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Cite this article: Powell LE, Isler K, Barton RA. 2017 Re-evaluating the link between brain size and behavioural ecology in primates. *Proc. R. Soc. B* **284**: 20171765. http://dx.doi.org/10.1098/rspb.2017.1765

Received: 7 August 2017
Accepted: 25 September 2017

Subject Category:
Neuroscience and cognition

Subject Areas:
behaviour, cognition, evolution

Keywords:
brain size, primate, ecology, group size, home range

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Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.3899422.

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Re-evaluating the link between brain size and behavioural ecology in primates

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Comparative studies have identified a wide range of behavioural and ecological correlates of relative brain size, with results differing between taxonomic groups, and even within them. In primates for example, recent studies contradict one another over whether social or ecological factors are critical. A basic assumption of such studies is that with sufficiently large samples and appropriate analysis, robust correlations indicative of selection pressures on cognition will emerge. We carried out a comprehensive re-examination of correlates of primate brain size using two large comparative datasets and phylogenetic comparative methods. We found evidence in both datasets for associations between brain size and ecological variables (home range size, diet and activity period), but little evidence for an effect of social group size, a correlation which has previously formed the empirical basis of the Social Brain Hypothesis. However, reflecting divergent results in the literature, our results exhibited instability across datasets, even when they were matched for species composition and predictor variables. We identify several potential empirical and theoretical difficulties underlying this instability and suggest that these issues raise doubts about inferring cognitive selection pressures from behavioural correlates of brain size.

1. Introduction

Absolute brain size varies almost a thousand-fold across the order Primates [1], and the adaptive significance of this variation has been the subject of intense interest. As neural tissue imposes costs [2], evolutionary increases in brain size are assumed to confer benefits in terms of enhanced cognitive abilities [3,4]. Although this assumption has received support from studies demonstrating positive associations between brain size and cognitive performance [5–9], the selection pressures responsible are still poorly understood.

A classic approach to this problem is to examine which specific aspects of lifestyle correlate with brain size across species. In primates, two broad categories of hypothesis have been tested in this way; ecological and social. Ecological hypotheses mainly relate to the foraging demands of a species' ecological niche [10–13]. Effects of diet [14–20], home range size [13,19,21], terrestriality [22] and activity period [23,24] on brain or brain component size have been reported, and explanations for such effects invoke a range of information-processing capacities, including spatial or spatio-temporal memory and visual processing [19,23,25,26]. By contrast, the Social Brain Hypothesis (SBH) proposes that the principal selection pressure responsible for variation in primate brain size is the cognitive demands of managing social relationships within bonded groups [27–32], a hypothesis that has received considerable empirical support [30–32]. Relationships between sociality and brain size have also been reported in other mammalian taxa such as Ungulates [33,34] and Carnivora [14,34–36].

However, some studies have failed to find a statistical link between brain size and sociality [14,19,20,36], and apparent exceptions, in terms of large-brained but not conspicuously social taxa, suggest that factors other than sociality may have been influential [14,37,38]. In particular, a recent analysis by DeCasien *et al*. [20]

found that diet, and not social group size, correlates with brain size in primates. DeCasien *et al*. point to several possible explanations for the correlation with diet that invoke the cognitive basis of foraging skills. Shultz & Dunbar [34] had earlier acknowledged that primate brain size correlates with diet, but argued (i) that this reflects energetic constraints on brain size rather than selection on foraging skills, and (ii) that brain size correlates with sociality independently of diet. The regression models supporting the latter conclusion were based on relatively small sample sizes, and, using a larger sample size, DeCasien *et al*. [20] failed to find an independent effect of social group size after accounting for body size and diet, as well as for phylogenetic uncertainty. On the other hand, Shultz & Dunbar [34] incorporated a wider range of ecological variables into their model. Here we combine the strengths of these studies and evaluate the possible effects of their use of different datasets; that is, we use phylogenetic comparative analysis applied to large sample sizes, we incorporate all the key behavioural-ecological predictors examined in previous studies, and we account for phylogenetic uncertainty. Although error variance in predictors theoretically has a major impact on the results of regression analyses, and is likely to be considerable in the case of behavioural measures collated from field studies conducted by different researchers using different methods on different populations, almost nothing is known about the effects of this problem on determining the behavioural correlates of brain size. A novel feature of our study is therefore that we assess the robustness of results by replicating analyses across datasets. A lack of such robustness would have significant implications for attempts to infer selection pressures from analyses that neglect this issue.

2. Material and methods

(a) Data sources

Brain size (endocranial volume) and body mass were obtained from previously published compilations [18,39–41]. While it might be argued that the SBH specifically invokes the neocortex as the relevant brain structure [31–33], proponents of the SBH refer to the hypothesis as an explanation for brain size and have used both overall brain and neocortex size [33,42], arguing that brain size and neocortex size are closely related because the neocortex comprises a large proportion of whole brain volume [34,43]. Using brain size markedly increases sample sizes and statistical power. Nevertheless, we recognize that these two measures could theoretically give different results (see Discussion).

Two datasets on primate behavioural ecology were analysed. The first (hereafter referred to as 'dataset 1') is a previously unpublished dataset compiled from the literature by K.I., providing updated, high quality data on primate behavioural ecology; favouring wild samples over captive, larger samples over smaller, original contributions over compilations, and more recent sources over older ones (see the electronic supplementary material 2 for data and sources) [18,39–41]. For sexually dimorphic species (size difference $> 10\%$), female values for endocranial volume (hereafter 'ECV') and body mass were used. For all other species, means were calculated across males and females. If available, body mass was taken from the same specimens as ECV. Otherwise, the largest available sample of wild body mass data was used. Dataset 1 includes information on diet composition (the percentage of time spent feeding on different dietary items), size of sleeping groups and of foraging groups, day ranges, and home range sizes. Dataset 2 was compiled from the literature by Nunn & van Schaik [44]. It provides values for female body mass, activity period, substrate use and diet. As body size in dataset 2 is derived only from female specimens, for comparability we also ran an analysis on dataset 1 using only female body size estimates (electronic supplementary material 1, table S13). Datasets 1 and 2 are not independent, as their sources overlap. Therefore, in order to test for robustness of results across strictly independent datasets, we also created subsets of the data by randomly selecting different species from each original dataset.

(b) Selection of ecological variables

Five behavioural-ecological variables were selected for analysis, based on the previous literature [19,21,25,30,31,45,46]: two continuous variables (home range size (ha) and social group size) and three dichotomous categorical variables: activity period (nocturnal/diurnal), substrate use (terrestrial/arboreal) and diet (folivore/non-folivore). Rather than presenting quantitative estimates, Nunn & van Schaik [44] classified species' diet categories based on the food type that occupied the largest proportion of feeding time. We therefore used the same criterion to categorize diet in dataset 2. However, diet is subject to marked intraspecific variation in relation to seasonal and local differences in the relative abundance of different food types [47]. Hence, categorizing species' diet according to percentage of feeding time can create anomalies, in which closely related species with similar foraging niches are placed in different categories owing simply to the quantitative estimates being based on insufficient or inaccurate samples. We therefore ran an additional separate analysis for dataset 1 in which folivores were more strictly defined as only those species with clear physiological specializations for folivory (electronic supplementary material 1, S16) [48,49]. As in previous analyses [11,23,24], diurnal species were defined as those that regularly forage and are active during the day, therefore including the few cathemeral lemurs which are more diurnal than their strictly nocturnal close relatives [50,51].

(c) Selection of group size data

Dataset 2 [44] provides both 'population group size' and 'foraging group size'. The authors define population group size as '. . .the animals that come together frequently, usually to sleep together and among which foraging units have highly overlapping ranges.' (p. 202), whereas foraging group sizes include the smaller, temporary parties or subgroups that form in response to immediate daily foraging conditions. Since the SBH relates to communities of individuals that associate habitually, we used population group size from dataset 2. Dataset 1 (K. Isler 2017, unpublished dataset, University of Zurich) recorded both sleeping and foraging group size. A third group size measure ('combi group size') takes the largest of the sleeping and foraging group figures. Combi group size therefore reflects the number of individuals who regularly associate, and is thus essentially definitionally the same as population group size from dataset 2. We therefore used combi group size in our primary analyses of dataset 1. However, we also reran the analyses with sleeping group size only (where available) and found no qualitative difference in results (see the electronic supplementary material 1, table S12). While group size may be a relatively indirect measure of primate social complexity [46,52], it is the one that forms the foundation of work on the SBH [31,46], and as we intended to revisit the conclusions of that work it is necessary to use the same metrics as used in those papers.

(d) Statistical analysis

Both analyses used the same endocranial volume data; only the behavioural-ecological data differed. Dataset 1 and the R code used in this study are available in the electronic supplementary material (electronic supplementary material 2 and electronic supplementary

material 3 respectively). We used phylogenetic generalized least-squares regression (PGLS) to analyse the correlated evolution of the five behavioural-ecological variables and endocranial volume. Data were analysed in the R [53] packages 'ape'[54], 'picante'[55], 'caper'[56] and 'nlme'[57]. Pagel's λ [58] is a scaling parameter, used to scale the variance co-variance matrix according to the expected variance given a phylogenetic tree, thus accounting for the confounding effect of phylogenetic relatedness in comparative studies [59]. λ was estimated by maximum likelihood. For the PGLS analyses, the phylogeny used was the consensus tree incorporating branch length estimates from the 10 k Trees Project [60]. Body mass was included as a covariate in the regression to control for its effects on endocranial volume following Freckleton [61], Smith [62] and Garcia-Berthou [63]. This method of body size correction is preferred over analysis of residuals as it avoids biased parameter estimates [61]. Including body mass as a covariate also has the benefit of controlling for any effects of body mass on other predictors, which is likely to be a particular issue for home range size. The granularity of the environment as perceived by the animal is likely to be dependent upon its size. For example, an increase of 1 ha would likely have very different implications for a 50 g mouse lemur than for an 85 kg gorilla.

All continuous variables (endocranial volume, body mass, group size and home range size) were log10 transformed prior to analysis to satisfy the assumption of normality. Prior to the analysis, we inspected the distribution of the response and predictor variables and found them to be approximately symmetrically distributed. We inspected diagnostic plots for the model and found no evidence of violation of the assumptions of normality or homogeneity of residuals [64]. Models were checked for outliers with a studentised residual with an absolute value greater than 3 [65]. None were found. We checked for collinearity between predictors in our models. Although statistically significant partial correlations were present for all predictors, none were above 0.67. Absolute correlations of less than 0.8 are deemed not to represent significant collinearity issues [66]. Variance inflation factors (VIFs) [64] were less than 1.4 in all cases which further reassured us that collinearity was not a significant problem in this case [67].

(e) Model comparisons

To assess the fit of the PGLS models, we constructed models which varied in complexity; from an allometric model in which body size was the sole predictor, models including body size and each predictor alone, and then added parameters to the model according to their p value (low to high). We then compared the Akaike's information criterion (AIC) [68] for each model using the native 'AIC' function in R [53]. The AIC takes in to account the size of the sample and the number of predictors; penalizing complex, over-parameterised models [64]. Lower values of the AIC indicate better fitting, more parsimonious models. We also used log likelihood ratio tests [69], run using the 'lrtest' function in the lmtest package [70] in R [53].

(f) Accounting for phylogenetic uncertainty

The PGLS analyses are based on a single consensus tree of the primates, but phylogenetic relationships are not known with certainty. To account for this issue and to additionally test whether this potential source of error in comparative studies has a significant impact on identifying correlates of brain size, we performed Bayesian phylogenetic regressions [71] accounting for shared ancestry by integrating over a posterior sample of 1000 primate phylogenetic trees taken from the 10 k Trees Project website [60]. We conducted these analyses using BayesTraitsV3 [72]. To account for the level of phylogenetic signal in our data we estimated the tree scaling parameter λ [72]. We used a uniform prior of −100 to 100 for all regression coefficients and a uniform prior of 0 to 1 for λ. We ran the analyses for 1 010 000 iterations, sampling every 1000 iterations removing the first 100 000 iterations as burn-in. To determine the significance of our regression coefficients we used pMCMC values which can be interpreted in a similar way to frequentist p-values [73].

Table 1. Phylogenetic least-squares (PGLS) regressions examining the effects of five behavioural-ecological variables on endocranial volume. (*=significant at the $\alpha < 0.05$ level; **=significant at the $\alpha < 0.01$ level; ***=significant at the $\alpha < 0.001$ level.)

	dataset 1 ($n = 144$)		dataset 2 ($n = 104$)	
predictor	t_{137}	p	t_{97}	p
intercept	−5.5	<0.001***	11.3	<0.001***
body size	18.6	<0.001***	13.3	<0.001***
activity period	2.5	<0.05*	1.9	0.06
terrestriality	0.4	0.69	−0.3	0.8
folivory	−1.7	0.08	0.1	0.9
group size	1.7	0.1	0.1	0.9
home range size	2.4	<0.05*	2.8	<0.01**
model summary:				
λ	0.988		0.997	
R^2	0.8		0.75	

3. Results

(a) PGLS

Table 1 presents the results of PGLS analyses on the two full datasets. In all cases λ was close to 1, indicating that the data are consistent with a Brownian motion model of trait evolution [74]. A simple allometric model regressing endocranial volume on body size alone explained 77% of the variation in dataset 1 and 73% in dataset 2. The full model (comprising all five behavioural-ecological variables) was highly significant in both dataset 1 ($\lambda = 0.99$, $r^2 = 0.8$, $p < 0.0001$) and dataset 2 ($\lambda = 1$, $r^2 = 0.75$, $p < 0.0001$).

In dataset 1 home range size and activity period were both associated with endocranial volume after accounting for the effects of body size (positive associations between brain size and home range size and diurnality respectively) ($\lambda = 0.99$, $t_{6,108} = 2.1$, $p < 0.05$). The model based on dataset 2 (K. Isler 2017, unpublished dataset, University of Zurich) also showed a significant positive partial correlation with home range size, ($\lambda = 0.99$, $t_{6,97} = 2.8$, $p < 0.01$), but the partial correlations with activity period did not reach significance ($p = 0.06$), and no other behavioural-ecological variables were significantly correlated with brain size while accounting for these effects.

When each dataset was matched to include the same species and the same endocranial volume data, results changed, and again differed between datasets. Table 2 indicates significant partial correlations for diet in dataset 1 and for home range size in dataset 2. In both cases, the effect of activity period was now non-significant.

We next performed PGLS analyses on the datasets: (i) after they had been made completely independent from each other, and (ii) after they had been reduced to include only species that appeared in Stephan *et al.*'s 1981 brain component volumes dataset [75]. Again, results differed between the datasets and

Table 2. Phylogenetic least-squares (PGLS) regressions examining the effects of five behavioural-ecological variables on endocranial volume with datasets matched for species. (*=significant at the $\alpha < 0.05$ level; ***=significant at the $\alpha < 0.001$ level.)

	dataset 1 ($n = 99$)		dataset 2 ($n = 99$)	
predictor	t_{92}	p	t_{92}	p
intercept	−5.8	<0.001***	11	<0.001***
body size	16.9	<0.001***	13	<0.001***
activity period	1.8	0.1	1.9	0.1
terrestriality	0.3	0.8	−0.2	0.8
folivory	−2.2	<0.05*	0.1	0.9
group size	1	0.3	0.1	0.9
home range size	1.3	0.2	2.5	<0.05*
model summary:				
λ	0.99		1	
R^2	0.81		0.75	

from the results reported above (see the electronic supplementary material 1, tables S4 and S9 for full results). Folivory showed a significant negative association with brain size in independent dataset 1, whereas there were no significant predictors after accounting for body mass in independent dataset 2. Similarly, no significant associations were found in the full multiple regressions on either dataset when they were matched to the Stephan *et al*. [75] species list. However, because the sample sizes in these analyses were small relative to the number of predictors, we used model comparisons to determine which combinations of predictors are best supported (see below).

(b) Model comparison

To establish which combination of variables model endocranial volume best in each dataset, we employed a model comparison approach using AIC [68] and log likelihood ratio tests [69]. We first subjected the full datasets to model comparison (electronic supplementary material 1, tables S2 and S3).

AIC values indicate that the model offering the best and most parsimonious explanation of dataset 1 was one which included activity period, home range size, diet and group size. (model ix, table S2 in the electronic supplementary material 1). Following Burnham and Anderson (2002) [69], an AIC difference (Δi) of less than 2 was considered to indicate substantial empirical support (p. 70). The best model was therefore not a significantly better fit to the data than models vii, viii and x ($\Delta i < 2$). AIC differences between the models fitted to dataset 2 (electronic supplementary material 1, table S3) showed that a model containing home range size and activity period was the best fit to the data, but model vi which included only body size (the covariate) and home range size provided a comparable fit ($\Delta i < 2$). Model viii (home range size, activity period and terrestriality) also gave a comparable fit according to the $\Delta i < 2$ rule, but a log likelihood ratio test showed that this addition of terrestriality did not significantly improve the fit (electronic supplementary material 1, table S3). In summary, these results show that endocranial volume is best modelled by different combinations of variables in the two datasets. Home range size was consistently present in the best models ($\Delta i < 2$) across the two datasets, appearing in all seven of the best models. Group size appeared in only two of the seven best models and only when accompanied by home range size, folivory and activity period.

As described above, the inclusion of different species in each dataset may result in the composition of the best models varying between datasets. We therefore also subjected the species matched datasets to model comparison, as detailed in tables S5 and S6 in the electronic supplementary material 1.

The model comparisons for the species matched datasets show broad agreement with those of the non-matched, full datasets in the electronic supplementary material 1, tables S2 and S3. The best models still consistently included home range size, appearing in every model with substantial support (i.e. where $\Delta i < 2$) save one (model viii, table S5 in the electronic supplementary material 1). Group size appeared in only one of the best models, again together with home range size, folivory and activity period.

PGLS model comparisons for the Stephan *et al*. [75] sample of species identified social group size as a significant predictor: in both datasets, group size and folivory were included in the best model. The addition of home range size was found not to improve the fit in either dataset (tables S10 and S11, electronic supplementary material 1).

(c) Accounting for phylogenetic uncertainty

A Bayesian phylogenetic regression of the full datasets replicated the qualitative results of the PGLS analyses. In dataset 1, home range size (posterior mean = 0.0247, 95% CI = 0.0241 to 0.0253, pMCMC = 0.0066) and activity period (posterior mean = 0.1327, 95% CI = 0.1293 to 0.262, pMCMC = 0.0154) both had pMCMC values of less than 0.05 (electronic supplementary material 1, table S14), indicating that these traits are well supported [72]. Home range size was the only predictor with strong support in dataset 2 (posterior mean = 0.0426, 95% CI = 0.0416 to 0.0436, pMCMC = 0.0007, electronic supplementary material 1, table S15). Figures S14*a*, S14*b* and S15 in the electronic supplementary material 1 show the posterior distributions of estimates of those traits that had pMCMC < 0.05.

4. Discussion

We have re-examined the correlates of brain size in primates, using two large comparative datasets, and incorporating multiple potentially relevant behavioural variables within phylogenetic statistical models. Our results indicate that, even holding constant statistical methods, phylogeny, set of predictor variables, response variable data, and species sample, the behavioural and ecological correlates of brain size are sensitive to the use of different predictor datasets. Accounting for phylogenetic uncertainty did not affect this outcome.

This lack of robustness raises doubts about inferences from behavioural-ecological correlates of brain size based on analyses of single datasets, and may help to explain divergent results between studies. To the extent that we find stability, there is stronger evidence for correlations with ecological factors, notably home range size, than for social group size, as found in Clutton-Brock and Harvey's pioneering study [17].

Our results are also broadly in line with the more recent study of DeCasien *et al*. [20], in finding stronger and more robust associations with ecological factors related to foraging than with social group. However, our inclusion of additional variables and datasets also reveals differences. DeCasien *et al*. identified frugivorous diets as the key correlate of large brain size, but did not examine home range size. By contrast, we found home range size rather than diet to be the most consistent correlate of brain size, but note that this varied between datasets, suggesting their effects are hard to separate, perhaps because diet and ranging together form an adaptive 'syndrome': more frugivorous and (less folivorous) diets are strongly associated with more patchily distributed resources and larger home ranges [44]. The manner in which diet is categorized also appears to have an impact; when only species with biological adaptations to leaf processing are classified as folivorous, diet additionally becomes a significant predictor of brain size (electronic supplementary material 1; S16*a* and *b*). We also found some evidence for an association between activity period and large brain size, though this effect was small and variable across datasets, the potential reasons for which we discuss below.

Evidence for a correlation between brain size and social group size after accounting for effects of other variables was weak. We found that this well-known correlation appears largely dependent on the particular sample of species in the Stephan dataset [75]. One elaboration of the SBH accounts for dietary correlates of brain size in primates as a reflection of energetic constraints [31,34,43]. In this view, sociality selects for bigger brains and diet must become more frugivorous to provide the additional energy required to meet the costs. However, this hypothesis would presumably predict stronger correlations with diet than with home range size, which we do not find. In addition, we do not find support for the claim that social group size and brain size are robustly correlated after accounting for the effects of ecological variables [34,43]. We agree with Dunbar & Shultz [43] that, in principle, comparative analysis should differentiate between selection pressures and constraints, but it remains unclear how this can be achieved in practice. While path analysis has been suggested as a possible solution [31,43], it is essentially a protocol for arranging a set of regression coefficients according to some causal hypotheses; it cannot be used to discover causality from correlational data [76], it cannot solve the problem of instability across datasets, and it is as vulnerable to underlying issues with the data as are the regression analyses on which it is based. In summary, while it remains plausible that sociality is related to cognitive evolution in primates, we suggest that this can no longer be claimed on the basis of a strong or robust correlation between brain size and group size that remains after controlling for other variables.

Why are results unstable, and what implications does this have for using them to infer selection on cognitive abilities? We highlight three empirical issues (data quality, statistical power and intrinsic intraspecific variability) as well as theoretical difficulties with brain size as a global measure of cognitive capacities. Data quality and replicability are major issues for comparative studies because of the diversity of sources and of the methods used by different researchers to collect the primary data [77–79]. Furthermore, many behaviours vary extensively within and between populations of the same species, and comparative studies routinely collapse this intraspecific variation into species-specific means. The validity of these mean values depends on the extent to which the variation has been sampled to a comparable extent across species, and on the assumption that interspecific variation is substantial by comparison. For example, group size in different populations of terrestrial or semi-terrestrial cercopithecine species varies widely, depending on habitat, reflecting facultative adjustment of behaviour to local ecological conditions. Group size in yellow baboons (*Papio cynocephalus*) was found to vary between 8 and 44 within one study population [80]; the contrasts between *Papio* populations or sub-species is even more marked, with estimates of group size varying approximately 20-fold [81] and of home range size approximately 100-fold [82]. Phylogenetic methods which control for intraspecific variation by incorporating the uncertainty in to the error term are now available [83]. Future work could exploit this development, if and when sufficient reliable data for sampling intraspecific variance become available for a large sample of species. However, this would in one sense only make the problem we have highlighted worse: the inflation of error terms that inevitably result can be expected to reduce the likelihood of finding significant correlations. The point we wish to emphasize here, however, is that current inferences in the literature about the selection pressures driving the evolution of brain size made using the standard approach of analysing single datasets appear to be unreliable. This point has important implications both for interpreting the existing literature, and for the design of future studies. Where variables are prone to measurement error and/or extensive intraspecific variation, such as is particularly likely to be the case with many behavioural variables, we recommend careful attention to data quality, testing the stability of results across datasets and/or incorporation of uncertainty in estimation of species-typical mean values.

In addition, statistical power is a serious issue where a range of predictors are considered with moderate or small numbers of species, as is not uncommonly the case in published comparative studies. In this situation (model overfitting) we can expect models with high coefficients of determination but poor generalizability from one dataset to another. This is a particular issue with the relatively small dataset of Stephan *et al*. [75], which has been the main empirical foundation for the claim that social group size is the strongest predictor of brain and/or neocortex size [30,31,43,84]. When datasets 1 and 2 were matched to the species in the Stephan *et al*. data, the best models identified by our model comparisons did include group size (electronic supplementary material 1, tables S10*a*–S11*b*), in contrast with our results for the larger datasets. Hence, in accord with the suggestion of Parker that this dataset may be biased in favour of the SBH [13], we recover a clear correlation with group size only when analysis is restricted to these species. It therefore seems that the differences in patterns of correlations between studies [20,31] are at least partly owing to different species sampling and/or different predictor variables, rather than simply to use of different brain measures (overall brain size versus neocortex size).

The fact that an effect of home range size emerges through two different types of analysis and two different (albeit not independent) datasets may make it tempting to interpret ranging as the 'true' correlate of primate brain size, and to suggest, as others have done, that large brains reflect selection on spatial memory [33,85]. We, however, urge caution in this respect. First, we cannot unambiguously separate the effects of home range size, diet and activity period. Second, and in

our view more importantly, overall brain size does not necessarily reflect the ways in which different selection pressures acted on different neural systems [3,23,86]. For example, we found evidence that diurnality is associated with larger brains, but this result was weak and lacking consistency across datasets. Evolutionary transitions between nocturnal and diurnal niches are known to correlate with the relative size of visual and olfactory brain regions [23]. Crucially, visual and olfactory regions show opposite evolutionary patterns (the former being relatively large and the latter relatively small in diurnal species), so that overall brain size fails to adequately capture the influence of sensory niche on information-processing capacities [23]. In this case, the relatively weak and variable effects of activity period on overall brain size can only be interpreted by understanding the divergent responses of underlying neural systems. Similarly, recent evidence reveals a striking difference in the pattern of brain component evolution in apes compared to other anthropoid primates, with increased cerebellar relative to cortical expansion in the former [74]. These different neural causes of brain size variation in different clades can be presumed to have different cognitive implications, presenting a difficulty for the attempt to relate overall brain size to individual selection pressures [3] or to some general cognitive ability. While large brain regions such as the mammalian neocortex and avian pallium inevitably have a relatively strong impact on overall brain size [87], these components themselves consist of multiple functional systems that evolve in a mosaic fashion in response to different selection pressures [23,87–92]. Making sense of the behavioural and ecological correlates of brain size will therefore depend on the difficult task of understanding the complex and clade-specific ways in which brain size reflects variation in specific neural systems.

Data accessibility. The data supporting this article (which are not available directly from the literature) have been uploaded as the electronic supplementary material.

Authors' contributions. R.A.B. and L.E.P. conceived of the project and wrote the manuscript; L.E.P. and K.I. collected the data; L.E.P. and R.A.B. analysed the data. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. L.E.P. is funded by a Durham Doctoral Studentship provided by the University of Durham.

Acknowledgements. The authors would like to thank Chris Venditti for his invaluable advice on Bayesian methods, the Primatology discussion group at the University of Durham for advice on drafts, and the AnthroTree workshop at Duke University, North Carolina for providing training in phylogenetic methods to L.E.P.

References

1. Barton RA. 2012 Embodied cognitive evolution and the cerebellum. *Phil. Trans. R. Soc. B* **367**, 2097–2107. (doi:10.1098/rstb.2012.0112)
2. Aiello LC, Wheeler P. 1995 The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199. (doi:10.1086/204350)
3. Healy SD, Rowe C. 2007 A critique of comparative studies of brain size. *Proc. R. Soc. B* **274**, 453–464. (doi:10.1098/rspb.2006.3748)
4. Weisbecker V, Blomberg S, Goldizen AW, Brown M, Fisher D. 2015 The evolution of relative brain size in marsupials is energetically constrained but not driven by behavioral complexity. *Brain Behav. Evol.* **85**, 125–135. (doi:10.1159/000377666)
5. MacLean EL *et al*. 2014 The evolution of self-control. *Proc. Natl Acad. Sci. USA* **111**, E2140–E2148. (doi:10.1073/pnas.1323533111)
6. Benson-Amram S, Dantzer B, Stricker G, Swanson EM, Holekamp KE. 2016 Brain size predicts problem-solving ability in mammalian carnivores. *Proc. Natl Acad. Sci. USA* **113**, 2532–2537. (doi:10.1073/pnas.1505913113)
7. Kotrschal A, Rogell B, Bundsen A, Svensson B, Zajitschek S, Brännström I, Immler S, Maklakov AA, Kolm N. 2013 Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. *Curr. Biol.* **23**, 168–171. (doi:10.1016/j.cub.2012.11.058)
8. Kotrschal A, Corral-Lopez A, Amcoff M, Kolm N. 2015 A larger brain confers a benefit in a spatial mate search learning task in male guppies. *Behav. Ecol.* **26**, 527–532. (doi:10.1093/beheco/aru227)
9. MacLean EL *et al*. 2012 How does cognition evolve? Phylogenetic comparative psychology. *Anim. Cogn.* **15**, 223–238. (doi:10.1007/s10071-011-0448-8)
10. Mars RB, Neubert F-X, Verhagen L, Sallet J, Miller KL, Dunbar RIM, Barton RA. 2014 Primate comparative neuroscience using magnetic resonance imaging: promises and challenges. *Front. Neurosci.* **8**, 298.
11. Barton RA. 2006 Primate brain evolution: Integrating comparative, neurophysiological, and ethological data. *Evol Anthropol Issues, News, Rev.* **15**, 224–236. (doi:10.1002/evan.20105)
12. Harvey PH, Rambaut A. 2000 Comparative analyses for adaptive radiations. *Phil. Trans. R. Soc. Lond. B* **355**, 1599–1605. (doi:10.1098/rstb.2000.0721)
13. Parker ST. 2015 Re-evaluating the extractive foraging hypothesis. *New Ideas Psychol.* **37**, 1–12. (doi:10.1016/j.newideapsych.2014.11.001)
14. Swanson EM, Holekamp KE, Lundrigan BL, Arsznov BM, Sakai ST. 2012 Multiple determinants of whole and regional brain volume among terrestrial carnivorans. *PLoS ONE* **7**, e38447. (doi:10.1371/journal.pone.0038447)
15. Walker R, Burger O, Wagner J, Von Rueden CR. 2006 Evolution of brain size and juvenile periods in primates. *J. Hum. Evol.* **51**, 480–489. (doi:10.1016/j.jhevol.2006.06.002)
16. Harvey PH, Clutton-Brock TH, Mace GM. 1980 Brain size and ecology in small mammals and primates. *Proc. Natl Acad. Sci. USA* **77**, 4387–4389. (doi:10.1073/pnas.77.7.4387)
17. Fish JL, Lockwood CA. 2003 Dietary constraints on encephalization in primates. *Am. J. Phys. Anthropol.* **120**, 171–181. (doi:10.1002/ajpa.10136)
18. van Woerden JT, van Schaik CP, Isler K. 2010 Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. *Am. Nat.* **176**, 758–767. (doi:10.1086/657045)
19. Clutton-Brock TH, Harvey PH. 1980 Primates, brains and ecology. *J. Zool.* **190**, 309–323. (doi:10.1111/j.1469-7998.1980.tb01430.x)
20. DeCasien AR, Williams SA, Higham JP. 2017 Primate brain size is predicted by diet but not sociality. *Nat. Ecol. Evol.* **1**, 112. (doi:10.1038/s41559-017-0112)
21. Milton K, May ML. 1976 Body weight, diet and home range area in primates. *Nature* **259**, 459–462. (doi:10.1038/259459a0)
22. Sawaguchi T. 1990 Relative brain size, stratification, and social structure in anthropoids. *Primates* **31**, 257–272. (doi:10.1007/BF02380947)
23. Barton RA, Purvis A, Harvey PH. 1995 Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Phil. Trans. R. Soc. Lond. B* **348**, 381–392. (doi:10.1098/rstb.1995.0076)
24. Barton RA. 1996 Neocortex size and behavioural ecology in primates. *Proc. R. Soc. B* **263**, 173–177. (doi:10.1098/rspb.1996.0028)
25. Milton K. 1988 Foraging behaviour and the evolution of primate intelligence. In *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans* (eds RW Byrne, A Whiten), pp. 285–305. New York, NY: Clarendon Press/Oxford University Press.
26. Barton RA. 1998 Visual specialization and brain evolution in primates. *Proc. R. Soc. Lond. B* **265**, 1933–1937. (doi:10.1098/rspb.1998.0523)

27. Whiten A, Byrne RW. 1988 Tactical deception in primates. *Behav. Brain Sci.* **11**, 233–273. (doi:10.1017/S0140525X00049682)
28. Jolly A. 1966 Lemur social behavior and primate intelligence. *Science* **153**, 501–506. (doi:10.1126/science.153.3735.501)
29. Humphrey NK. 1976 The social function of intellect. In *Growing points in ethology* (eds PPG Bateson, RA Hindle), pp. 303–317. Cambridge, UK: Cambridge University Press.
30. Dunbar RIM. 1992 Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* **22**, 469–493. (doi:10.1016/0047-2484(92)90081-J)
31. Dunbar RIM, Shultz S. 2007 Evolution in the social brain. *Science* **317**, 1344–1347. (doi:10.1126/science.1145463)
32. Barton R, Dunbar RIM. 1997 Evolution of the social brain. In *Machiavellian intelligence II* (eds A Whiten, RW Byrne), pp. 240–263. Cambridge, UK: Cambridge University Press.
33. Shultz S, Dunbar RIM. 2006 Both social and ecological factors predict ungulate brain size. *Proc. R. Soc. B* **273**, 207–215. (doi:10.1098/rspb.2005.3283)
34. Shultz S, Dunbar RIM. 2007 The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proc. R. Soc. B* **274**, 2429–2436. (doi:10.1098/rspb.2007.0693)
35. Pérez-Barbería FJ, Shultz S, Dunbar RIM. 2007 Evidence for coevolution of sociality and relative brain size in three orders of mammals. *Evolution* **61**, 2811–2821. (doi:10.1111/j.1558-5646.2007.00229.x)
36. Holekamp KE, Dantzer B, Stricker G, Shaw Yoshida KC, Benson-Amram S. 2015 Brains, brawn and sociality: a hyaena's tale. *Anim. Behav.* **103**, 237–248. (doi:10.1016/j.anbehav.2015.01.023)
37. van Schaik CP, Isler K, Burkart JM. 2012 Explaining brain size variation: from social to cultural brain. *Trends Cogn. Sci.* **16**, 277–284. (doi:10.1016/j.tics.2012.04.004)
38. Byrne RW. 2006 Parsing behaviour: a mundane origin for an extraordinary ability? In *The roots of human sociality* (eds S Levinson, N Enfield), pp. 478–502. Oxford, UK: Berg.
39. Isler K, Christopher Kirk E, Miller JMA, Albrecht GA, Gelvin BR, Martin RD. 2008 Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *J. Hum. Evol.* **55**, 967–978. (doi:10.1016/j.jhevol.2008.08.004)
40. van Woerden JT, Willems EP, van Schaik CP, Isler K. 2012 Large brains buffer energetic effects of seasonal habitats in catarrhine primates. *Evolution* **66**, 191–199. (doi:10.1111/j.1558-5646.2011.01434.x)
41. van Woerden JT, van Schaik CP, Isler K. 2014 Brief communication: seasonality of diet composition is related to brain size in new world monkeys. *Am. J. Phys. Anthropol.* **154**, 628–632. (doi:10.1002/ajpa.22546)
42. Shultz S, Dunbar R. 2010 Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proc. Natl Acad. Sci. USA* **107**, 21 582–21 586. (doi:10.1073/pnas.1005246107)
43. Dunbar RIM, Shultz S. 2017 Why are there so many explanations for primate brain evolution? *Phil. Trans. R. Soc. B* **372**, 20160244. (doi:10.1098/rstb.2016.0244)
44. Nunn CL, van Schaik CP. 2002 A comparative approach to reconstructing the socioecology of extinct primates. In *Reconstructing behavior in the primate fossil record* (eds JM Plavcan, RF Kay, WL Jungers, CP van Schaik), pp. 159–215. Boston, MA: Springer US.
45. Barton RA. 1999 The evolutionary ecology of the primate brain. In *Comparative primate socioecology* (ed. PC Lee), p. 167. Cambridge, UK: Cambridge University Press.
46. Dunbar RIM. 1998 The social brain hypothesis. *Evol. Anthropol. Issues, News, Rev.* **6**, 178–190. (doi:10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)
47. Melin AD, Young HC, Mosdossy KN, Fedigan LM. 2014 Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. *J. Hum. Evol.* **71**, 77–86. (doi:10.1016/j.jhevol.2014.02.009)
48. Chivers DJ, Hladik CM. 1980 Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *J. Morphol.* **166**, 337–386. (doi:10.1002/jmor.1051660306)
49. Hladik CM. 1978 Adaptive strategies of primates in relation to leaf eating. In *The ecology of arboreal folivores* (ed. GG Montgomery), pp. 373–395. Washington, DC: Smithsonian Institution Press.
50. Griffin RH, Matthews LJ, Nunn CL. 2012 Evolutionary disequilibrium and activity period in primates: a Bayesian phylogenetic approach. *Am. J. Phys. Anthropol.* **147**, 409–416. (doi:10.1002/ajpa.22008)
51. Donati G, Santini L, Razafindramanana J, Boitani L, Borgognini-Tarli S. 2013 (Un-)expected nocturnal activity in 'diurnal' *Lemur catta* supports cathemerality as one of the key adaptations of the lemurid radiation. *Am. J. Phys. Anthropol.* **150**, 99–106. (doi:10.1002/ajpa.22180)
52. Fischer J, Farnworth MS, Sennhenn-Reulen H, Hammerschmidt K. 2017 Quantifying social complexity. *Anim. Behav.* **130**, 57–66. (doi:10.1016/j.anbehav.2017.06.003)
53. R Development Core Team. 2015 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
54. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
55. Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010 Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464. (doi:10.1093/bioinformatics/btq166)
56. Orme D *et al.* 2013 caper: comparative analyses of phylogenetics and evolution in R. See https://doi.org/10.1093/bioinformatics/btq166.
57. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team. 2015 Linear and nonlinear mixed effects models, R package version 3.1-122. See https://cran.r-project.org/package=caper.
58. Pagel M. 1999 The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Syst. Biol.* **48**, 612–622. (doi:10.1080/106351599260184)
59. Nunn CL. 2011 *The comparative approach in evolutionary anthropology and biology*, 380 p. Chicago, IL: The University of Chicago Press.
60. Arnold C, Matthews LJ, Nunn CL. 2010 The 10kTrees website: a new online resource for primate phylogeny. *Evol. Anthropol. Issues, News, Rev.* **19**, 114–118. (doi:10.1002/evan.20251)
61. Freckleton RP. 2002 On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J. Anim. Ecol.* **71**, 542–545. (doi:10.1046/j.1365-2656.2002.00618.x)
62. Smith RJ. 1999 Statistics of sexual size dimorphism. *J. Hum. Evol.* **36**, 423–458. (doi:10.1006/jhev.1998.0281)
63. Garcia-Berthou E. 2001 On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *J. Anim. Ecol.* **70**, 708–711. (doi:10.1046/j.1365-2656.2001.00524.x)
64. Quinn GP, Keough MJ. 2002 *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press.
65. Field A, Miles J, Field Z. 2012 *Discovering statistics using R*. London, UK: Sage.
66. Garland T. 2012 Can PGLS cope with collinearity between explanatory variables? [Internet]. [R-sig-phylo] (Online forum comment). 2012 [cited 2015 Jan 5]. Available from http://www.mail-archive.com/r-sig-phylo@r-project.org/msg02093.html.
67. Mundry R. 2014 Statistical issues and assumptions of phylogenetic generalized least squares. In *Modern phylogenetic comparative methods and their application in evolutionary biology* (ed. LZ Garamszegi), pp. 131–153. Heidelberg, Germany: Springer.
68. Akaike H. 1974 A new look at the statistical model identification. *IEEE Trans Automat Contr.* **19**, 716–723. (doi:10.1109/TAC.1974.1100705)
69. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
70. Zeileis A, Hothorn T. 2002 Diagnostic checking in regression relationships. *R News.* **2**, 7–10.
71. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
72. Pagel M, Meade A. 2016 BayesTraits Manual (V3) [Internet]. [cited 2017 May 18]. See http://www.evolution.rdg.ac.uk/BayesTraitsV3/Files/BayesTraitsV3.Manual.pdf
73. Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* **33**, 1–22. (doi:10.18637/jss.v033.i02)
74. Barton RA, Venditti C. 2014 Explosive evolution of the cerebellum in humans and other

great apes. *Curr. Biol.* **24**. (doi:10.1016/j.cub.2014.08.056)
75. Stephan H, Frahm H, Baron G. 1981 New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatol.* **35**, 1–29. (doi:10.1159/000155963)
76. Denis DJ, Legerski J. 2003 Causal modeling and the origins of path analysis. In *Annual Convention of the American Psychological Association*. Toronto, Canada: ICAAP.
77. Patterson SK, Sandel AA, Miller JA, Mitani JC. 2014 Data quality and the comparative method: the case of primate group size. *Int. J. Primatol.* **35**, 990–1003. (doi:10.1007/s10764-014-9777-1)
78. Borries C, Gordon AD, Koenig A. 2013 Beware of primate life history data: a plea for data standards and a repository. *PLoS ONE* **8**, e67200. (doi:10.1371/journal.pone.0067200)
79. Borries C *et al*. 2016 Transparency, usability, and reproducibility: guiding principles for improving comparative databases using primates as examples. *Evol. Anthropol. Issues, News, Rev.* **25**, 232–238. (doi:10.1002/evan.21502)
80. Stacey PB. 1986 Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol.* **18**, 175–187. (doi:10.1007/BF00290821)
81. Dunbar RIM. 1992 Time: a hidden constraint on the behavioural ecology of baboons. *Behav. Ecol. Sociobiol.* **31**, 35–49. (doi:10.1007/BF00167814)
82. Barton RA, Whiten A, Strum SC, Byrne RW, Simpson AJ. 1992 Habitat use and resource availability in baboons. *Anim. Behav.* **43**, 831–844. (doi:10.1016/S0003-3472(05)80206-4)
83. Ives AR, Midford PE, Garland T. 2007 Within-species variation and measurement error in phylogenetic comparative methods. *Syst. Biol.* **56**, 252–270. (doi:10.1080/10635150701313830)
84. Kudo H, Dunbar RIM. 2001 Neocortex size and social network size in primates. *Anim. Behav.* **62**, 711–722. (doi:10.1006/anbe.2001.1808)
85. Dunbar RIM, Shultz S. 2007 Understanding primate brain evolution. *Phil. Trans. R. Soc. B* **362**, 649–658. (doi:10.1098/rstb.2006.2001)
86. Barton RA, Harvey PH. 2000 Mosaic evolution of brain structure in mammals. *Nature* **405**, 1055–1058. (doi:10.1038/35016580)
87. Sayol F, Lefebvre L, Sol D. 2016 Relative brain size and its relation with the associative pallium in birds. *Brain Behav. Evol.* **87**, 69–77. (doi:10.1159/000444670)
88. Montgomery SH, Mundy NI, Barton RA. 2016 Brain evolution and development: adaptation, allometry and constraint. *Proc. R. Soc. B* **283**, 20160433. (doi:10.1098/rspb.2016.0433)
89. Moore JM, DeVoogd TJ. 2017 Concerted and mosaic evolution of functional modules in songbird brains. *Proc. R. Soc. B* **284**, 20170469. (doi:10.1098/rspb.2017.0469)
90. Carlisle A, Selwood L, Hinds LA, Saunders N, Habgood M, Mardon K, Weisbecker V. 2017 Testing hypotheses of developmental constraints on mammalian brain partition evolution, using marsupials. *Sci. Rep.* **7**, 97. (doi:10.1038/s41598-017-02726-9)
91. Barton RA. 2007 Evolutionary specialization in mammalian cortical structure. *J. Evol. Biol.* **20**, 1504–1511. (doi:10.1111/j.1420-9101.2007.01330.x)
92. Logan CJ *et al*. 2017 Beyond brain size. *bioRxiv*. (doi:10.1101/145334)