

Both social and ecological factors predict ungulate brain size

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Among mammals, the members of some Orders have relatively large brains. Alternative explanations for this have emphasized either social or ecological selection pressures favouring greater information-processing capacities, including large group size, greater foraging efficiency, higher innovation rates, better invasion success and complex problem solving. However, the focal taxa for these analyses (primates, carnivores and birds) often show both varied ecological competence and social complexity. Here, we focus on the specific relationship between social complexity and brain size in ungulates, a group with relatively simple patterns of resource use, but extremely varied social behaviours. The statistical approach we used, phylogenetic generalized least squares, showed that relative brain size was independently associated with sociality and social complexity as well as with habitat use, while relative neocortex size is associated with social but not ecological factors. A simple index of sociality was a better predictor of both total brain and neocortex size than group size, which may indicate that the cognitive demands of sociality depend on the nature of social relationships as well as the total number of individuals in a group.

Keywords: social brain; behavioural flexibility; cognitive capacity; social complexity

1. INTRODUCTION

Although an extreme example of encephalization, humans are not the only species with a brain that is large relative to their body size. Other primates, cetaceans and elephants all have relatively large brains compared to other mammals (Jerison 1973) and there is considerable variation both between species and between higher taxonomic groups (van Dongen 1998). However, even within those taxa that are relatively small brained, brain size has been increasing over evolutionary time (Jerison 1973). As brain tissue is extremely costly (Aiello & Wheeler 1995), and as costly traits that provide no adaptive benefit are rarely maintained, we can assume there must be an adaptive explanation for the evolution of larger brains.

The functional hypotheses that have been proposed centre around two main concepts: ecological competence (e.g. Reader & Laland 2002) and the 'social brain' hypothesis (Dunbar 1992, 1998; Barton 1996; Dunbar & Bever 1998).

The hypotheses of ecological competence predict that increased cognitive ability allows individuals to solve more complex ecological problems, such as those involved in foraging tasks (e.g. Parker & Gibson 1977) or in managing and processing spatial and temporal information about resource availability (e.g. Clutton-Brock & Harvey 1980). One variation focuses on behavioural flexibility, where an individual's ability to respond appropriately to novel environmental conditions is dependent on its cognitive capacity (Lefebvre *et al.* 1997). Behaviourally flexible individuals should be at a selective advantage as they can

potentially use a wide variety of resources as well as seek out and exploit novel ones (Bateson 2004). Although intuitively appealing, it is often very difficult to measure these behaviours in a way that would allow the hypothesis to be tested, because flexibility can be expressed through a myriad of behaviours. The most commonly cited indicators of ecological problem solving are tool use (e.g. Lefebvre *et al.* 2002; Reader & Laland 2002) and use of extractive foraging (removing food items from an embedded matrix; e.g. Gibson 1986). Similarly, the frequency of documented behavioural innovations has been used as a measure of behavioural flexibility (e.g. Lefebvre *et al.* 1997; Reader & Laland 2002).

The social brain hypothesis argues that an individual's ability to manage complex relational information is dependent on its cognitive capacity, and, hence, on some aspect of brain size (Dunbar 1998). Individuals with superior cognitive capacity should be able to keep track of more individual relationships and be able to respond appropriately during interactions with other individuals. Ultimately, of course, the effective management of social relationships is concerned with solving problems of ecological relevance (survival and successful reproduction), but the social brain hypothesis differs from the ecological ones in that it assumes that the ecological problems are solved communally or by social learning rather than by individual learning. Cognitive demands should increase with group size, as the minimum number of potential relationships that have to be processed should be proportional to the number of individuals in the group (Dunbar 1992; Barton 1996). However, the complexity and nature of these relationships may vary in different types of group. Large aggregations are often unstable (e.g. migratory wildebeest herds and wader flocks, fish schools); individuals in these large aggregations do not

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Table 1. Ecological and social parameters used to predict relative brain size in ungulates.

parameter	description
sociality	<i>non-social</i> : species described as generally observed alone <i>social</i> : species with pair bonds or generally observed in groups
social system	<i>non-social</i> <i>monogamous</i> : species with pair bonds, or stable overlapping male and female territories <i>harem/seasonal</i> groups with generally one adult male and several to many females or unstable seasonal aggregations <i>large mixed</i> : stable groups with several adult males and females
group size	log of the geometric mean of the observed range of group sizes
habitat	<i>open</i> : species found in savannah or grassland habitats <i>closed</i> : species found primarily in closed forest or woodland <i>mixed</i> : species found either in open and closed habitats or species that are found in woodland/savannah matrices
diet	<i>grazer</i> : at least 75% of diet composed of grasses <i>browser</i> : at least 75% of diet composed of browse <i>grazer/browser</i> : at least 75% of diet composed of these two groups <i>browser/frugivore</i> : at least 75% of diet composed of these two groups <i>omnivore</i> : diet not dominated by any food type

necessarily form stable bonds or have repeated interactions with all other members of the group. In contrast, members of stable, cohesive groups interact regularly with other group members (e.g. many primates, non-migratory passerines, social carnivores). Dominance or affiliative relationships, and perhaps even coalitions, can emerge between group members in order to stabilize interactions. In many species of ungulates and carnivores, relationships are managed through territorial marking (Gosling & Roberts 2001). Even 'solitary' individuals regularly interact with individuals using a common or adjacent home range. In such cases, individuals manage more information and inter-individual relationships than would be predicted by looking at overall group size on its own. Therefore, to understand the cognitive demands of sociality, it may be necessary to consider the nature and complexity of social relationships and not just the total number of group members.

Both of the main hypotheses for brain size evolution have received considerable support from previous comparative analyses. Primates and birds with relatively larger brains have been shown to have higher rates of learning and innovation (Lefebvre *et al.* 1997, 2004; Reader & Laland 2002). Social group size is correlated with brain size in primates (Sawaguchi & Kudo 1990; Dunbar 1992, 1998; Barton 1996), carnivores and some insectivores (Dunbar & Bever 1998) and cetaceans (Connor *et al.* 1998; Marino 2002). However, ecological and social intelligence are not necessarily mutually exclusive: there is some evidence that species with cognitively demanding social environments are also better able to solve foraging and other complex problems (Reader & Laland 2002). Primates, especially, show high levels of social complexity, but are also able to exploit a wide variety of resources, use tools and engage in extractive foraging. Thus, finding a correlation between ecology and brain size does not negate the possibility of large brains initially evolving in response to social pressures, or vice versa (Dunbar 1992).

Following this logic, we examined the relationship between brain size and social complexity in ungulates. Ungulates are an ideal group to test theories of cognitive evolution because, unlike the taxa that have been the primary focus of studies of brain size evolution hitherto

(e.g. primates, Dunbar 1992; Barton 1996; carnivores, Dunbar & Bever 1998 and birds, Beauchamp & Fernández-Jurcic 2004; Burish *et al.* 2004), they do not typically display complex foraging strategies or use extractive foraging. The majority of ungulates are folivores and as such their food resources are typically more evenly dispersed in time and space (Harvey *et al.* 1980) than those of carnivorous or frugivorous species (e.g. most primates). Thus, the ecological predictors that could be expected to drive brain size evolution are much more restricted. On the other hand, ungulates do display a wide variety of social and reproductive behaviour; some species are almost exclusively solitary (e.g. tapirs *Tapirus* and water deer *Hydropotes*) while, in others, most individuals are members of large stable social groups (e.g. buffalo *Syncerus* and horses *Equus*).

2. MATERIAL AND METHODS

(a) Data collection

A summary of predictor variables can be found in table 1. We use three different measures of social complexity: group size, social system and sociality. By taking into account the stability of social relationships and total group size, the different social systems can be ordered according to social complexity, such that complexity increases as follows: non-social, monogamy, harem/seasonal groups and stable mixed sex herds. We have also included diet and habitat use as two criteria to control for the ecological variation between species. Information on sociality, group size, diet and habitat use were taken from Jarman (1974), Kingdon (1997), Nowak (1999) and Brashares *et al.* (2000). The quality of social behaviour data varied considerably across species. It was possible to obtain only ranges of observed numbers of individuals in aggregations for many species. In these cases, we used the geometric mean (as it gives a better estimate of central tendency when the upper limit is strongly skewed) of the group size range reported for each species as an estimate of species characteristic group size. The group size estimates include observations of seasonal and temporary aggregations, as well as lone individuals.

A complete list of the species included in the analysis can be found in electronic supplementary material. We collected

information on both total brain (81 species) and neocortex size (38 species) along with associated body sizes for individuals. Brain and body size data were taken from several different sources (Mangold-Wirz 1966; Oboussier & Schliemann 1966; Jerison 1973; Kruska 1973; Haarmann 1975). We excluded domestic species from the analyses as these species undergo considerable body size increase or brain size reduction following domestication (Kruska 1987). Since most evolutionary changes in overall brain size result from changes to the neocortex (Barton & Harvey 2000) and this region is thought to be responsible for 'executive functions' (Keverne *et al.* 1996), we compiled information on both total brain mass and neocortex mass. Residuals were calculated using reduced major axis regression (RMA) of log brain/neocortex size against log body size. We used RMA regression for two reasons, based on the arguments of Raynor (1985) and Sokal & Rohlf (1995). In calculating residuals, we are interested in the deviation from the observed correlation between brain size for each species rather than body size as a predictor of brain size. Additionally, as both brain size and body size for each species are subject to measurement error, RMA regression is more appropriate for interpreting allometric relationships, as least-squares regression underestimates the slope when there is error in the independent variable (Harvey & Pagel 1991). Neocortex data were available for many fewer species, and one reference (Oboussier & Schliemann 1966) provided neocortex surface area rather than volume or weight. Residuals were, therefore, calculated separately for neocortex volume and neocortex surface area, and the source was included as a factor in all models. As neocortex ratios (mass of neocortex/mass of other brain components) rather than neocortex residuals have been shown to have the strongest association with group size in primates (Dunbar 1992, 1998), we have also calculated these where possible (using log-transformed estimates of brain and neocortex size).

(b) Statistical analyses

The relationship between behavioural and ecological characters and brain neocortex size were first explored using non-phylogenetic univariate analyses (ANOVA or linear regression). However, comparative analyses of adaptation across multiple species analyses must also consider the patterns of phylogenetic relatedness between species. Autocorrelation between variables is likely to increase when two species are closely related, because there is a higher probability that they share characteristics by descent rather than in response to selection. To test for phylogenetic autocorrelation, we analysed the data using phylogenetic generalized least squares (PGLS; Grafen 1989; Martins 1999; Garland & Ives 2000). PGLS analyses fit models that incorporate the expected covariance among species using generalized least squares. The correlation between error terms is, thus, altered to reflect the degree of phylogenetic relatedness among the species. The PGLS approach was executed in R (Ihaka & Gentleman 1996) using the analysis of phylogenetics and evolution (APE) package (Paradis *et al.* 2004) and code provided by R. P. Duncan and T. Blackburn.

Phylogenetic independent contrasts (PIC) are the most commonly used method to account for phylogenetic relationships. PIC analysis assumes that the expected covariance between two species is directly proportional to their relatedness (i.e. time since divergence). PGLS analyses that incorporate a covariance structure based on Brownian

evolution have been shown to be exactly equivalent to PIC analyses (Rohlf 2001). However, PGLS analyses offer two main advantages. First, if the assumed evolutionary model of Brownian motion is incorrect, a statistical model incorporating phylogenetic information may not fit the data as well as one assuming that traits evolved independently. Traditional applications that perform PIC analyses do not check these assumptions (Freckleton *et al.* 2002), nor do they easily allow for deviations from Brownian motion to be incorporated into the analysis. PGLS allows the covariance matrix to be modified to accommodate the degree to which trait evolution deviates from Brownian motion, through a measure of phylogenetic correlation, λ (Pagel 1999; see also Freckleton *et al.* 2002). A Brownian motion model of evolution assumes that $\lambda=1$ (traits are directly proportional to relatedness), while in models that assume phylogenetic independence $\lambda=0$ (no correlation between traits and phylogenetic relatedness). λ can be optimized by maximizing the maximum-likelihood value of PGLS models using different values of λ . We compared the log likelihood of models using the optimized λ with the log likelihood of models assuming either no phylogenetic signal ($\lambda=0$) or Brownian motion evolution ($\lambda=1$) to test whether there is significant phylogenetic dependence in the data (Freckleton *et al.* 2002).

Ungulate phylogeny was constructed from Gatesy *et al.* (1997), Flagstad *et al.* (2001) and Murphy *et al.* (2001) (see electronic supplementary material). As branch lengths for this composite phylogeny are not known, we assumed proportional branch lengths (calculated in the APE package in R).

(c) Model selection

Where there was no significant difference between the optimized λ models and non-phylogenetic models, a General Linear Model (GLM) was used to relate social and ecological variables to brain size. Minimum adequate models, retaining only significant predictor variables, were identified using forward and backward stepwise GLMs.

Where the optimized λ for phylogenetic autocorrelation differed significantly from both non-phylogenetic models and Brownian motion models, all reported models use the optimized λ value. Because GLS output does not include standard parametric measures of model fit, we used an information theoretic approach (AIC—Akaike Information Criteria, Akaike 1973; Burnham & Anderson 2002) to identify the model that provided the best fit to the data by constructing a set of candidate models derived from the original hypotheses and comparing the resulting AIC values. The relative weight of evidence for each candidate model was calculated using the following equation: $w_i = \exp(-1/2\Delta_i) / \sum \exp(-1/2\Delta_i)$. Although AIC values were used to discriminate between models, we have provided marginal *F*-test statistics for the factors included in each model as an indication of the relative contribution of each variable to the overall fit of the model. To explore the partial effects of each factor in the models, we saved residuals from models incorporating factors we wished to control for.

3. RESULTS

(a) Brain size

The initial univariate analyses indicated that social species have larger residual brain sizes than solitary species ($F_{1,76} = 5.67$, $p = 0.02$). Relative brain size also varied by

social system, with solitary species having the smallest brains and monogamous species having the largest ($F_{3,74}=7.07$, $p<0.001$). Relative brain size was not associated with habitat use ($F_{2,75}=1.59$, $p=0.21$), log group size ($r^2=0.01$, $F_{1,76}=0.11$, $p=0.74$) or diet ($F_{4,73}=1.24$, $p=0.30$).

For all PGLS models of brain size, the log likelihood of models with an optimized λ was significantly different from both non-phylogenetic and Brownian motion models (table 2). We, therefore, used these optimized values for all subsequent models. The four best performing models all included social system as a predictor. Together, these four models had a standardized summed weight of 0.84. The remaining nine models had a combined weighting of 0.16. Habitat was significant as a single predictor, but the model fit was relatively poor compared to models incorporating social system. Log group, sociality and diet all received very little support in univariate tests, but performed slightly better when incorporated with ecological variables in multivariate models (table 2). The predictive power of group size may be associated with habitat as they covary (ANOVA, $F_{2,33}=10.52$, $p<0.001$). However, this relationship is not in the expected direction if their effects were additive, as brain sizes are smallest in open habitats where group sizes are largest.

In order to look at the partial effects of the sociality variables, we saved the residuals from the model incorporating habitat and phylogenetic autocorrelation (figure 1a,b). In *post hoc* analyses, LSD pairwise comparison of these residuals indicated that solitary species have smaller partial residual brain sizes than monogamous species (mean difference = -0.17 ± 0.05 s.e., $p<0.001$) and harem/seasonal (mean difference = -0.14 ± 0.04 , $p<0.001$), but not large mixed groups (mean difference = -0.03 ± 0.05 , $p=0.55$). Monogamous species have larger relative brain sizes than large mixed groups (mean difference = -0.14 ± 0.05 , $p=0.006$), but not harem/seasonal species (mean difference = -0.04 ± 0.04 , $p=0.37$). Harem/seasonal species have larger brains than large mixed species (mean difference = 0.11 ± 0.04 , $p=0.01$). Therefore, species found in monogamous and harem groups had larger brains than non-social and species found in large mixed groups. Using the residuals from the phylogenetic model incorporating social system only, we see that species found in mixed habitats had the largest brains, followed by those in closed habitats, while species in open habitats had the smallest relative brain size (figure 1c). However, none of the pairwise comparisons were significant.

(b) Neocortex

For both measures of neocortex (residuals and ratio), non-phylogenetic models fit the data better ($\lambda=0$), except in the case of habitat ($\lambda=0.18$, table 3a). However, even in the habitat model, the log likelihood of the optimized λ model does not differ significantly from the non-phylogenetic model ($\chi^2=0.18$, $p=0.67$). Therefore, all neocortex analyses were completed on non-phylogenetic models. Sociality was significantly associated with neocortex residuals and ratios (figure 2a); neocortex residuals were also associated with social system (table 3a,b, figure 2b). There was no significant association between neocortex measures and total group size. Similarly, there was no

significant relationship between neocortex measurements and habitat use or diet (table 3a,b).

Log neocortex size was significantly associated with log brain size, but the slope relationship was slightly greater than 1 ($r^2=0.998$, $\beta=1.07$), indicating that the neocortex of ungulate species increases nonlinearly with total brain size.

4. DISCUSSION

Across analyses of both brain and neocortex size, there was a consistent association between brain size and sociality, and the best-fit models all include social system. Surprisingly, in contrast to social system or sociality, the effect of group size was rather inconsistent. Group size was not significantly associated with neocortex size, nor was there a significant association with total brain size. As a relationship between group size and brain size has been found in a number of other taxa, we may need to ask whether group size is the most relevant measure of social complexity across all taxa. An unstable herd of several thousand antelope may not present the same cognitive demands as a smaller stable group, where individuals interact on a regular basis. Additionally, in species that have unstable grouping patterns, as with many ungulates, group size is somewhat nebulous; estimating a characteristic group size may be more complex than taking the geometric mean of observed numbers of individuals in aggregations. Therefore, our estimated group size appears to have limited bearing on cognitive demands, but this may be a result of the different nature of relationships between individuals across groups or may reflect that among these species group size itself is a somewhat artificial construct.

Social complexity was not the only factor associated with relative brain size in ungulates. **Habitat was also significantly associated with brain size in the PGLS analyses.** There are several possible explanations as to how habitat could relate to brain size: (i) it is more difficult to detect predators in closed and mixed habitats, thus increased sensory ability, anti-predator defences and general awareness will benefit individuals in risky environments and (ii) increased habitat complexity will demand better spatial awareness for individuals to be able to negotiate their way within a home range. Interestingly, despite the strong association between total brain size and habitat, there is no significant relationship between habitat and neocortex size. This may suggest that another region in the brain is more strongly associated with habitat. One possibility would be the hippocampus, as this region of the brain is most strongly associated with spatial memory (O'Keefe & Nadle 1978). A possible extension of this work would be to relate different brain components, especially the hippocampus, to measures of spatial complexity such as habitat, home range size and territoriality.

The statistical analyses we used highlight several important issues as to how phylogeny is incorporated into different statistical methods. In all of the models of total brain size, the optimized lambda value differed significantly from not only the non-phylogenetic model, but also from a Brownian motion model. Conventional approaches to phylogenetic comparisons assume that Brownian motion is the most conservative model for the

Table 2. General Linear Model results for social and ecological factors. Both parametric significance and information criteria values are presented. (F =tests to illustrate relative contribution of each parameter to the model. $p(\chi^2_0)$ represents the probability of the likelihood of the model with an optimized λ being same as the non-phylogenetic model and $p(\chi^2_1)$ represents the probability of the likelihood of the model with an optimized λ being same as a model assuming Brownian motion.)

model	parameters	F	d.f.	p	λ	$p(\chi^2_0)$	$p(\chi^2_1)$	AIC	ΔAIC	weight
1	social system	3.63	3,72	0.02	0.75	<0.001	<0.001	-119.00	0	0.352
	habitat	2.60	2,72	0.08						
2	social system	2.82	3,68	0.05	0.83	0.002	0.003	-118.24	0.76	0.241
	habitat	2.24	2,68	0.11						
	diet	1.49	4,68	0.21						
3	social System	3.82	3,74	0.01	0.75	<0.001	<0.001	-117.13	1.87	0.138
4	social system	3.78	3,70	0.01	0.86	0.001	0.003	-116.66	2.34	0.109
	diet	1.71	4,70	0.16						
5	sociality	3.86	1,74	0.05	0.70	<0.001	<0.001	-114.63	4.37	0.040
	habitat	4.18	2,74	0.02						
6	log group	2.32	1,74	0.13	0.82	<0.001	<0.001	-114.36	4.64	0.035
	habitat	4.47	2,74	0.01						
7	habitat	3.43	2,75	0.04	0.84	<0.001	<0.001	-113.85	5.15	0.027
8	log group	1.32	1,70	0.25	0.86	<0.001	<0.001	-113.59	5.41	0.024
	diet	1.56	4,70	0.19						
	habitat	4.21	2,70	0.02						
9	sociality	1.77	1,70	0.19	0.78	<0.001	<0.001	-113.48	5.52	0.022
	habitat	4.10	2,70	0.02						
	diet	1.50	4,70	0.21						
10	diet	1.59	4,73	0.19	0.82	<0.001	<0.001	-109.94	9.06	0.004
11	social	0.78	1,76	0.38	0.69	<0.001	<0.001	-109.87	9.13	0.004
12	log group	0.06	1,76	0.80	0.76	<0.001	<0.001	-109.39	9.61	0.003
13	log group	0.01	1,72	0.92	0.82	<0.001	<0.001	-107.95	11.05	0.001
	diet	1.54	4,72	0.20						

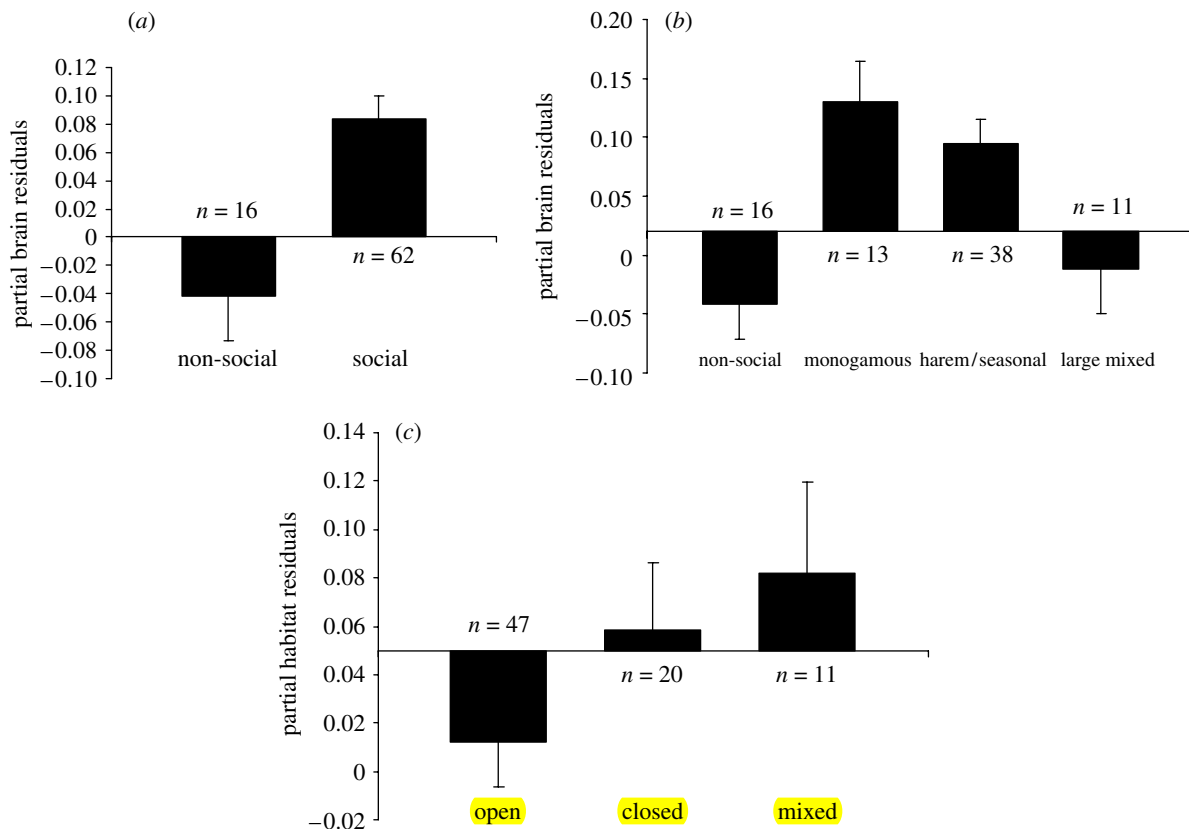


Figure 1. The relationship between total brain size and ecological and social factors. The data shown are residuals of a log body/–log brain RMA regression controlling for phylogeny and other factors (see text for details) as explained: (a) the partial effects of sociality on relative brain size in ungulates; (b) the partial effect of different social systems on brain size; (c) the relationship between habitat use and relative brain size. In each case, the results control for the effects of phylogeny as well as habitat (in the case of (a) and (b)) and sociality (in the case of (c)), after removing the effects of phylogeny and sociality.

correlated evolution of characteristics, and is, therefore, very robust for avoiding Type I errors. However, from these results, it seems likely that using such an extreme mode of evolution can obscure relationships between variables. Using a PGLS approach with an optimized lambda allows the covariance explicitly due to phylogenetic relationships to be removed, but does not introduce additional error to the data. Additionally, in cases where the phylogenetic signal is minimal, we can determine whether it is necessary to control for phylogeny at all.

This leads to the question as to why there was no phylogenetic signal in analyses of the neocortex? There are two possible explanations. One functional explanation is that the neocortex is the region of the brain that has undergone the most recent evolutionary change and variation in neocortex volume is largely responsible for changes in overall brain size (Passingham 1973; Barton & Harvey 2000). **As brain size can vary up to 100-fold within taxonomic groups (Clark *et al.* 2001), the neocortex will be much more labile between species than any other component.** The second (statistical) explanation is that there may not be enough power in small phylogenies to estimate the covariance between species accurately (Freckleton *et al.* 2002). One possible test to determine whether the lack of a phylogenetic signal is the result of a functional or statistical process is to increase the sample size of the phylogeny. As neocortex data are limited for ungulates, other taxa could be incorporated into a larger analysis, or the test could be done on a taxon with better brain information, such as primates. However, even if the

lack of phylogenetic signal is a statistical artefact, the factors that were significant predictors of total brain size did not vary before and after controlling for phylogeny, and this should also be true of neocortex values.

The hypothesis addressed by this analysis assumes that brain size adaptively responds to ecological and behavioural traits. The reverse logic is that brain size and ecology determine whether or not a species is social and what the optimal group size should be. This effectively posits two evolutionary relationships between group size and brain size, the first predicts that **brain size evolves as a response to external ecological factors, but a large brain may facilitate sociality.** The second argument is that groups evolve in response to ecological factors such as predation or resource distribution; and sociality may drive a secondary increase in brain size, but a large brain is not a prerequisite for sociality. A correlated change test (Pagel 1999) could be used to separate the pattern of evolution between these two traits.

These results add considerable support to previous conclusions that social cognition is a principal driving force behind brain size evolution. However, this paper extends the results of previous studies in several ways. First, it shows that social group type may be at least as, if not more important than, total group size. As the stability and complexity of social bonds increase, the cognitive demands required for maintaining those relationships is also expected to increase. For taxa where most groups are stable, such as primates, we would expect a monotonically increasing relationship between social complexity and

Table 3. Results of univariate ANOVA and regression analyses of ecological and behavioural characteristics on neocortex residuals and ratios.

(a) neocortex residuals

parameter			mean/ coefficient	s.d.	N	F	d.f.	p	λ
sociality	sociality	yes	0.02	0.17	29	6.64	1,34	0.01	0
		no	-0.19	0.30	7				
ecology	social system	solitary	-0.19	0.30	7	3.89	3,32	0.02	0
		monogamous	0.09	0.16	12				
		harem/seasonal	-0.01	0.15	13				
		large stable	-0.18	0.13	4				
		GM group size	0.03						
ecology	diet	grazer	-0.11	0.14	6	1.54	3,32	0.22	0
		browser	0.05	0.15	12				
		grazer/browser	0.05	0.10	7				
		browser/frugivore/ omnivore	-0.04	0.31	11				
		habitat	open	-0.03	0.15				
closed	-0.05	0.31	11						
mixed	0.04	0.17	8						

(b) neocortex ratios

parameters		mean/coefficient	s.d.	N	F	d.f.	p
sociality	yes	1.97	0.35	3	12.39	1,17	0.03
	no	1.19	0.32	16			
GM group size		0.25		19	1.56	1,18	0.23
social system	solitary	1.19	0.32	3	4.91	3,15	0.014
	monogamous	2.06	0.44	3			
	harem/seasonal	2.03	0.38	9			
	large stable	1.74	0.16	4			
diet	grazer	1.96	0.53	4	2.59	3,15	0.09
	browser	2.08	0.52	5			
	grazer/browser	1.83	0.14	7			
	browser/frugivore/omnivore	1.30	0.42	3			
habitat	open	1.95	0.39	12	1.02	2,16	0.38
	closed	1.59	0.86	3			
	mixed	1.70	0.10	4			

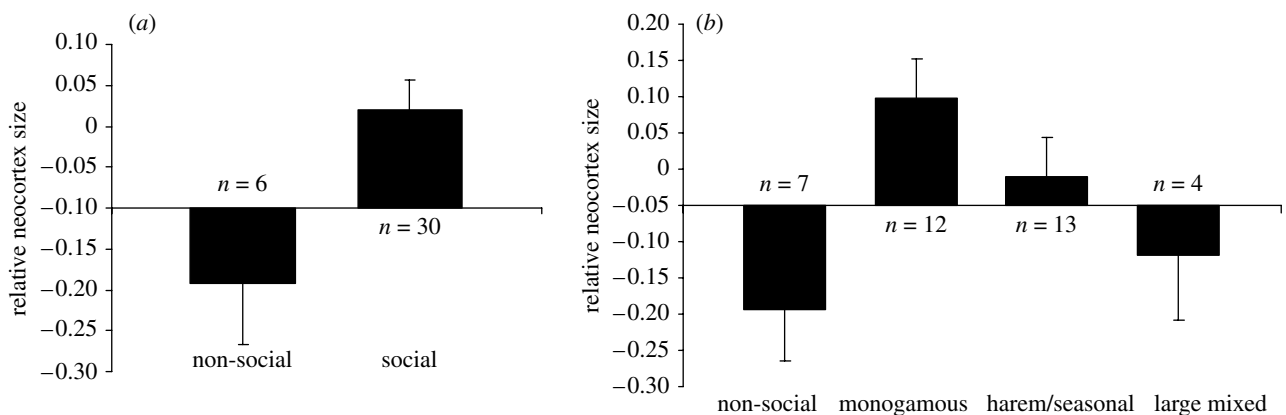


Figure 2. The relationship between (a) sociality and (b) social system and relative neocortex size. The neocortex data shown are residuals from a log body/log neocortex RMA regression.

group size. Thus, in the case of primates, any analyses of brain size and sociality incorporating social complexity rather than group size are likely to reach similar conclusions. However, group structure is not so consistently related to group size in other taxa, especially those

which form large schools or herds such as many birds, fish and ungulates. The lack of a relationship between group size and forebrain size in birds reported by [Beauchamp & Fernández-Jurcic \(2004\)](#), thus, may be the result of a violation of the implicit assumption that group size is

equivalent to social complexity. That social complexity is more important than group size in birds is further supported by Burish *et al.* (2004), who find that structure and flexibility of social systems are strongly associated with brain size and architecture in birds. It seems intuitively likely that the cognitive capacity needed to handle ephemeral associations with several thousand flock members may not be proportionally greater than that required for maintaining a close pair bond between individuals in a monogamous relationship or in a small cohesive group. The evidence from ungulates and birds indicate that the nature of relationships between individuals rather than total group size *per se* may be better indications of the cognitive demands necessary to cope with different kinds of sociality. Future investigations into the nature of individual relationships across vertebrate social systems could clarify the relationship between social complexity and cognition.

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