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Primate brain size is predicted by diet but not sociality

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The social brain hypothesis posits that social complexity is the primary driver of primate cognitive complexity, and that social pressures ultimately led to the evolution of the large human brain. Although this idea has been supported by studies indicating positive relationships between relative brain and/or neocortex size and group size, reported effects of different social and mating systems are highly conflicting. Here, we use a much larger sample of primates, more recent phylogenies, and updated statistical techniques, to show that brain size is predicted by diet, rather than multiple measures of sociality, after controlling for body size and phylogeny. Specifically, frugivores exhibit larger brains than folivores. Our results call into question the current emphasis on social rather than ecological explanations for the evolution of large brains in primates and evoke a range of ecological and developmental hypotheses centred on frugivory, including spatial information storage, extractive foraging and overcoming metabolic constraints.

Primates, especially anthropoids, have relatively large brains compared to other mammals. These observations have led researchers to propose various explanations for the evolution of increased brain size in the primate lineage. Accordingly, numerous comparative analyses have been undertaken with the goal of identifying social and/or ecological variables that explain interspecific variation in overall brain size, or of specific brain regions[1].

Early studies suggested that ecological factors, such as diet, explain relative brain size variation in non-human primates[2–5]. This is consistent with the idea that processing of meat and other foods contributed to subsequent increases in hominin brain size[6,7] by fulfilling corresponding higher energy requirements[8–11]. Later comparative studies emphasized the role of social factors. In particular, the social brain hypothesis posits that social complexity is the primary driver of cognitive complexity among primates, and that social pressures associated with maintaining group cohesion ultimately led to the evolution of the large human brain[12–15]. This hypothesis has been supported by studies indicating positive relationships between relative brain and/or neocortex size and mean group size[2,14–17].

However, research investigating the relationships between relative brain size and different social and mating system types, which may differ in their relative social complexity, has produced highly conflicting results[17,18]. Some studies have shown that polygynandrous primate species have the largest brains[3,17], consistent with the idea that systems that promote the most interactions and relationships between the greatest numbers of individuals might be the most cognitively demanding. Conversely, other studies have shown that monogamous species have the largest brains[18], and have argued that monogamy may require greater deception and manipulation abilities[18] for obtaining extra-pair copulations, produce a relatively high cost of cuckoldry, and/or require conflict resolution and coordination abilities for bond maintenance[17].

These conflicting results suggest that methodological issues may have led different researchers to different conclusions. Throughout the comparative study of primate brain size evolution, species sample sizes used in analyses have been small and idiosyncratic, while the statistical techniques available have improved considerably since early analyses. For example, many early studies used residuals as data, which can cause bias if the control variable co-varies with other variables in the analysis; the use of multiple regression with the confounding variable incorporated as a covariate is now recommended instead[19]. In addition, many studies used a phylogeny[20] that has become outdated and set all branch lengths to 1—a relatively radical branch length transformation that presumes an evolutionary pattern in which changes occur at the time of speciation in both daughter species.

We assembled a much larger and more representative sample of primates (>140 spp., more than tripling the sample size of previous studies) and tested whether multiple measures of sociality (mean group size, social and mating system separately) explain variation in brain size after controlling for body size, diet and phylogenetic history. Although some studies have used relative neocortex size rather than whole brain size, this information is not available for a large sample of primate species; in any case, the neocortex scales hyper-allometrically with brain size[21]. In its original form, the social brain hypothesis was formulated to explain primate intelligence[12,13] and was later discussed as an attempt to explain brain size[14,15,22]. The subsequent focus on the neocortex was not always based on a priori reasoning, but because neocortex analyses sometimes showed the strongest correlations with the social variables under examination[14]. Regions outside the neocortex are also involved in complex cognitive functions (for example, cerebellum[23], hippocampus[24], striatum[25]) and studies show that overall brain size predicts global cognitive ability across non-human primates[24,26]. Furthermore, studies by the main proponents of the social brain hypothesis continue to present analyses of relative total brain size[17,22,24], consistent with the interpretation that the social brain hypothesis does indeed aim to explain evolutionary increases not only in neocortex ratio, but in overall brain size.

Results

For each sociality measure, the full model (including all predictors) included brain size as the dependent variable, and body size, either diet category or percent frugivory and alternative sociality measures

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Table 1 | Results for diet and group size models (spp. $n = 140$): brain (log) ~ body (log) + diet + group size (log).

Branch length comparisons	dBIC	Weight
Lambda = 0.968	**0.0**	**0.95**
Kappa = 0.698	6.1	0.05
Delta = 1.469	11.1	<0.01
All branch lengths = 1	42.1	<0.001
Sequential SS ANOVA	**Mean sq.**	***P* value**
Body (log)	**0.2213**	**$<2 \times 10^{-16}$**
Diet	**0.0012**	**0.02**
Group (log)	0.0000	0.74
Residuals	0.0004	
Model comparisons	**dBIC**	**Weight**
Body (log)	0.0	0.92
Body (log) + diet	5.2	0.07
Body (log) + diet + group (log)	10.0	0.01

There is strong evidence that the model incorporating a maximum-likelihood value of lambda provides relatively better model fit than models incorporating other branch length transformations. Non-lambda models exhibit higher BIC values (by >6) and very low weights, which represent the relative likelihood of a model given the BIC values of all models in the comparison. Body size and diet explain a significant amount of variation in brain size after controlling for phylogeny and are highlighted in bold. Group size does not explain additional variation, as this variable exhibits a low mean square value and a non-significant *P* value ($P > 0.05$). Compared with a model including only body size, there is strong evidence that the model including body size, diet and group size provides relatively poor fit, while there is only weak evidence of such for the model including both body size and diet. The model including group size exhibits a higher BIC value (by >6) and very low weight, indicating low relative likelihood of this model. Notes: branch length comparisons are estimated using maximum-likelihood, with others set to 1. dBIC, difference in BIC value from best fit model (dBIC > 6 indicates strong evidence of relatively poor model fit)[29]; mean sq., mean squares. Sequential sum of squares (SS) ANOVA represents Type I ANOVA of best fit model including all predictor variables. Model comparisons were constructed using maximum-likelihood lambda. Corrected significant *P* value cut-off = 0.05/6 = 0.0083.

Table 2 | Results for diet and social system models (spp. $n = 142$): brain (log) ~ body (log) + diet + social system.

Branch length comparisons	dBIC	Weight
Lambda = 0.961	**0.0**	**0.98**
Kappa = 0.635	7.7	0.02
Delta = 2.012	15.9	<0.001
All branch lengths = 1	42.2	<0.001
Sequential SS ANOVA	**Mean sq.**	***P* value**
Body (log)	**0.2232**	**$<2 \times 10^{-16}$**
Diet	**0.0013**	**0.01**
Social system	0.0002	0.60
Residuals	0.0003	
Model comparisons	**dBIC**	**Weight**
Body (log)	0.0	0.91
Body (log) + diet	4.6	0.09
Body (log) + diet + social system	17.6	<0.001

See Table 1 legend for explanatory information. Social system does not explain additional variation, as this variable exhibits a low mean square value and a non-significant *P* value ($P > 0.05$). Compared with a model including only body size, there is strong evidence that the model including body size, diet and social system provides relatively poor fit, while there is only weak evidence of such for the model including both body size and diet.

as predictors. We employed phylogenetic generalized least squares (PGLS) regression and incorporated phylogenetic uncertainty by using two recent consensus phylogenies[27,28] and testing across a Bayesian block of alternative trees for one of them[27], using maximum-likelihood model averaging, Bayesian phylogenetic mixed models and a fully Bayesian phylogenetic regression analysis. We compared different branch length transformations and full versus reduced models using the Bayesian information criterion (BIC)[29]. The possible effect of within-species group size variation was tested via resampling. Consensus tree analyses were repeated within certain subgroups (anthropoids, catarrhines) and also using female-only brain and body size data to account for possible effects of grade shifts in the nature of sociality and sexual dimorphism, respectively. Finally, we reconstructed ancestral states to visualize the evolutionary context of brain size evolution and sociality.

Contrary to the predictions of the social brain hypothesis, our results indicate that none of the sociality measures examined here explain relative brain size variation in primates, which is predicted only by diet, with frugivores having relatively larger brains than folivores. Results from analyses across all primates incorporating the 10kTrees consensus tree[27] are presented here in detail because this set provides the largest species sample size. Maximum-likelihood estimates of lambda were used for branch length transformations because other models, particularly those with branch lengths set to 1 (as in most previous studies), were worse fitting (Tables 1–4). In all cases, Type I ANOVAs for models including all predictors indicate that, while body size and diet each explain a significant amount of brain size variation, none of the sociality measures examined explain additional variation (Tables 1–3). This pattern of significance remains when percent frugivory is included in the model instead of diet category (Supplementary Tables 1–3), and when the order in which diet and sociality variables are entered into the model is switched (Supplementary Tables 5–10). Phylogenetic uncertainty does not affect these patterns, as both consensus trees (Tables 1–3; Supplementary Tables 1–18), most maximum-likelihood models tested across the block of 1,000 trees (Supplementary Tables 19–26), Bayesian phylogenetic mixed models (Supplementary Tables 30–37) and fully Bayesian phylogenetic regression analyses (Supplementary Tables 27–29) provide statistically indistinguishable results. Within-species variation also does not affect these results, as the resampling analysis of the full group size models confirmed the lack of effect for group size (model with diet category: median estimate = −0.003, 95% confidence interval (CI) = −0.021 to 0.017; model with percent frugivory: median estimate = 0.021, 95% CI = −0.008 to 0.047). These results are not confounded by sexual dimorphism as analyses run using female-only brain and body size data produced similar results (Supplementary Tables 38–59). Although some sociality measures seem to explain a significant amount of variation within a small set of subgroup analyses, these are probably owing to model assumption violations and are not consistent when different phylogenies or diet proxies are used (see Supplementary Text).

Furthermore, for each sociality proxy, the model including all predictors is not a good fit relative to models including either body size alone or body size and diet (Tables 1–3; Supplementary Tables 1–3, 11–13 and 15–17), whereas the last two are statistically indistinguishable from each other (Tables 1–4; Supplementary Tables 1–4, 11–14 and 15–18). After correcting for multiple comparisons, frugivores and frugivore/folivores exhibit significantly larger brains than folivores (Table 4), with model estimates suggesting that frugivores exhibit 25% (95% CI = 8–44%) more brain tissue than folivores of the same body weight. According to primate brain cellular scaling rules as determined by the isotropic fractionator method[30], this predicted difference amounts to an increase of around 1.08 billion total neurons for a frugivore of average body weight. Relatively more neurons for the same body mass probably indicates increased processing power that is not simply related to maintenance and control of the body[31]. In some supplementary analyses, omnivores also exhibit significantly larger brains than folivores (Supplementary Tables 58, 66 and 80). These results are supported by the significant

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Table 3 | Results for diet and mating system models (spp. $n = 142$): brain (log) ~ body (log) + diet + mating system.

Branch length comparisons	dBIC	Weight
Lambda = 0.963	**0.0**	**0.98**
Kappa = 0.653	7.3	0.03
Delta = 1.533	15.7	<0.001
All branch lengths = 1	41.8	<0.001
Sequential SS ANOVA	**Mean sq.**	***P* value**
Body (log)	**0.2241**	**$<2 \times 10^{-16}$**
Diet	**0.0013**	**0.01**
Mating system	0.0005	0.19
Residuals	0.0003	
Model comparisons	**dBIC**	**Weight**
Body (log)	0.0	0.91
Body (log) + diet	4.6	0.09
Body (log) + diet + mating system	17.9	<0.001

See Table 1 legend for explanatory information. Mating system does not explain additional variation, as this variable exhibits a low mean square value and a non-significant *P* value ($P > 0.05$). Compared with a model including only body size, there is strong evidence that the model including body size, diet and mating system provides relatively poor fit, while there is only weak evidence of such for the model including both body size and diet.

Table 4 | Results for diet models (spp. $n = 144$): brain (log) ~ body (log) + diet.

Branch length comparisons	dBIC	Weight
Lambda = 0.967	**0.0**	**0.97**
Kappa = 0.637	6.7	0.04
Delta = 1.703	15.5	<0.001
All branch lengths = 1	43.2	<0.001
Sequential SS ANOVA	**Mean sq.**	***P* value**
Body (log)	**0.2248**	**$<2 \times 10^{-16}$**
Diet	**0.0012**	**0.02**
Residuals	0.0004	
Model comparisons	**dBIC**	**Weight**
Body (log)	0.0	0.91
Body (log) + diet	4.7	0.09
Multiple comparisons	**Estimate**	***P* value**
Frugivores vs folivores	**0.097**	**0.002**
Frugivore/folivores vs folivores	**0.099**	**0.004**
Omnivores vs folivores	0.074	0.037
Frugivore/folivores vs frugivores	0.002	0.931
Omnivores vs frugivores	−0.023	0.269
Omnivores vs frugivore/folivores	−0.025	0.297

See Table 1 legend for explanatory information. Compared with a model including only body size, there is only weak evidence that a model including body size and diet provides relatively poor fit. Only frugivores and frugivore/folivores exhibit significantly larger relatively brain size than folivores, after correcting for the number of comparisons, and these comparisons are highlighted in bold. The estimated intercept differences between categories are also provided here.

and positive effect of percent frugivory (Supplementary Tables 1–4, 15–18, 23–29 and 34–37). Phylogenetic uncertainty does not affect these differences between dietary categories (Supplementary Tables 14, 22 and 33). Ancestral reconstructions of relative brain size (encephalization quotient, EQ) and the aforementioned sociality measures (Fig. 1; Supplementary Figs 1 and 2) highlight notable departures from the predictions of the social brain hypothesis.

Discussion

The results presented here are consistent with a range of ecological and developmental hypotheses centred on frugivory, including: (1) necessity of spatial information storage and retrieval[3,4]; (2) cognitive demands of 'extractive foraging' of fruits and seeds[5]; and (3) higher energy turnover and enhanced diet quality for energy needed during fetal brain growth[8–11]. Together, it seems that frugivory not only provides selective pressures on cognitive processing[3–5], but compensates for the costs of a metabolically expensive brain via facilitating higher energy turnover and/or lower energy allocation to digestion[8–11]. There are many examples of closely related species with similar body sizes, group sizes and social systems that exhibit corresponding brain size and dietary differences (for example, *Ateles* versus *Alouatta*; Supplementary Table 107). Notably, ancestral reconstructions elsewhere suggest these changes were not driven by reductions in body size[32]. Results suggesting that omnivorous anthropoid, but not strepsirrhine, species have large brains relative to folivores probably reflect different behavioural strategies related to faunivory. While omnivorous strepsirrhines usually feed on insects, a relatively abundant food source, omnivorous anthropoids often additionally hunt vertebrates (such as *Cebus capucinus*[33]). Although frugivores tend to have relatively smaller guts, recent work indicates no negative correlation between relative size of the brain and digestive tract after controlling for fat-free mass[34]. The lack of relationship between relative brain size and sociality indicated here is consistent with previous studies limited to strepsirrhines[35] and on non-primate taxa (for example, cetaceans[36], carnivores[37], birds[38]), and suggests that assumptions underlying the primate social brain hypothesis and its associated predictions should be re-evaluated.

First, complex social behaviours (for example, coalitions, reciprocation) that were previously assumed to be unique to primates have now been found in other taxa that do not exhibit relatively large brains compared to other members of their order (such as spotted hyenas[39]). Therefore, the premise that social complexity necessarily requires cognitive complexity may not always hold, as social living challenges might not require flexible cognitive solutions in real-time, but could be solved using simpler evolved rules-of-thumb[40]. Observational and simulation studies have suggested that simple associative rules may actually explain many complex patterns of behaviour[40].

Second, the hypothesis that complex social environments are more cognitively demanding than properties of the physical environment is partially derived from the idea that the former is more unstable than the latter and requires more processing power to navigate[41]. This has not been demonstrated quantitatively[41], and studies indicating a positive relationship between relative brain size and survival in mammalian species introduced into new environments suggest that long-term environmental variability could select for behavioural versatility[42].

Difficulties associated with assigning appropriate proxies of social complexity and cognitive complexity should not be underestimated. For example, mean group size is, 'at best, a crude proxy' of social complexity[43], because larger groups may not be characterized by a corresponding increase in the number of differentiated relationships/interactions[44]. Future studies using more sophisticated proxies may provide better support for the social brain hypothesis. However, our results call into question the current emphasis on social rather than ecological explanations for the evolution of large brains in primates. Rapid expansion of the hominoid cerebellum suggests technical intelligence was at least as important as social intelligence in human cognitive evolution[45]. Furthermore, numerous studies suggest that the neural substrates of tool use may represent evolutionary precursors for the evolution of language in humans[46,47]. Technical innovations also allowed for the increased incorporation of meat in the diet, and the advent of cooking meat

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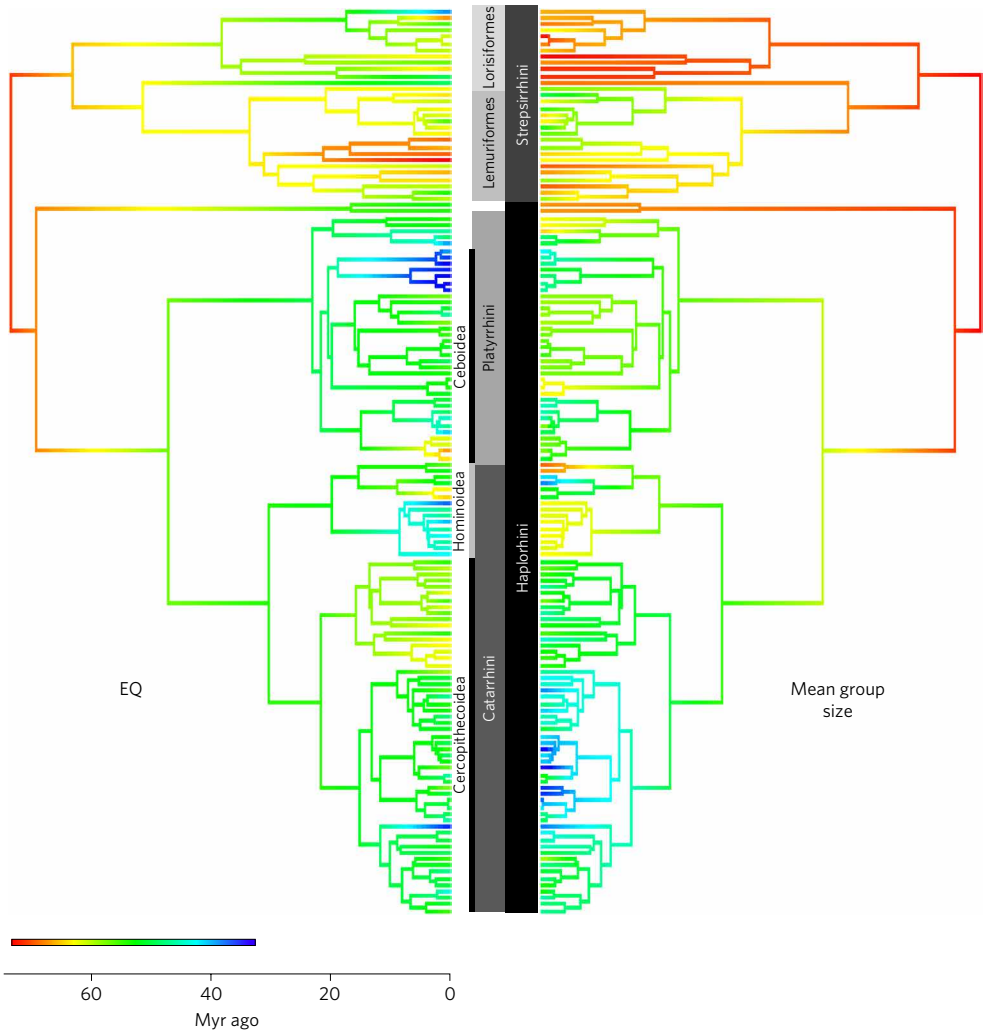

Figure 1 | Ancestral reconstructions of primate EQ (left) and mean group size (right). Lower values for EQ and mean group size are shown in redder colours; higher values are shown in blue ($n = 140$ species). Examples of departures from predictions of the social brain hypothesis include gibbons, which exhibit a decrease in group size since their last common ancestor with the great apes (associated with transitioning to monogamy) and an increase in relative brain size (concurrent with decreased body size and maintenance or slight increase in absolute brain size[32]). Similarly, although cebids and the aye-aye have not increased group size, their relative brain size has increased (possibly in relation to their extractive foraging behaviours[5]).

and other foods[6,7]. Together with the present study, this body of comparative work suggests that both human and non-human primate brain evolution was primarily driven by selection on increased foraging efficiency, with associated changes then perhaps providing the scaffolding for subsequent development of social skills.

Methods

Data collection and compilation. We compiled all species averaged data on brain and body weights from published literature sources (Supplementary Data: 'Brain Data' and 'Body Data' tabs). Brain weights represent averages of the following: (1) brain weights recorded in several original sources (compiled in ref. [48]); and (2) endocranial volumes (ECV) recorded in ref. [49], which were converted to masses by multiplying by a factor of 1.036 g cm^{-3} (the specific gravity of brain tissue[50]). The final value used for each species represents an average of the values provided across studies, weighted according to the study sample size (Supplementary Data: 'Brain Pivot' and 'Brain Final' tabs). This dataset was supplemented with secondary source data[51]. The female-only dataset represents brain and body weights of sexed specimens from ref. [49]. The subset of species for which both brain weight and ECV were available ($n = 79$) was tested for bias due to different collection methods. Agreement was concluded given that: (1) corrected ECV and weight measurements were highly correlated ($R^2 = 0.99$); (2) the mean difference (corrected ECV – weight) was 0.62 g with a 95% CI including zero (−1.81 to 3.05 g); and (3) there was low correlation ($R^2 = 0.20$) between the mean value of the two methods and the difference. As body weights were unavailable for many specimens in the original studies, they represent averages from the *CRC Handbook of Mammalian Body Masses*[52], and the AnAge[53] and PanTHERIA[54] databases. Additional data from secondary sources[51,55,56] were added to supplement this dataset, and were calculated as the mean values of males and females. In the course of compiling this dataset, we excluded juveniles, emaciated individuals and 'low-quality' data (indicated in the AnAge database[53]) when this information was available.

We assigned dietary categories according to previous designations in the published literature[3,55,57–61] and used a four category scheme, which includes folivore, frugivore/folivore, frugivore and omnivore (Supplementary Data: 'Diet Data' tab). Percent frugivory per species was obtained from ref. [62] (Supplementary Data: 'Diet Data' tab). We assigned social and mating systems after consolidating assignments listed in published literature sources[3,17,18,35,63–66] (Supplementary Data: 'System Data' tab). Social system categories represent the four-way categorization scheme typically used in primate studies[67], including solitary, pair-living, harem polygyny and polygynandry. Mating system categories include spatial polygyny, monogamy, polyandry, harem polygyny and polygynandry. These two categorization schemes, social system and mating system, were used to conform to previous studies using either one, and because primate social organizations and mating systems describe distinct categorization schemes that are not always congruent, although are often used interchangeably. Group size data were collected from numerous primary and secondary sources[35,59,67–74]. Average group size per species was calculated after removing duplicate values (Supplementary Data: 'Group Size Pivot' tab). This resulted in an average of 4.7 group size data points per species.

No simple universally accepted rule exists regarding the ratio of sample size to the number of predictors; however, a commonly used rule states that the

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number of cases should be at least 10 times the number of estimated terms[75]. Across all models included in these analyses, the maximum number of terms to be estimated is 10 (mating system models including all predictors: 1 = intercept, 1 = body size (log) coefficient, 3 = diet category coefficients, 4 = mating system coefficients, 1 = branch length transformation parameter), and all sample sizes exceed 100 species.

Statistical analyses. All statistical analyses were carried out in R 3.2.2. Humans (*Homo sapiens*) were excluded from all analyses because we are an outlier with regard to brain size and, consequently, excluding humans or presenting results with humans omitted is common practice in comparative studies of brain size[18].

For each of the three sociality measures (mean group size, social system, mating system), two sets of models were constructed to incorporate either dietary category or percent frugivory as the diet measure. In each set, three different models were constructed, each of which had brain size as the dependent variable and either body size, body size + diet, or body size + diet + sociality proxy as predictors. All continuous variables except percent frugivory were log-transformed before analyses. Interaction terms were not included for the sake of interpretability and to prevent over-parameterization[76]. Assumptions of the linear model, with the exception of uncorrelated errors (see below), were tested and confirmed. Although the expected relationship between body size and diet[77] was confirmed in this sample, all variance inflation factors throughout the linear models did not exceed 3.3, a cut-off commonly employed[78] as it indicates the point at which $R^2 = 0.70$ between variables. Although residual variances tend to differ between dietary categories and social and mating systems, multiple regression models assume the error variance is constant across values predicted from the model, and plots of residuals versus predicted values support this assumption.

Species represent non-independent cases because they may share traits due to phylogenetic inertia, so we tested for phylogenetic signal in linear model residuals by estimating values of Pagel's lambda (λ). Although it has been common practice in comparative biology to test the independent and dependent variables for phylogenetic signal to justify analysis using phylogenetic methods, PGLS assumes that the regression model residuals, not the traits under investigation, follow a multivariate normal distribution with variances and covariances that are proportional to the species' phylogenetic relationships. As significant phylogenetic signal was detected, PGLS regression was employed in all cases. We used the topologies and branch lengths from the GenBank taxonomy consensus tree provided on the 10kTrees website[27] (version 3) and also repeated all analyses using the molecular phylogeny from ref. [28].

Model comparisons were conducted using BIC, rather than Akaike information criterion, as the former uses a more conservative penalty for additional terms and is more likely to suggest the most parsimonious model, or the one with the fewest number of parameters that need to be estimated. Sequential analysis of variance (Type I ANOVA) was used to identify variables that explained a significant amount of brain size variation.

In some of the analyses limited to catarrhines, maximum-likelihood estimations of lambda produced by the PGLS models resulted in a value of zero. It is unlikely that these traits should be modelled using ordinary least squares regression (equivalent to lambda = 0) and that this result is due to decreased sample size. The log-likelihood plots of lambda illustrate this, as they are very flat (see Supplementary Fig. 3 for example). Consequently, these models were run using a value of lambda obtained by calculating its 95% CI (represented by red lines in Supplementary Fig. 3), extracting 100 equally spaced values of lambda within this interval and averaging them with each value weighted according to its likelihood.

We also considered the influence of uncertainty in phylogenetic relationships by using 1,000 different trees from 10kTrees, which were created using Bayesian phylogenetic methods and sampled in proportion to their probability[27]. We examined the full (all predictors) PGLS models for each sociality and diet measure combination separately for each tree. Type I ANOVA was conducted on each of the resulting models, and the range of P values for each predictor was compared with those produced by analyses incorporating the consensus tree. We also examined the PGLS model including body size and diet separately for each tree to confirm brain size differences between dietary categories. We applied model averaging, as this procedure takes into account the varying degree of fit of the models to estimate regression coefficients[79]. For each model, we allowed the phylogenetic scaling factor (lambda) to take the value of its maximum-likelihood[19].

We also fitted regression models using the 'Continuous' program in BayesTraits V2[80]. As this function can use only continuous variables, we ran models using percent frugivory and group size (log) as proxies of diet quality and sociality, respectively. This program allowed us to generate posterior distributions of PGLS regression models (regression coefficients and scaling parameters) that account for phylogenetic non-independence of species data. The analysis sampled the tree block of 1,000 trees in proportion to their posterior probability to account for phylogenetic uncertainty, and the scaling parameter lambda was sampled during the Markov chain Monte Carlo (MCMC) regression analysis. Uniform, uninformative priors were used, as these reflect the assumption that all possible values of the parameters are equally likely a priori[81], and this analysis was run for 2 million iterations, sampling every 200 iterations, with a burn-in of 200,000. MCMC diagnostics were run using the 'coda' package in R[82]. We report the posterior means of the variables included in each model and their 95% CI[83], and the probability that each explanatory parameter value is >0 (P_{MCMC}) as all have been hypothesized to have positive associations with brain size.

Finally, we considered the possible effect of phylogenetic uncertainty by using Bayesian mixed models to test across a random sample of 100 different trees from the previous set of 1,000 10kTrees phylogenies. This was implemented using the R package 'MCMCglmm'[84] and modified R code from ref. [85]. This procedure uses an MCMC estimation approach and accounts for phylogenetic non-independence by including the phylogenetic relationships among species as a random variable. We confirmed convergence between model chains using the Gelman–Rubin statistic, with all models required to have a potential scale reduction factor below 1.1 (ref. [86]). The effective sample sizes for all terms across all models were >1,000. In line with previous work[84,85], we used an uninformative inverse-Wishart distribution and a parameter expanded previously, with a half-Cauchy distribution for the random factor. Each model was fitted to each of the 100 trees, and the model outputs were combined to create coefficient distributions.

We implemented a resampling procedure as a way to incorporate within-species variation in group size. This procedure involves randomly choosing one group size datum for each species and setting it as the species-specific estimate[16,87]. Using this resampling scheme, we created 1,000 species-specific datasets that were subsequently analysed using the full (all predictors) group size PGLS model. Some iterations encountered optimization errors, which relate to calculating the maximum-likelihood of lambda. These were ignored and resampling continued until we produced 1,000 models[16]. To make inferences across these models, we determined the 95% CI of the derived group size term coefficients.

Before ancestral reconstruction analyses, polytomies in the phylogenetic tree were resolved using the 'multi2di' function in the R package 'ape'[88]. Maximum-likelihood ancestral state reconstructions of continuous traits (relative brain size, mean group size) were estimated using the 'fastAnc' function in the R package 'phytools'[89]. The EQ[31] was used as a measure of relative brain size, and the equation was derived from our dataset ($n = 144$ species) using the allometric formula $E = kP^{\alpha}$, where E is brain mass, P is body mass, k is the proportionality constant, α is the allometric exponent and the final equation is $E = 0.085 \times P^{0.775}$. The root node was set[22] to reflect a species characterized by solitary foraging (group size = 1) and a relative brain size (EQ = 0.41) based on estimates of early Eocene fossil primate brain and body weights (*Smilodectes gracilis*[90]: brain = 9.84 g, body = 1,600 g, EQ = 0.38; *Tetonius homunculus*[91]: brain = 1.55 g, body = 161 g, EQ = 0.45; see Supplementary Data: 'Fossil Data' tab).

Reconstructions for discrete variables (social and mating system) were conducted using an empirical Bayesian method in which the transition matrix is fixed at its most likely value, executed by the 'make.simmap' function in R package 'phytools'[89]. The function first fits a continuous-time reversible Markov model for the evolution of the trait in question, and then simulates stochastic character histories using that model and the tip states on the given tree[89]. To provide information regarding reconstruction uncertainty, marginal ancestral reconstructions were performed at each node by computing the set of empirical Bayes posterior probabilities that each node is in each state over 500 simulations. The root node prior probabilities were set to assume spatial polygyny and solitary foraging as the ancestral states for mating system and social system, respectively. Different transition rate models were considered using BIC, including: (1) an equal rates model, in which a single parameter governs all evolutionary transition rates; (2) a symmetrical rates model, in which forward and reverse evolutionary transitions between states are constrained to be equal; and (3) an all-rates-different model, where each rate is given a unique parameter. The symmetrical rates model was ultimately used for both reconstructions as it exhibited the lowest BIC value.

Data availability. The authors declare that all data supporting the findings of this study are available within the paper and its Supplementary Information files.

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Author contributions

A.R.D. designed the project and performed the analyses with input from J.P.H. and S.A.W. A.R.D. and S.A.W. collected the data. All three authors wrote the manuscript.

Additional information

Supplementary information is available for this paper.

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Competing interests

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