873	20,681	95,503	2·22	—	23·4	7·5	80	400	1000
Cebus	3100	46,429	13,088	66,939	2·36	1·19	18·1	5·7	37·5	148·1	2000
Saimiri	660	15,541	4938	22,572	2·21	0·55	32·5	7·9	12·3	106·1	2425
Macaca	7800	63,482	16,817	87,896	2·6	1·27	39·6	14·3	63	1500	1428
Cercocebus	7900	68,733	20,555	97,603	2·38	1·53	15·4	7	61	227	1270
Papio	25,000	140,142	35,971	190,957	2·76	1·99	51·2	11·4	63	2695	5400
Cercopithecus[7]	4850	47,550	13,272	67,035	2·44	1·02	23·9	8·2	48·1	28·8	1336
Miopithecus	1200	26,427	7610	377,760	2·33	—	65·5[8]	15·4	43	120	2300
Erythrocebus	7800	77,141	18,398	103,167	2·96	—	28·1	7·9	52	420	3290
Pygathrix	7500	48,763	16,341	72,530	2·05	—	—	—	—	—	—
Nasalis	14,000	62,685	21,924	92,797	1·75	—	14·4	6·3	—	130	—
Procolobus[9]	7000	50,906	15,933	73,818	2·22	—	35	13·4	8	67·3	587
Hylobates	5700	65,800	21,504	97,505	2·08	1·37	3·4	1	58·5	49	1502
Gorilla	105,000	341,444	100,480	470,359	2·65	3·58	7	3	2	800	400
Pan	46,000	291,592	68,611	382,103	3·22	3·26	53·5	13	68	2150	3900
Homo	65,000	1006,525	188,449	1251,847	4·10	8·52	—	—	—	—	—

[1] Mean of adult male and adult female body weight, from Harvey *et al.* (1986).

[2] From Stephan *et al.* (1981). N = neocortex volume; H = volume of hind brain (medulla + cerebellum + mesencephalon + diencephalon); T = total brain volume.

[3] Neocortex ratio = (neocortex volume)/(total brain volume − neocortex volume).

[4] Jerison's (1973) "extra cortical neurons" index.

[5] Mean values from relevant chapters in Smuts *et al.* (1986).

[6] From Richard (1985) or Clutton-Brock & Harvey (1977), with preference given to the first.

[7] Generic values obtained by averaging data from two species (three for *Galago*). Stephan *et al.* (1981) list two species for *Saguinus*, but I was unable to identify *S. tamarin* and therefore omitted it from the analyses.

[8] Evidence given by Gautier-Hion (1971) suggests that group sizes are larger in populations living commensally with humans; therefore only groups listed by Gautier-Hion (1971) as living in undisturbed habitats were used when calculating the mean in this case.

[9] *Procolobus* = *Colobus badius.*

behavioural data were taken only from those species whose brain sizes were estimated by Stephan *et al.* (1981).

Species averages have been taken for all variables where possible, even though all the hypotheses state that cognitive capacity (as indexed by relative neocortex volume) imposes a limit on the maximum value for a specific behavioural or demographic variable. One reason for using averages is that most behavioural and demographic variables are influenced by a number of factors (see, for example, Dunbar, in press), so that considerable variation is found even within a given species. Even if a cognitive constraint does exist for a particular behavioural variable, it is likely that those populations inhabiting more marginal habitats will be forced to behave at the very limits of their capacities, leading to some overshoot on optimal values on these variables. In addition, group size is often subject to demographic lag ("frictional") effects, because groups cannot always undergo fission as soon as they exceed the optimal group size; often they have to wait until their size has increased sufficiently to produce daughter groups above some minimum size. Our principal concern is with the maximum size of group that the animals can manage as a cohesive unit, rather than with the absolute maximum group size. Some baboon populations, for example, live in enormous groups, but these groups are invariably very unstable and frequently fragment (see Sharman, 1981; Dunbar, in press). Taking an average across as many populations of a given taxon as possible should partial out the effects of these contextual variables and give us a better estimate of the maximum size at which groups are still cohesive.

Most analyses of brain size in vertebrates have used some variant of Jerison's (1973) Encephalisation Quotient (EQ) as their measure of relative brain size (e.g., Clutton-Brock & Harvey, 1980; Martin, 1981; Gittleman, 1986; Harvey *et al.*, 1987; Pagel & Harvey, 1988). EQ is generally measured as the ratio of actual brain size to that predicted for an animal of the same body size by some general relationship—that for basal insectivores in the case of Stephan (1972), the two-thirds power of body weight in Jerison (1973) and Bauchot (1982), and the best-fit regression line for the taxon under consideration in most other cases. However, Deacon (1990*b*) has recently argued that most of these indices are undermined by the fact that there is no unbiased baseline against which to assess allometric trends. In particular, the use of residuals from the regression line against body weight fails to recognise that, if the selection factors acting on brain size and body size differ, the two components will evolve at different rates. Willner (1989), for example, has pointed out that brain growth terminates much earlier than somatic growth, and is thus likely to be evolutionarily more conservative than body size (see also Deacon, 1990*a*). Indeed, body mass is known to be subject to considerable environmental influence even within species (Dunbar, 1990; Altmann *et al.*, in press). One consequence of this is that body mass may change ahead of brain size, so that using body size as the baseline may result in uninterpretable estimates of predicted size for brain parts. (I shall suggest that this does in fact seem to be the case in primates.) This may be one reason why it is brain size rather than body size that acts as the biological constant determining many life history and ecological variables (Harvey & Clutton-Brock, 1985; Harvey *et al.*, 1987; Pagel & Harvey, 1988; Deacon, 1990*b*).

Sawaguchi & Kudo (1990) attempt to avoid this problem by using total brain volume as the baseline from which to calculate residuals for neocortex size. Unfortunately, this particular measure ends up plotting neocortex size against itself, especially in the large-bodied anthropoids where the neocortex accounts for the bulk of the animal's total cranial capacity (see Willner, 1989; Deacon, 1990*b*). Nonetheless, the preceeding considerations suggest that some aspect of brain size would be a more appropriate baseline than body weight.

In order to circumvent problems of interpretation, I first considered a number of different ways of characterising differences in neocortex size between taxa. These include: (1) absolute neocortex volume; (2) relative neocortex volume (measured as the residual of neocortex volume regressed on *either* body mass *or* the rest of the brain); and (3) neocortex ratio (calculated as the ratio of neocortex volume to the volume of *either* the rest of the brain *or* the volume of the hindbrain). The "rest of brain" is taken to be the total brain volume less the volume of the neocortex; for present purposes, the hindbrain has been defined rather loosely and taken to be the combined volumes of the medulla, cerebellum, mesencephalon and diencephalon, as given by Stephan *et al.* (1981). Note that my primary concern in the first instance is to find the best predictor of the behavioural/demographic variables, rather than to determine the precise value of the functional relationship (as is normally the case in most allometric scaling analyses: see Harvey & Pagel, 1991).

It is now widely recognised that comparative analyses on a species-by-species basis can introduce significant biases (Harvey & Mace, 1982; Harvey & Pagel, 1991). Harvey & Mace (1982) recommended analysis at the genus, rather than species, level as a means of overcoming this problem (see also Ridley, 1986). More recently, Cheverud *et al.* (1985) have advocated the use of autocorrelation techniques as the best means of removing the effects of phylogenetic inertia. Alternative methods are given by Harvey & Pagel (1991), who recommend the method of independent contrasts. Although these procedures have a great deal to recommend them, their use is, however, dependent on the adequacy of the available phylogenies (e.g., Ely & Kurland, 1989).

In fact, these problems are mainly important only in so far as the aim of the analysis is to identify the relative contributions of selection and phylogenetic inertia to the observed variation in a given character. In the present case, concern is only with the factors that drive evolutionary change. As noted above, this problem is approached by examining the extent to which brain size constrains a species' ability to alter its behaviour. From this point of view, it does not matter whether phylogenetic inertia or selection pressure is responsible for a given species' current brain size, since the immediate interest lies in the *consequences* of brain size, not its causes. Once we have established that such a relationship exists, we are then in a position to infer something about the selection pressures that have influenced changes in brain size within the primate lineage. (Note, however, that this second claim is an inference; it cannot, strictly speaking, be tested directly by comparative analyses). This is not to deny that phylogenetic inertia has been responsible for part of the variation we currently observe in a character. It is merely to point out that our interest as evolutionary biologists is often not so much in what has been responsible for the contemporary variation in a trait, but what has caused these traits to change from the ancestral condition in those cases where change has occurred. Given that our central question is "Why do some primates now have *bigger* brains than others?", we are essentially interested in the covariance of one trait with another. This in itself would be some justification for an analysis at the species level: most behavioural variables are too labile in their ontogeny to be inherited in the simple sense implied by the conventional concerns over the statistical independence of traits. Although covariation of two traits with some third variable may still pose a serious problem (body size is the most likely culprit), this can easily be dealt with by partialling out the effects of the more obvious confounding variables.

As it happens, Stephan *et al.* (1981) measured brain volumes for only one representative species from each genus in most cases. Here, therefore, Ridley's (1986) advice has been followed: the data for those genera represented by more than one species were averaged and

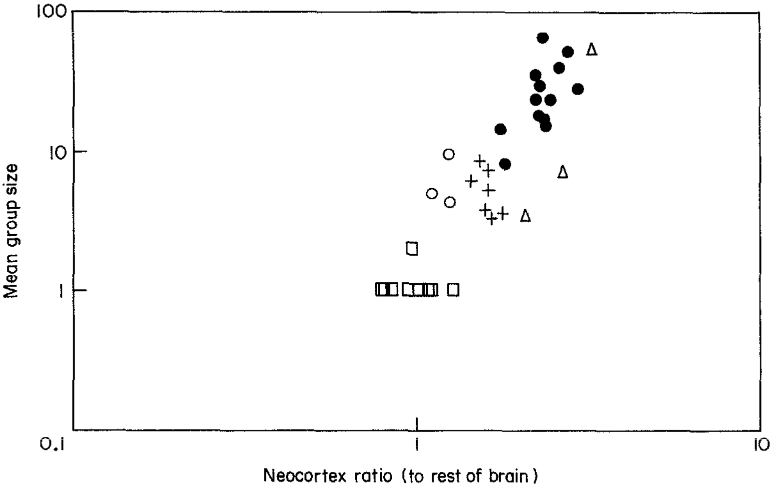

Figure 1. Mean group size for individual genera plotted against neocortex ratio (relative to rest of brain; i.e., total brain volume less neocortex). (●) Polygamous anthropoids; (+) monogamous anthropoids; (○) diurnal prosimians; (□) nocturnal prosimians; (△) hominoids. Source: Table 1.

analysis carried out at the genus level. With so few cases in which a genus is represented by more than one species, it is not clear that a great deal would be gained by using a more sophisticated approach.

The final methodological issue concerns the statistical analysis. There have been a number of recent discussions as to which methods give the best estimate for underlying relationships in comparative analyses of this kind (see for example Harvey & Mace, 1982; Rayner, 1985; Harvey & Pagel, 1991). In general, the performance of the three most common techniques for line-fitting (least-squares regression, major axis and reduce major axis) depends both on the assumptions that are made about the error variances and on the covariance between the two variables. In general, the three methods agree in their estimates of the slope parameter only when $r^2 > 0{\cdot}9$, with regression analysis, in particular, tending to underestimate the slope when the covariance is low. Harvey & Pagel (1991) specifically reject the use of the reduced major axis on the grounds that it ignores information contained in the covariance (and so can yield a slope estimate even when two variables are uncorrelated). Nonetheless, it is used here in preference to major axis analysis because Kendall & Stuart (1979) have shown that, if the errors are unknown, then the reduced major axis gives the maximum-likelihood estimate of the functional relation. Aiello (1992) has shown that the major axis tends to overestimate the slope under exactly those conditions where regression analysis tends to underestimate it (namely, when $r^2 < 0{\cdot}9$), whereas reduced major axis tends to yield intermediate values. Rayner (1985) also recommends the reduced major axis in preference to other techniques in situations (such as the present) where the error variances are unknown, because it is the only one of the three techniques that is independent of the error correlation.

All data were log-transformed for analysis.

Results

Tests of the social hypotheses

Mean group size is plotted against various indices of relative neocortex size in Figures 1 and 2. In each case, there is a significant regression between group size and neocortex size across the range of primate genera (Table 2). However, it is clear that the neocortex ratio (against the rest of the brain) gives much the best fit to the data (Table 2). The reduced major axis equation in this case is:

$$\mathrm{Log}_{10}(N) = 0{\cdot}093 + 3{\cdot}389\log_{10}(C_R) \qquad (1)$$

($r^2=0{\cdot}764$, $P<0{\cdot}001$), where N is the mean group size and C_R is the neocortex ratio. Analysis of the data for anthropoids only yields virtually identical results, suggesting that there are no major grade differences in this respect. The equation for neocortex volume discounted against body mass seems to be exceptionally poor. However, it is clear from Figure 2(c) that much of this is apparently due to what seems to be a grade shift by the nocturnal prosimians and the monogamous anthropoids: these seem to have much smaller group sizes for neocortex size than would be expected for all other primates. Exclusion of these two groups yields an equation which is both significant and in the same range on r^2 as most of the other analyses (Table 2). Table 2 also gives the results of a similar analysis using Jerison's (1973) "extra cortical neurons" index, N_c; although the sample of species is much smaller (and is limited to anthropoids), the results are essentially the same. Exclusion of *Gorilla* from the analysis markedly improves the goodness of fit in this case. In fact, *Gorrilla* turns out to have a relatively small brain with an enormous cerebellum (see Stephan *et al.*, 1981); since Jerison (1973) estimated N_c from total brain volume, his index grossly overestimates the true volume of the neocortex in this particular case.

Since neocortex ratio also correlates with body size and body size in turn correlates with group size (Figure 3; $r^2=0{\cdot}461$), it is necessary to partial out the effects of body size on this relationship. Table 3 confirms that the relationship between neocortex ratio and group size is independent of the correlation between neocortex ratio and body size.

Although it is generally the case that the different measures of relative neocortex size have much the same relationship to group size, there are marked differences between them in the proportion of variance in group size that they explain. The interpretation of these differences is not always clear, though it at least seems reasonable to infer that the use of body size as a baseline is confounded by the fact that body size can change in either direction ahead of (or even independently of) brain size (see also Willner, 1989; Deacon, 1990*b*). Because neocortex ratio gives by far the best fit to the data, in subsequent sections only the results for this index of relative neocortex size will be presented.

Tests of the ecological hypotheses

The percentage of fruit in the diet is plotted against neocortex ratio in Figure 4. It is clear that these variables are unrelated to each other.

In contrast, the absolute size of the range area does correlate with neocortex ratio [Figure 5(a); $r^2=0{\cdot}593$], as does the absolute length of the day journey [Figure 5(b); $r^2=0{\cdot}295$]. However, both of these ecological variables correlate with body size and ecological grain effects are known to be important; an area of 1 ha will appear to be a relatively small area to a 25 kg primate, but a very significant area to a 500 g animal. If the relationship between body size and both these ecological variables is removed by calculating residuals from the reduced major axis regression for each variable against body weight, the apparent relationship to neocortex ratio is lost in both cases [Figures 6(a) & (b); $r^2=0{\cdot}017$ for range size and $r^2<0{\cdot}001$ for day journey length].

Group size is also a determinant of both range size and day journey length in primates (Clutton-Brock & Harvey, 1977; Dunbar, 1988). It is therefore necessary to partial out the

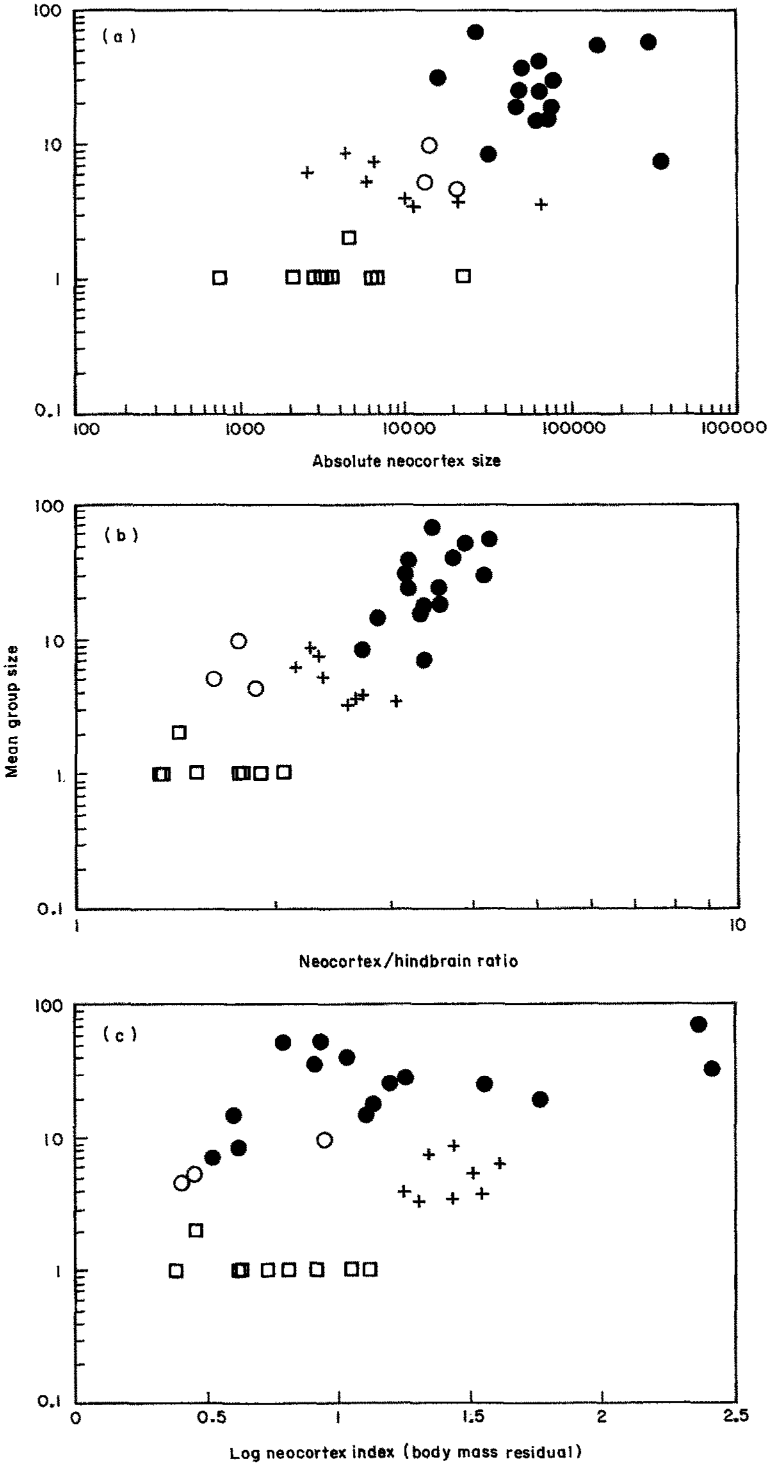
(a)
100
10
1
0.1
100
1000
10000
100000
100000
Absolute neocortex size
(b)
Mean group size
100
10
1
0.1
1
10
Neocortex/hindbrain ratio
(c)
100
10
1
0.1
0
0.5
1
1.5
2
2.5
Log neocortex index (body mass residual)

Figure 2a, b, c.

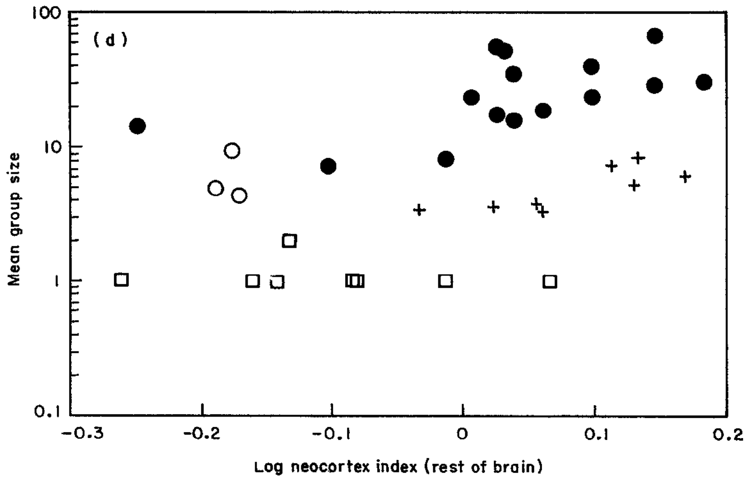

Figure 2d.

Figure 2. Mean group size for individual genera plotted against: (a) absolute neocortex volume, (b) neocortex ratio (relative to the hindbrain; i.e., medulla + cerebellum + mesencephalon + diencephalon), (c) neocortex index (residual against body mass) and (d) neocortex index (residual against rest of brain). Symbols and source as Figure 1.

Table 2 Regression statistics (reduced major axis) for relationships shown in Figures 1 & 2

Independent variable	Equation	r^2	t_{33}	P[1]
Neocortex volume	$\log (N) = -3{\cdot}067 + 0{\cdot}910 \log (C)$	0·547	6·309	<0·001
Neocortex ratio (*vs.* rest of brain)	$\log (N) = 0{\cdot}093 + 3{\cdot}389 \log (C_R)$	0·764	10·349	<0·001
Neocortex ratio (*vs.* hindbrain)[2]	$\log (N) = -0{\cdot}615 + 3{\cdot}672 \log (C_H)$	0·719	9·198	<0·001
Neocortex index[3] (residual *vs.* body mass)	$\log (N) = 1{\cdot}000 + 1{\cdot}981 \log (N_W)$	0·003	0·92	>0·20
(polygamous genera only)	$\log (N) = 1{\cdot}255 + 1{\cdot}761 \log (N_W)$	0·307	2·75	<0·02
Neocortex index[4] (residual *vs.* rest of brain)	$\log (N) = 0{\cdot}844 + 11{\cdot}084 \log (N_R)$	0·286	3·64	<0·01
Jerison's index, N_C[5]	$\log (N) = 1{\cdot}094 + 1{\cdot}271 \log (N_C)$	0·195	1·63	~0·10
(excluding *Gorilla*)	$\log (N) = 1{\cdot}172 + 1{\cdot}390 \log (N_C)$	0·392	2·54	<0·05

[1] Two-tailed.

[2] Hindbrain = medulla + cerebellum + mesencephalon + diencephalon.

[3] Reduced major axis equation for neocortex volume regressed on body mass:
$\log (C) = 1{\cdot}242 + 0{\cdot}911 \log (W)$
($N = 38$, $r^2 = 0{\cdot}911$, $P < 0{\cdot}001$), where C = neocortex volume (in cm^3) and W = body mass (g).

[4] Reduced major axis equation for neocortex volume regressed on rest of brain:
$\log (C) = -0{\cdot}950 + 1{\cdot}289 \log (R)$
($N = 38$, $r^2 = 0{\cdot}974$, $P < 0{\cdot}001$), where R = Total brain volume − neocortex volume (in cm^3).

[5] From Jerison (1973): analysis is based only on the 13 anthropoid genera common to both Stephan *et al.* (1981) and Jerison (1973). (N.B. Jerison's index, N_c, uses a slope of 0·67 as a baseline from which to derive the expected number of extra cortical neurons for an animal of a given body weight.)

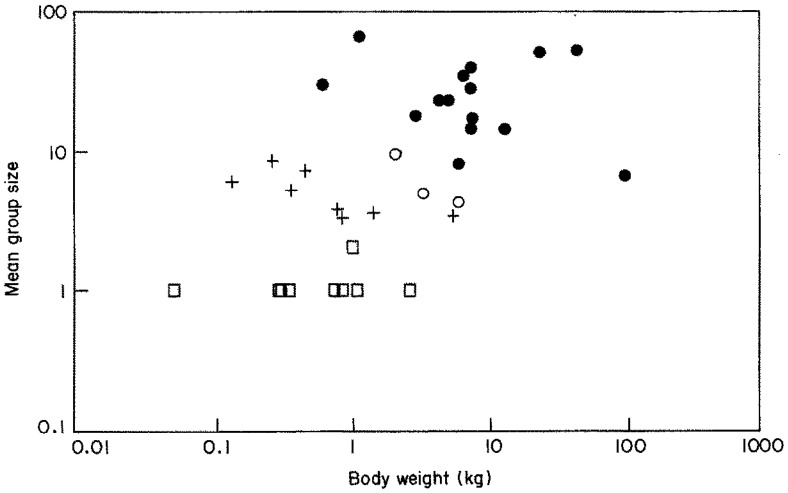

Figure 3. Mean group size for individual genera plotted against mean body size. Symbols and source as Figure 1.

Table 3 **Partial correlations against body weight for relationship between neocortex ratio and group size**

Comparison	Correlation coefficient Pairwise r	 Partial r (*vs.* body mass)	 P
Neocortex ratio *vs.* Body mass	0·676	0·323	>0·05
Neocortex ratio *vs.* Group size	0·870	0·774	<0·001
Group size *vs.* Body mass	0·636		

effects of the inter-correlations between neocortex ratio, group size and each of these three ecological variables. The results for neocortex ratio are given in Table 4. The correlations between neocortex ratio and both the percentage of fruit in the diet and the day journey length tend towards $r = 0$ when the correlation with group size is removed. While the same is true for range size, the partial correlation nonetheless remains significant. One reason may be that body mass creates ecological grain effects that also need to be removed. We can remove this effect by recalculating the correlations using the residual of the dependent variable on body mass rather than the raw values. Doing so results in partial correlations (taking both body mass and group size into account) that are negative (Table 4). This is clearly contrary to the hypothesis, which requires a positive correlation in each case. (As there is no reason to expect body size to influence fruit consumption directly, this partial correlation is not given). Once again, it seems that it is the correlation between neocortex ratio and group size that seems to be responsible for the apparent relationship between these ecological variables and neocortex size.

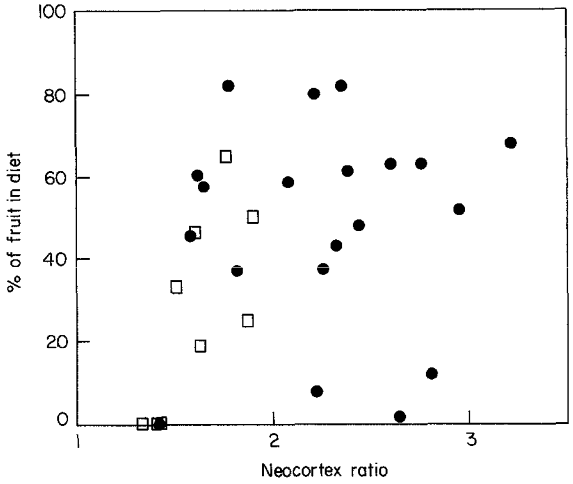

Figure 4. Mean percentage of fruit in the diet plotted against neocortex ratio for individual genera. (●) Anthropoids; (□) prosimians. Source: Table 1.

Two statistical points should be noted here. First, residuals from the reduced major axis line have been calculated, mainly because it seems to produce a better fit (see Methods section). However, as Harvey & Pagel (1991) point out, least squares regression is the only one of the three line-fitting techniques that yields residuals that are uncorrelated with the independent variable. Second, Deacon's (1990*b*) concerns about the use of body size as the baseline for scaling analyses has been ignored in these cases, because ecological grain effects, unlike both life history variables and brain size, are a *direct* effect of body size (see Peters, 1983; Schmidt-Nielson, 1984); indeed, it is difficult to place any alternative interpretation on the notion of ecological scaling effects in these cases.

Tests of the "extractive foraging" hypothesis

Figure 7(a) suggests that extractive foragers do not have significantly larger neocortex ratios than non-extractive foragers (means of 2·51 and 1·69, respectively; $t = 1{\cdot}763$ with unequal variances, $\mathrm{df} = 36$, $P > 0{\cdot}05$). Omitting humans from the calculation reduces the mean for extractive foragers to 2·19 ($t = 1{\cdot}225$, $\mathrm{df} = 35$, $P > 0{\cdot}2$). In contrast, extractive foragers do seem to have significantly larger neocortices for body size than non-extractive foragers (Figure 7(b): mean residual of neocortex volume regressed on body mass is 1·274 and 0·522, respectively; $t = 4{\cdot}983$, $\mathrm{df} = 36$, $P < 0{\cdot}001$). However, the distributions in Figure 7(b) suggest that most of the difference is due to the fact that prosimians generally have smaller neocortex indices than anthropoids, but are disproportionately more often represented among the non-extractive foragers. Reanalysis of the data for anthropoids only reveals that the differences between extractive and non-extractive foragers are not, in fact, significant (mean residuals of 1·360 and 1·186, respectively; $t = 0{\cdot}562$, $\mathrm{df} = 22$, $P > 0{\cdot}2$).

Tests of hypotheses about group size

The preceeding analyses indicate that increases in neocortex size are related to changes in group size rather than changes in ecological niche or patterns of resource exploitation. There are, however, at least three different ways in which group size might be constrained by

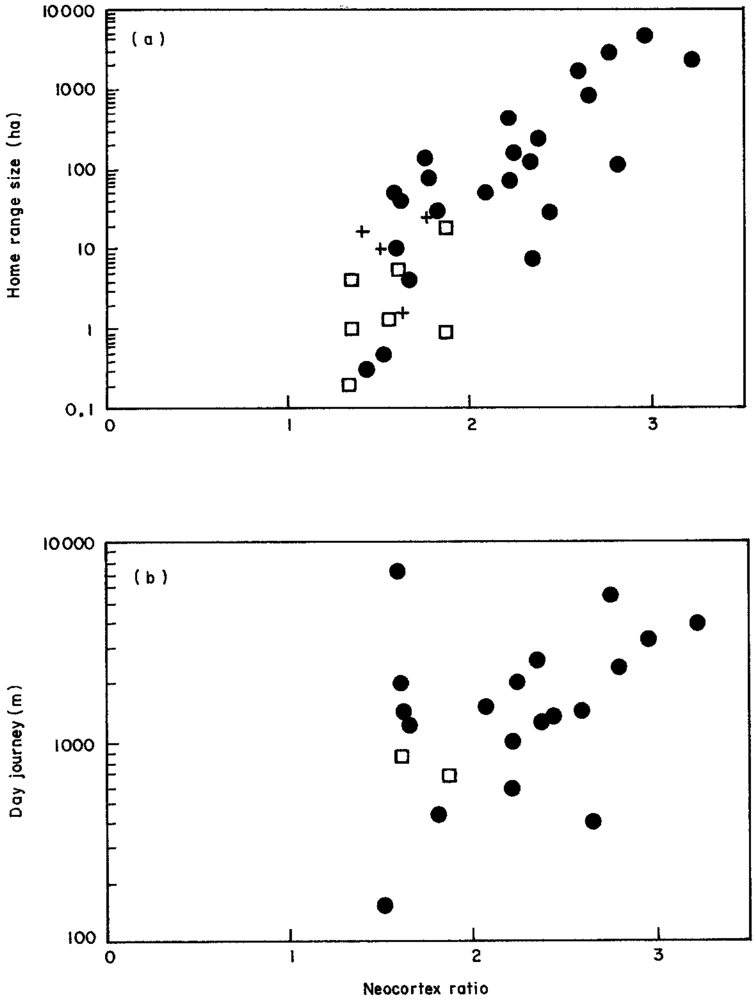

Figure 5. (a) Mean range size and (b) mean day journey length plotted against neocortex ratio for individual genera. (●) Anthropoids; (□) prosimians; (+) solitary (males). Source: Table 1.

neocortex size. In this section, I attempt to determine which of these is the most likely explanation.

Two different aspects of group size might be important. One is the absolute group size and the other is the possibility that it is female group size, rather than total group size, that is important.

The suggestion that the number of females might be important derives from the observation that it is females that form the core of most primate societies, whereas males are by and large peripheral members of the groups (see for example Wrangham, 1980; Dunbar, 1988). If primate groups are held together mainly by the relationships between groups of females [and this is likely to apply most strongly in the case of female-bonded species (*sensu* Wrangham, 1980)], then regressing number of females in the group against neocortex size should produce an improvement in the goodness of fit compared to the regression for total group size. The data in Figure 8 yield the following reduced major axis equation:

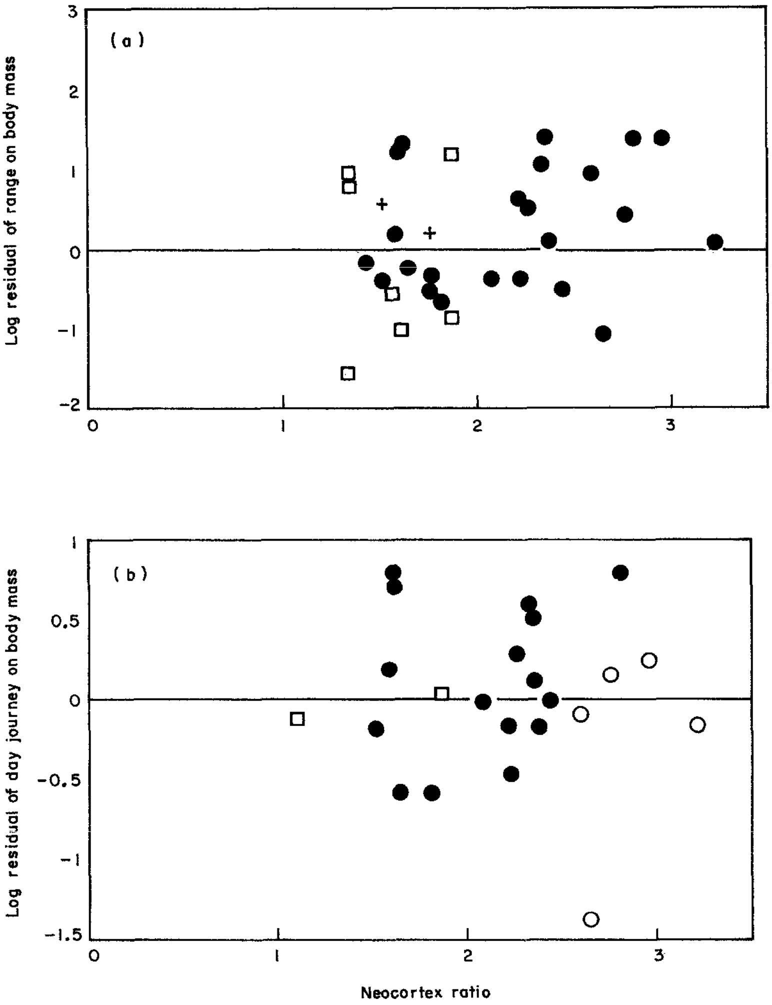

Figure 6. Residuals against body mass for (a) range size and (b) day journey length plotted against neocortex ratio for individual genera. (●) Arboreal anthropoids; (○) terrestrial anthropoids; (□) prosimians; (+) solitary species (males only).

$$\mathrm{Log}_{10}(N_f) = -0.124 + 2.661 \log_{10}(C_R) \qquad (2)$$

where N_f is the mean number of reproductive-age females in the group. Although the slope parameter is significant, this equation accounts for considerably less of the variance in the data than does total group size ($r^2 = 0.568$), suggesting that it is total group size rather than female group size that is the limiting factor.

The slope of the relationship between group size and neocortex ratio in equation (1) is greater than unity, suggesting that the information overload is not due to either the absolute number of personal relationships or the absolute number of dyadic relationships within the group as a whole that each individual has to be able to remember. This suggests: (a) that large groups are probably created by the hierarchical clustering of smaller cliques; and (b)

Table 4 **Partial correlations between neocortex ratio (against rest of brain) and various ecological variables, taking group size and body mass into account**

			Spearman r_S	
Comparison	N^1	Pairwise r	Partial (*vs.* N)	Partial (*vs.* $N+W$)^2
C_R *vs.* % fruit	29	0·503*	0·298	—
C_R *vs.* range size	32	0·793*	0·524*	−0·345
C_R *vs.* day journey	22	0·294	0·047	−0·599

$*P<0{\cdot}05$ one-tailed as a positive correlation.

^{1}Sample size.

^{2}Partial correlation between residual of dependent variable on body mass and neocortex ratio, given group size.

that the cognitive limitations lie in the quality of the relationships involved in the structuring of these cliques. Without more detailed information on clique size, however, it is not possible to test this last hypothesis at present.

Discussion

Of the two main arguments that have been deployed to account for the evolution of large brain size in primates, only the social intellect hypothesis receives support from these results. The evidence is quite unequivocal in that neocortical volume is not related to either the degree of folivory or the size of area that needs to be mapped.

Thus, even if the *initial* impetus towards an increase in relative brain size in primates may have been ecological, it seems clear that, once initiated, the process of brain evolution was accelerated by the fact that an enlarged cortex created new opportunities in other (specifically social) domains. It now seems clear that a large part of this impetus lay in the especially intense nature of primate inter-personal relationships that allow these animals both to form highly effective coalitions (Harcourt, 1988, 1989) and to exploit their knowledge of how other individuals are likely to behave (Whiten & Byrne, 1988; Cheney & Seyfarth, 1990). That this newly acquired cognitive capacity should subsequently be used in the ecological domain as well in some cases, need not, however, be surprising. Natural selection often exploits "windows of opportunity" of this kind when evolutionary processes make them available.

These analyses raise a number of important issues, namely (1) the meaning (or interpretation) of the different measures of relative neocortex size, (2) the significance of individual deviations from the regression line relating neocortex size and group size and (3) the question of precisely what aspect of social relationships is limited by neocortex size.

It is not possible to determine from these analyses alone where the cognitive limitations lie. Nonetheless, the fact that the ratio of neocortex volume to the rest of the brain is the best predictor of group size strongly suggests that it is the absolute size of the neocortex (and hence the number of available neurons) that may be the key constraint. This in turn would seem to imply an additive model of neural processing capacity as opposed to the more conventional model of a proportional increase assumed in most of the literature on allometric scaling (see

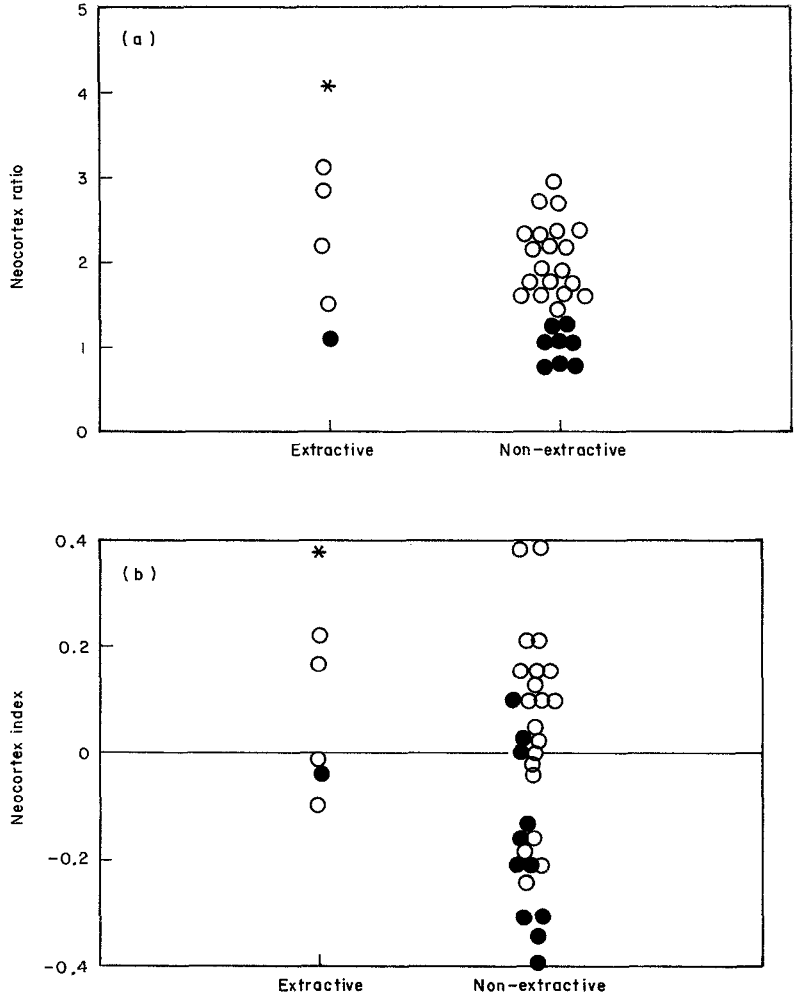

Figure 7. (a) Neocortex ratio and (b) neocortex index (relative to body mass) for extractive and non-extractive foragers. Extractive foraging genera are: *Daubentonia*, *Callithrix*, *Cebus*, *Papio* and *Pan*. The asterisk indicates *Homo*. (●) Prosimians; (○) anthropoids. Source: Table 1.

Byrne, in press). In other words, a 10% increase in neocortex volume has more functional significance in a large species than in a small species. One correlate seems to be that, if you need a larger neocortex (brain), then you have to evolve a larger body mass in order to achieve this. This may reflect a developmental constraint.

A comparison of the results for the different indices of neocortex size in relation to group size (Figures 1 & 2) suggests that, despite the overall consistency of the relationship between the various indices of relative neocortex size and group size, there are some striking differences. In particular, a comparison of the distributions for neocortex ratio (relative to rest of brain; Figure 1) and the neocortex index [relative to body weight; Figure 2(c)] suggests that changes in body size may have occurred ahead of changes in brain size, thereby markedly increasing the amount of scatter in the data when neocortex volume is given as a function of body size.

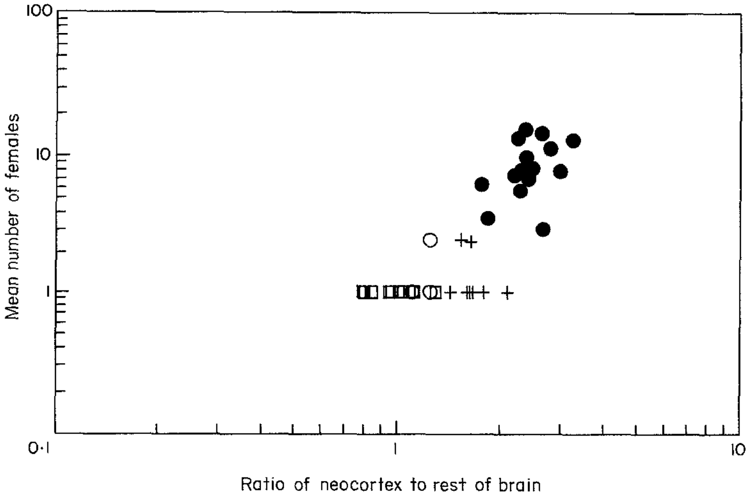

Figure 8. Mean number of reproductive females per group for individual genera plotted against neocortex ratio (against rest of brain). Source: Table 1.

Nonetheless, there are illuminating consistencies in the pattern of this scatter. Figure 2(c) suggests that the more terrestrial catarrhines (*Papio* and *Pan*, but not *Erythrocebus*) lie on a grade elevated above the regression line for other polygamous anthropoids, implying that they have undergone a rapid increase in body size (presumably in response to the increased risk of predation encountered in more open terrestrial habitats). Conversely, the monogamous anthropoids (both hylobatids and ceboids) appear to lie on a grade below that for polygamous arboreal anthropoids, suggesting that they have, as a group, undergone a relatively rapid reduction in body size. Indeed, in contrast to the other groups, their distribution is globular rather than linear. The fact that all these species fall much closer to the regression line for neocortex ratio (Figure 1) strongly suggests that it is body size that has changed, not brain (or neocortex) size. Note that all the callitrichids also fall into this group, despite the fact that their mating system includes a variety of non-monogamous mating systems (see Goldizen, 1987).

Similar results may be noted in the prosimians. The diurnal prosimians appear to fall on the same regression line for neocortex index (residual from body weight) as the arboreal anthropoids, whereas the nocturnal prosimians all fall on a lower grade. As with the monogamous anthropoids, this appears to be associated with a marked reduction in body size. The large range in neocortex index in this latter group could be interpreted in either of two ways. One is that these nocturnal genera are constrained into a solitary way of life by some aspect of their feeding ecology or habitus (such as the difficulty of maintaining contact between group members at night or the need to remain cryptic). The other is that the true group size is much larger than the value of one that I assumed for these "solitary" species.

The assumption that these species are genuinely asocial, even though solitary, has in fact been questioned. Clark (1985), for instance, has argued that *Galago crassicaudatus* populations consist of "communities" of some 10–15 individuals who know each other well and have well defined social relationships with each other (interpolating the neocortex index for this species into regression equations given in Table 2 for polygamous primates would in fact yield a predicted group size of 10·4). Clark's evidence, however, does not suggest that galago "supergroups" involve quite the same kinds of sophisticated interactions as those found in the more social primates (see also Harcourt, 1988). In fact, the group size predicted for *G. crassicaudatus* by their neocortex ratio (equation 1) is exactly 1·1 animals. This leads me to favour the hypothesis that it is body size that has changed in these species, rather than group size that has been underestimated. If so, then the evidence from neocortex size at least tends to confirm the general view that a solitary lifestyle may be primitive to the Order Primates (see Charles-Dominique, 1978; Charles-Dominique & Martin, 1970).

Although phyletic dwarfism has been inferred on morphological evidence for some platyrrhine taxa (notably the callitrichids; see Ford, 1980; Martin, 1989), the hylobatids have not usually been considered to have undergone a marked reduction in body size. In fact, there is some evidence to suggest that the ancestors of the gibbon may have been rather larger than the extant species; the late Miocene gibbon-like hominoid *Laccopithecus robustus* is estimated to have been about 12 kg in weight (Fleagle, 1988; Yuerong *et al.*, 1989)—ca. 2·5 times larger than the average gibbon, and only slightly larger than the extant "giant" gibbon (*Hylobates symphalangus*). The equations given in Table 2 suggest that, given their observed neocortex size, a body size of 24 kg would be required to bring the smaller hylobatids into line with the other polygamous primates in Figure 2(c). If the ancestral body weight was in fact 12 kg, this would imply that body weight has declined at about twice the rate at which brain size has reduced in these taxa.

It is clear, however, that group size has declined even faster than body size in the hylobatids, since the observed group size is still less than that predicted by neocortex ratio in Figure 1. The group size predicted for hylobatids by equation (1) is 13·96, nearly three times larger than the observed group size. Groups of this size would be expected to be single male polygamous groups (see Ridley, 1986; Andelman, 1986; Dunbar, 1988), and would thus imply some degree of sexual dimorphism in body size. Willner (1989) has shown that the degree of sexual dimorphism in brain size within the hylobatids is consistent with a relatively recent reduction in body size dimorphism. This would imply that the ancestral hylobatids lived in polygamous groups, which would in turn, once again, imply larger groups. Some evidence that the ancestral gibbons might indeed have been dimorphic is provided by Yuerong *et al.* (1989); they have shown that at least one extinct hylobatid (*Laccopithecus robustus*) was both larger and more sexually dimorphic than living hylobatids. A subsequent reduction in body size and group size is consistent with the invasion of a terminal branch foraging niche (like that seen in the smaller modern hylobatids) from an ancestral niche that was more conventional for catarrhine primates. Ecological competition from the frugivorous macaques migrating into Asia from Africa and Europe during the early Pliocene may well have been the precipitating factor. Significantly, the only extant hylobatid that seems to have retained the ancestral body size (the siamang) is more folivorous than is typical for gibbons, and would thus face less competition from macaques than the more frugivorous smaller gibbons.

The orang-utan provides the one obvious exception to the general rule and some consideration should be given to it. Although there are no data available on its neocortex size, it is likely that the orang approaches the chimpanzee in neocortex size (as it in fact does in terms of Jerison's index, N_c). This would imply that it ought to be found in relatively large groups, yet it leads a semi-solitary existence. It would be easy to resolve this problem by accepting Mackinnon's (1974) argument that the orang is "socially degenerate". The evidence for both larger body size and even greater sexual dimorphism in the extinct subspecies and the more open terrestrial habitats occupied by these populations (see Mackinnon, 1974) does indeed imply relatively large polygamous groups in earlier times. However, consideration ought to be given to the alternative possibility that orang-utans do live in a more complex social world than that implied by a group size of 1–2. At least some of those who have worked on orang populations have suggested that the social system may in fact be a dispersed group (e.g., Schaller, 1965; Mackinnon, 1974). Although most other studies have generally denied the existence of social groups in any strict sense (e.g., Rodman, 1973; Horr, 1975; Rijksen, 1978; Galdikas, 1985; te Boekhorst *et al.*, 1990; Mitani *et al.*, 1991), the evidence from all these studies in fact suggests that each population does contain a stable core of some 6–15 individuals who occupy a given area through which more nomadic animals pass from time to time. In fact, the claim that orang-utans do not possess any formal social system rests on the fact that observed patterns of association between individuals suggest that groups form mainly when animals converge on food sources or oestrous females (te Boekhorst *et al.*, 1990; Mitani *et al.*, 1991), but this does not necessarily imply that the animals lack well defined relationships of a relatively complex type. Evidence of a rather different type than that provided by Mitani *et al.* (1991) or te Boekhorst *et al.* (1990) is needed to resolve this question. However, if the orang group size is genuinely in the order of 1–2 animals, this would imply that the species was more social in the evolutionarily recent past. That a species now lives in smaller groups than is predicted by neocortex size is not, of course, incompatible with the hypothesis, since this only specifies that there is an upper limit to group size.

The terrestrial primates are generally characterised by relatively large neocortices as well as large groups. This can be interpreted as reflecting the fact that there has been selection for large groups, which in turn has exerted a strong selection pressure for the evolution of a large neocortex. Two hypotheses for the evolution of large groups currently command attention in the literature; namely defence against predators and defence of food sources against conspecifics (see van Schaik, 1983; Wrangham, 1987; Dunbar, 1988). The strong correlation between terrestriality, large neocortex size, large body size and large groups suggests that predation risk is the more likely of these alternatives, since it is difficult to see why large groups should be needed to defend the food sources of terrestrial species but not those of arboreal species. The resource defence hypothesis can only be entertained if it can be shown that arboreal species exploit resources that differ radically in either availability or dispersion from those exploited by terrestrial species. This does not, of course, preclude the possibility that, once large groups have evolved, the opportunity that they offer to defend resources cannot be exploited as well (Dunbar, 1988; van Schaik, 1989).

Finally, the fact that the cognitive constraint stems from absolute group size rather than female group size was unexpected, especially given the fundamental importance of reproductive females as the core of most primate societies (see Wrangham, 1980; Dunbar, 1988). This strongly suggests that primate groups are closely integrated in structural terms. There remains, however, a fundamental issue concerning the mechanism that gives rise to the observed relationship. The evidence presented above suggests that the cognitive limitation may lie in the nature of the relationships themselves rather than their quantity. It is well known that primate groups often become unstable or highly substructured prior to fission (see, for example, Chepko-Sade & Sade, 1979; Cords & Rowell, 1986; Sugiyama & Ohsawa, 1982). There is also some evidence to suggest that dominance ranks become less stable in larger groups (see Mori, 1979; Dunbar, 1984), possibly because relationships are less clear cut when animals only interact with each other (or observe others interacting with third parties) at irregular intervals. One likely reason for this in proximate terms may well be that the animals cannot coordinate so many relationships in their mental state-space. These issues are beyond the scope of the present paper, but clearly merit more detailed study.

Acknowledgements

I am grateful to the many people who have commented on the various versions of this paper during its over-long gestation, in particular Leslie Aiello, Rob Barton, Dick Byrne, Sandy Harcourt, Hiroko Kudo, Phyllis Lee, Henry Plotkin and Andy Whiten.

References

Aiello, L. A. (1992). Size and shape in human evolution. *J. hum. Evol.* **22,** 127–147.

Altmann, J., Schoeller, D., Altmann, S. A., Muruthi, P. & Sapolsky, R. M. (in press). Body size and fatness in a free-living baboon population. *Brit. J. Nutr.*

Andelman, S. J. (1986). Ecological and social determinants of cercopithecine mating patterns. In (D. Rubenstein & R. Wrangham, Eds) *Ecological Aspects of Social Evolution*, pp. 201–216. Princeton: Princeton University Press.

Armstrong, E. (1985). Relative brain size in monkeys and prosimians. *Am. J. phys. Anthrop.* **66,** 263–273.

Armstrong, E., Clarke, M. R. & Hill, E. M. (1987). Relative size of the anterior thalamic nuclei differentiates anthropoids by social system. *Brain Behav. Sci.* **30,** 263–271.

Bauchot, R. (1982). Brain organisation and taxonomic relationships in Insectivora and Primates. In (E. Armstrong & D. Falk, Eds) *Primate Brain Evolution*, pp. 163–176. New York: Plenum Press.

te Boekhorst, I., Schurmann, C. & Sugardjito, J. (1990). Residential status and seasonal movements of wild orang-utans in the Gunung Leuser Reserve (Sumatra, Indonesia). *Anim. Behav.* **39,** 1098–1109.

Boesch, C. & Boesch, H. (1984). Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates* **25,** 160–170.

Byrne, R. W. (in press). Empathy in primate social manipulation and communication: a precursor to ethical behaviour. In (G. Thines, Ed.) *Biological Evolution and Emergence of Ethical Conduct.*

Byrne, R. & Whiten, A. (Eds) (1988). *Machiavellian Intelligence.* Oxford: Oxford University Press.

Charles-Dominique, P. (1978). Solitary and gregarious prosimians: evolution of social structures in primates. In (D. Chivers & K. Joysey, Eds) *Recent Advances in Primatology*, Vol. 3, pp. 139–149. London: Academic Press.

Charles-Dominique, P. & Martin, R. D. (1970). Evolution of lorises and lemurs. *Nature (Lond.)* **227,** 257–260.

Cheney, D. L. & Seyfarth, R. M. (1990). *How Monkeys See the World.* Chicago: University of Chicago Press.

Chepko-Sade, D. & Sade, D. S. (1979). Patterns of group splitting within matrilineal kinship groups: a study of social group structure in *Macaca mulatta* (Cercopithecidae: Primates). *Behav. Ecol. Sociobiol.* **5,** 67–86.

Cheverud, J. M., Dow, M. M. & Leutennegger, W. (1985). The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* **39,** 1335–1351.

Clark, A. B. (1985). Sociality in a nocturnal "solitary" prosimian: *Galago crassicaudatus. Int. J. Primatol.* **6,** 581–600.

Clutton-Brock, T. H. & Harvey, P. H. (1977). Species differences in feeding and ranging behaviour in primates. In (T. Clutton-Brock, Ed.) *Primate Ecology*, pp. 557–584. London: Academic Press.

Clutton-Brock, T. H. & Harvey, P. H. (1980). Primates, brains and ecology. *J. Zool. Lond.* **190,** 309–323.

Cords, M. & Rowell, T. E. (1986) Group fission in blue monkeys of the Kakamega Forest, Kenya. *Folia primat.* **46,** 70–82.

Deacon, T. W. (1990*a*). Problems of ontogeny and phylogeny in brain-size evolution. *Int. J. Primat.* **11,** 237–281.

Deacon, T. W. (1990*b*). Fallacies of progression in theories of brain-size evolution. *Int. J. Primat.* **11,** 193–236.

Dunbar, R. I. M. (1984). *Reproductive Decisions: an Economic Analysis of Gelada Baboon Social Strategies.* Princeton: Princeton University Press.

Dunbar, R. I. M. (1986). Social ecology of gelada baboons. In (D. I. Rubenstein & R. W. Wrangham, Eds) *Ecological Aspects of Social Evolution*, pp. 332–351. Princeton: Princeton University Press.

Dunbar, R. I. M. (1988). *Primate Societies.* Ithaca: Cornell University Press and London: Chapman & Hall.

Dunbar, R. I. M. (1989). Social systems as optimal strategy sets: the costs and benefits of sociality. In (V. Standen & R. Foley, Eds) *Comparative Socioecology*, pp. 73–88. Oxford: Blackwells Scientific Publications.

Dunbar, R. I. M. (1990). Environmental determinants of intraspecific variation in body weight in baboons (*Papio* spp.). *J. Zool. Lond.* **220,** 157–169.

Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia primat.* **57,** 121–131.

Dunbar, R. I. M. (in press). Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.*

Ely, J. & Kurland, J. A. (1989). Spatial autocorrelation, phylogenetic constraints and the causes of sexual dimorphism in primates. *Int. J. Primatol.* **10,** 151–171.

Fleagle, J. G. (1988). *Primate Adaptation and Evolution.* New York: Academic Press.

Ford, S. M. (1980). Callitrichids as phyletic dwarfs and the place of the Callitrichidae in Platyrrhini. *Primates* **21,** 31–43.

Galdikas, B. (1985). Orang utan sociality at Tanjung Puting. *Am. J. Primat.* **9,** 101–119.

Gautier-Hion, A. (1971). L'ecologie du talapoin du Gabon. *Terre Vie* **25,** 427–490.

Gibson, K. R. (1986). Cognition, brain size and the extraction of embedded food resources. In (J. G. Else & P. C. Lee, Eds) *Primate Ontogeny, Cognition and Social Behaviour*, pp. 93–104. Cambridge: Cambridge University Press.

Gibson, K. R. (1990). New perspectives on instincts and intelligence: brain size and the emergence of hierarchical mental constructional skills. In (S. T. Parker & K. R. Gibson, Eds) *"Language" and Intelligence in Monkeys and Apes*, pp. 97–128. Cambridge: Cambridge University Press.

Gittleman, J. (1986). Carnivore brain size, behavioural ecology and phylogeny. *J. Mammal.* **67,** 23–36.

Goldizen, A. W. (1987). Tamarins and marmosets: communal care of offspring. In (B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker, Eds) *Primate Societies*, pp. 34–43. Chicago: University of Chicago Press.

Harcourt, A. H. (1988). Alliances in contests and social intelligence. In (R. Byrne & A. Whiten, Eds) *Machiavellian Intelligence*, pp. 132–152. Oxford: Oxford University Press.

Harcourt, A. H. (1989). Sociality and competition in primates and non-primates. In (V. Standen & R. Foley, Eds) *Comparative Socioecology*, pp. 223–242. Oxford: Blackwell Scientific Publications.

Harvey, P. H. & Clutton-Brock, T. H. (1985). Lifehistory variation in primates. *Evolution* **39,** 559–581.

Harvey, P. H. & Mace, G. A. (1982). Comparisons between taxa and adaptive trends. In (King's College Sociobiology Group, Eds) *Current Problems in Sociobiology*, pp. 343–362. Cambridge: Cambridge University Press.

Harvey, P. H. & Pagel, M. (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Harvey, P. H., Kavanagh, M. & Clutton-Brock, T. H. (1980). Sexual dimorphism in primate teeth. *J. Zool. Lond.* **186,** 475–485.

Harvey, P. M., Martin, R. D. & Clutton-Brock, T. H. (1987). Life histories in comparative perspective. In (B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker, Eds) *Primate Societies*, pp. 181–196. Chicago: University of Chicago Press.

Hofman, M. A. (1982). Encephalisation in mammals in relation to the size of the cerebral cortex. *Brain Behav. Biol.* **20,** 84–96.

Hofman, M. A. (1983*a*). Energy metabolism, brain size and longevity in mammals. *Q. Rev. Biol.* **58,** 495–512.

Hofman, M. A. (1983*b*). Evolution of the brain in neonatal and adult placental mammals: a theoretical approach. *J. theoret. Biol.* **105,** 317–322.

Horr, D. (1975). The Borneo orang-utan: population structure and dynamics in relationship to ecology and reproductive strategy. In (L. Rosenblum, Ed.) *Primate Behaviour*, Vol. 4, pp. 307–323. New York: Academic Press.

Humphrey, N. K. (1976). The social function of intellect. In (P. Bateson & R. Hinde, Eds) *Growing Points in Ethology*, pp. 303–317. Cambridge: Cambridge University Press.

Jerison, H. J. (1973). *Evolution of the Brain and Intelligence*. New York: Academic Press.

Jolly, A. (1969). Lemur social behaviour and primate intelligence. *Science* **153,** 501–506.

Kawai, M., Dunbar, R. I. M., Ohsawa, H. & Mori, U. (1983). Social organisation of gelada baboons: social units and definitions. *Primates* **14,** 1–13.

Kendall, M. G. & Stuart, A. (1979). Functional and structural relationship. In *The Advanced Theory of Statistics. Vol. 2. Inference and Relationships*, pp. 391–409. London: Griffin.

Kling, A. S. (1986). Neurological correlates of social behaviour. *Ethol. Sociobiol.* **7,** 175–186.

Krebs, J., Sherry, D., Healy, S., Perry, V. & Vaccarino, A. (1989). Hippocampal specialisation of food-storing birds. *Proc. Natn. Acad. Sci. U.S.A.* **86,** 1388–1392.

Kummer, H. (1982). Social knowledge in free-ranging primates. In (D. Griffin, Ed.) *Animal Mind—Human Mind*, pp. 113–130. Berlin: Springer.

Mace, G. M. & Harvey, P. H. (1983). Energetic constraints on home range size. *Am. Nat.* **121,** 120–132.

Mackinnon, J. R. (1974). The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim. Behav.* **22,** 3–74.

MacLean, P. D. (1982). On the origin and progressive evolution of the triune brain. In (E. Armstrong & D. Falk, Eds) *Primate Brain Evolution*, pp. 291–316. New York: Plenum Press.

Martin, R. D. (1981). Relative brain size and metabolic rate in terrestrial vertebrates. *Nature (Lond.)* **293,** 57–60.

Martin, R. D. (1984). Body size, brain size and feeding strategies. In (D. J. Chivers, B. Wood & A. Bilsborough, Eds) *Food Acquisition and Processing in Primates*, pp. 73–103. New York: Plenum Press.

Martin, R. D. (1989). *Primate Origins and Evolution*. London: Chapman & Hall.

Milton, K. (1988). Foraging behaviour and the evolution of primate intelligence. In (R. Byrne & A. Whiten, Eds) *Machiavellian Intelligence*, pp. 285–305. Oxford: Oxford University Press.

Milton, K. & May, M. L. (1976). Body weight, diet and home range area in primates. *Nature (Lond.)* **259,** 459–462.

Mitani, J. C., Grether, G. F., Rodman, P. S. & Priatna, D. (1991). Associations among wild orang-utans: sociality, passive aggregations or chance? *Anim. Behav.* **42,** 33–46.

Mori, A. (1979). The social organisation of the provisioned Japanese monkey troops which have extraordinary large population sizes. *J. Anthrop. Soc. Nippon* **85,** 325–345.

Myers, R. E., Swett, C. & Miller, M. (1973). Loss of social group affinity following prefrontal lesions in free-ranging macaques. *Brain Res.* **64,** 257–269.

O'Keefe, J. & Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford: Clarendon Press.

Olton, D. (1985). Temporal context of spatial memory. *Phil. Trans. R. Soc.* **308,** 79–86.

Pagel, M. D. & Harvey, P. H. (1988). How mammals produce large-brained offspring. *Evolution* **42,** 948–957.

Parker, S. T. & Gibson, K. R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in great apes and cebus monkeys. *J. hum. Evol.* **6,** 623–641.

Passingham, R. (1973). Anatomical differences between the neocortex of man and other primates. *Brain Behav. Ecol.* **7,** 337–359.

Passingham, R. (1982). *The Human Primate*. San Francisco: Freeman.

Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.

Rayner, J. M. V. (1985). Linear relations in biomechanics: the statistics of scaling functions. *J. Zool. Soc. Lond.* **206,** 415–439.

Richard, A. (1985). *Primates in Nature*. San Francisco: Freeman.

Ridley, M. (1986). The number of males in a primate troop. *Anim. Behav.* **34,** 1848–1858.

Rijksen, H. (1978). A Field Study on Sumatran Orangutans (*Pongo pygmaeus abelii* Lesson 1827). Ph.D. Dissertation, University of Utrecht.

Robinson, J. G. & Jansen, C. H. (1987). Capuchins, squirrel monkeys and atelines: socioecological convergence with Old World primates. In (B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker, Eds) *Primate Societies*, pp. 69–82. Chicago: University of Chicago Press.

Rodman, P. (1973). Population composition and adaptive organisation among orang-utans of the Kutai Reserve. In (R. P. Michael & J. Crook, Eds) *Comparative Ecology and Behaviour of Primates*, pp. 383–413. London: Academic Press.

Sade, D. S. (1972). Sociometrics of *Macaca mulatta*. I. Linkages and cliques in grooming matrices. *Folia primat.* **18,** 196–223.

Sawaguchi, T. (1988). Correlations of cerebral indices for "extra" cortical parts and ecological variables in primates. *Brain Behav. Evol.* **32,** 129–140.

Sawaguchi, T. (1990). Relative brain size, stratification and social structure in anthropoids. *Primates* **31,** 257–272.

Sawaguchi, T. & Kudo, H. (1990) Neocortical development and social structure in primates. *Primates* **31,** 283–290.

van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour* **87,** 120–144.

van Schaik, C. P. (1989). The ecology of social relationships amongst females primates. In (V. Standen & R. Foley, Eds) *Comparative Socioecology*, pp. 195–218. Oxford: Blackwells Scientific Publications.

Schaller, G. (1965). Behavioural comparisons of the apes. In (I. DeVore, Ed.) *Primate Behaviour*, pp. 474–483. New York: Holt Rinehart & Winston.

Schmidt-Nielsen, K. (1984). *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press.

Sharman, M. (1981). Feeding, Ranging and Social Organisation of the Guinea Baboon. Ph.D. Dissertation, University of St. Andrews.

Sigg, H. & Stolba, A. (1981). Home range and daily march in a hamadryas baboon troop. *Folia primat.* **36,** 40–75.

Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R. & Struhsaker, T. (Eds) (1987). *Primate Societies*. Chicago: University of Chicago Press.

Stephan, H. (1972). Evolution of primate brains: a comparative anatomical investigation. In (R. Tuttle, Ed.) *Functional and Evolutionary Biology of Primates*, pp. 155–174. Chicago: Aldine-Atherton.

Stephan, H., Frahm, H. & Baron, G. (1981). New and revised data on volumes of brain structures in insectivores and primates. *Folia primat.* **35,** 1–29.

Sugiyama, Y. & Ohsawa, H. (1982). Population dynamics of Japanese monkeys at Ryozenyama. III. Female desertion of the troop. *Primates* **23,** 31–44.

Sussman, R. W. & Kinzey, W. G. (1984). The ecological role of the Callitrichidae: a review. *Am. J. phys. Anthrop.* **64,** 419–449.

Whiten, A. & Byrne, R. B. (1988). Taking (Machiavellian) intelligence apart. In (R. Byrne & A. Whiten, Eds) *Machiavellian Intelligence*, pp. 50–66. Oxford: Oxford University Press.

Willner, L. A. (1989). Sexual Dimorphism in Primates. Ph.D. Dissertation, University of London.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour* **75,** 262–300.

Wrangham, R. W. (1986). Ecology and social relationships in two species of chimpanzees. In (D. Rubenstein & R. Wrangham, Eds) *Ecological Aspects of Social Evolution*, pp. 352–378. Princeton: Princeton University Press.

Wrangham, R. W. (1987). Evolution of social structure. In (B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Strusaker, Eds) *Primate Societies*, pp. 282–296. Chicago: University of Chicago Press.

Yuerong, P., Waddle, D. M. & Fleagle, F. G. (1989). Sexual dimorphism in *Laccopithecus robustus*, a late Miocene hominoid from China. *Am. J. phys. Anthrop.* **79,** 137–158.