

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

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## 1 Abstract

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

17

18

## 19 Introduction

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

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

38 However, some studies have failed to find a statistical link between brain size and sociality  
39 (14,19,20,36), and apparent exceptions, in terms of large-brained but not conspicuously social  
40 taxa, suggest that factors other than sociality may have been influential (14,37,38). In  
41 particular, a recent analysis by DeCasien et al. (20) found that diet, and not social group size,  
42 correlates with brain size in primates. DeCasien et al. point to several possible explanations for

43 the correlation with diet that invoke the cognitive basis of foraging skills. Shultz & Dunbar (34)  
44 had earlier acknowledged that primate brain size correlates with diet, but argued (a) that this  
45 reflects energetic constraints on brain size rather than selection on foraging skills, and (b) that  
46 brain size correlates with sociality independently of diet. The regression models supporting the  
47 latter conclusion were based on relatively small sample sizes, and, using a larger sample size,  
48 DeCasien et al. (20) failed to find an independent effect of social group size after accounting  
49 for body size and diet, as well as for phylogenetic uncertainty. On the other hand, Shultz and  
50 Dunbar (34) incorporated a wider range of ecological variables into their model. Here we  
51 combine the strengths of these studies and evaluate the possible effects of their use of  
52 different data sets; that is, we use phylogenetic comparative analysis applied to large sample  
53 sizes, we incorporate all the key behavioural-ecological predictors examined in previous  
54 studies, and we account for phylogenetic uncertainty. Although error variance in predictors  
55 theoretically has a major impact on the results of regression analyses, and is likely to be  
56 considerable in the case of behavioural measures collated from field studies conducted by  
57 different researchers using different methods on different populations, almost nothing is  
58 known about the effects of this problem on determining the behavioural correlates of brain  
59 size. A novel feature of our study is therefore that we assess the robustness of results by  
60 replicating analyses across datasets. A lack of such robustness would have significant  
61 implications for attempts to infer selection pressures from analyses that neglect this issue.

62

## 63 [Materials and Methods](#)

### 64 [Data sources](#)

65 Brain size (endocranial volume) and body mass were obtained from previously published  
66 compilations (18,39–41). Whilst it might be argued that the SBH specifically invokes the

67 neocortex as the relevant brain structure (31–33), proponents of the SBH refer to the  
68 hypothesis as an explanation for brain size and have used both overall brain and neocortex size  
69 (33,42) arguing that brain size and neocortex size are closely related, because the neocortex  
70 comprises a large proportion of whole brain volume (34,43). Using brain size markedly  
71 increases sample sizes and statistical power. Nevertheless, we recognise that these two  
72 measures could theoretically give different results (see Discussion).

73 Two datasets on primate behavioural ecology were analysed. The first (hereafter referred to  
74 as ‘dataset 1’) is a previously unpublished dataset compiled from the literature by KI, providing  
75 updated, high quality data on primate behavioural ecology; favouring wild samples over  
76 captive, larger samples over smaller, original contributions over compilations, and more recent  
77 sources over older ones (see Electronic Supplementary Material 2 for data and sources)  
78 (18,39–41). For sexually dimorphic species (size difference > 10%), female values for  
79 endocranial volume (hereafter “ECV”) and body mass were used. For all other species, means  
80 were calculated across males and females. If available, body mass was taken from the same  
81 specimens as ECV. Otherwise, the largest available sample of wild body mass data was used.  
82 Dataset 1 includes information on diet composition (the percentage of time spent feeding on  
83 different dietary items), size of sleeping groups and of foraging groups, day ranges, and home  
84 range sizes. Dataset 2 was compiled from the literature by Nunn and van Schaik (44). It  
85 provides values for female body mass, activity period, substrate use, and diet. As body size in  
86 dataset 2 is derived only from female specimens, for comparability we also ran an analysis on  
87 dataset 1 using only female body size estimates (Electronic Supplementary Material 1 (ESM1),  
88 Table S13). Datasets 1 and 2 are not independent, as their sources overlap. Therefore, in order  
89 to test for robustness of results across strictly independent datasets, we also created subsets  
90 of the data by randomly selecting different species from each original dataset.

## 91 Selection of ecological variables

92 Five behavioural-ecological variables were selected for analysis, based on the previous  
93 literature (19,21,25,30,31,45,46): two continuous variables (home range size (ha) and social  
94 group size) and three dichotomous categorical variables: activity period (nocturnal/diurnal,  
95 substrate use (terrestrial/arboreal) and diet (folivore/non folivore). Rather than presenting  
96 quantitative estimates, Nunn and van Schaik (44) classified species' diet categories based on  
97 the food type that occupied the largest proportion of feeding time. We therefore used the same  
98 criterion to categorise diet in dataset 2. However, diet is subject to marked intraspecific  
99 variation in relation to seasonal and local differences in the relative abundance of different food  
100 types (47). Hence, categorising species' diet according to percentage of feeding time can create  
101 anomalies, in which closely related species with similar foraging niches are placed in different  
102 categories due simply to the quantitative estimates being based on insufficient or inaccurate  
103 samples. We therefore ran an additional separate analysis for dataset 1 in which folivores were  
104 more strictly defined as only those species with clear physiological specialisations for folivory  
105 (ESM1, S16) (48,49). As in previous analyses (11,23,24), diurnal species were defined as those  
106 that regularly forage and are active during the day, therefore including the few cathemeral  
107 lemurs which are more diurnal than their strictly nocturnal close relatives (50,51).

## 108 Selection of group size data

109 Dataset 2 (44) provides both 'population group size' and 'foraging group size'. The authors  
110 define population group size as "...the animals that come together frequently, usually to sleep  
111 together and among which foraging units have highly overlapping ranges." (p. 202), whereas  
112 foraging group sizes include the smaller, temporary parties or subgroups that form in response  
113 to immediate daily foraging conditions. Since the SBH relates to communities of individuals that  
114 associate habitually, we used population group size from Dataset 2. Dataset 1 (52) recorded

115 both sleeping and foraging group size. A third group size measure (“Combi Group Size”) takes  
116 the largest of the sleeping and foraging group figures. Combi Group Size therefore reflects the  
117 number of individuals who regularly associate, and is thus essentially definitionally the same as  
118 population group size from Dataset 2. We therefore used Combi Group Size in our primary  
119 analyses of dataset 1. However, we also reran the analyses with sleeping group size only (where  
120 available) and found no qualitative difference in results (see ESM1, Table S12). While group size  
121 may be a relatively indirect measure of primate social complexity (46,53), it is the one that  
122 forms the foundation of work on the SBH (31,46), and as we intended to revisit the conclusions  
123 of that work it is necessary to use the same metrics as used in those papers.

#### 124 [Statistical Analysis](#)

125 Both analyses used the same endocranial volume data; only the behavioural-ecological data  
126 differed. Dataset 1 and the R code used in this study are available in the electronic  
127 supplementary material (ESM2 and ESM3 respectively). We used phylogenetic generalised  
128 least squares regression (PGLS) to analyse the correlated evolution of the five behavioural-  
129 ecological variables and endocranial volume. Data were analysed in the R (54) packages  
130 “ape”(55), “picante”(56), “caper”(57) and “nlme”(58). Pagel’s  $\lambda$  (59) is a scaling parameter,  
131 used to scale the variance co-variance matrix according to the expected variance given a  
132 phylogenetic tree, thus accounting for the confounding effect of phylogenetic relatedness in  
133 comparative studies (60).  $\lambda$  was estimated by maximum likelihood. For the PGLS analyses, the  
134 phylogeny used was the consensus tree incorporating branch length estimates from the 10k  
135 Trees project (61). Body mass was included as a covariate in the regression to control for its  
136 effects on endocranial volume following Freckleton (62), Smith (63), and Garcia-Berthou (64).  
137 This method of body size correction is preferred over analysis of residuals as it avoids biased  
138 parameter estimates (62). Including body mass as a covariate also has the benefit of controlling

139 for any effects of body mass on other predictors, which is likely to be a particular issue for home  
140 range size. The granularity of the environment as perceived by the animal is likely to be  
141 dependent upon its size. For example, an increase of 1 hectare would likely have very different  
142 implications for a 50g mouse lemur than for an 85kg gorilla.

143 All continuous variables (endocranial volume, body mass, group size, and home range size)  
144 were log<sub>10</sub> transformed prior to analysis to satisfy the assumption of normality. Prior to the  
145 analysis, we inspected the distribution of the response and predictor variables and found them  
146 to be approximately symmetrically distributed. We inspected diagnostic plots for the model  
147 and found no evidence of violation of the assumptions of normality or homogeneity of residuals  
148 (65). Models were checked for outliers with a studentised residual with an absolute value >3  
149 (66). None were found. We checked for collinearity between predictors in our models. Although  
150 statistically significant partial correlations were present for all predictors, none were above  
151 0.67. Absolute correlations of less than .8 are deemed not to represent significant collinearity  
152 issues (67). Variance inflation factors (VIFs) (65) were less than 1.4 in all cases which further  
153 reassured us that collinearity was not a significant problem in this case (68).

#### 154 [Model comparisons](#)

155 To assess the fit of the PGLS models, we constructed models which varied in complexity; from  
156 an allometric model in which body size was the sole predictor, models including body size and  
157 each predictor alone, and then added parameters to the model according to their p value (low  
158 to high). We then compared the AIC (Akaike's Information Criterion) (69) for each model using  
159 the native "AIC" function in R (54). The AIC takes in to account the size of the sample and the  
160 number of predictors; penalising complex, over-paramaterised models (65). Lower values of  
161 the AIC indicate better fitting, more parsimonious models. We also used log likelihood ratio  
162 tests (70), run using the "lrtest" function in the lmtest package (71) in R (54).

## 163 Accounting for phylogenetic uncertainty

164 The PGLS analyses are based on a single consensus tree of the primates, but phylogenetic  
165 relationships are not known with certainty. To account for this issue and to additionally test  
166 whether this potential source of error in comparative studies has a significant impact on  
167 identifying correlates of brain size, we performed Bayesian phylogenetic regressions (72)  
168 accounting for shared ancestry by integrating over a posterior sample of 1000 primate  
169 phylogenetic trees taken from the 10k trees project website (61). We conducted these analyses  
170 using BayesTraitsV3 (73). To account for the level of phylogenetic signal in our data we  
171 estimated the tree scaling parameter  $\lambda$  (73). We used a uniform prior of -100 to 100 for all  
172 regression coefficients and a uniform prior of 0 to 1 for  $\lambda$ . We ran the analyses for 1,010,000  
173 iterations, sampling every 1000 iterations removing the first 100,000 iterations as burn-in. To  
174 determine the significance of our regression coefficients we used pMCMC values which can be  
175 interpreted in a similar way to frequentist p-values (74).

## 176 Results

### 177 PGLS

#### 178 (Table 1)

179 Table 1 presents the results of PGLS analyses on the two full datasets. In all cases  $\lambda$  was close  
180 to 1, indicating that the data are consistent with a Brownian motion model of trait evolution  
181 (75). A simple allometric model regressing endocranial volume on body size alone explained  
182 77% of the variation in dataset 1 and 73% in dataset 2. The full model (comprising all five  
183 behavioural-ecological variables) was highly significant in both dataset 1 ( $\lambda=0.99$ ,  $r^2=0.8$ ,  $p$   
184  $<0.0001$ ) and dataset 2 ( $\lambda=1$ ,  $r^2=.75$ ,  $p <0.0001$ ).

185 In dataset 1 home range size and activity period were both associated with endocranial volume  
186 after accounting for the effects of body size (positive associations between brain size and HRS

187 and diurnality respectively) ( $\lambda=0.99$ ,  $t_{6,108}=2.1$ ,  $p < 0.05$ ). The model based on dataset 2 (52) also  
188 showed a significant positive partial correlation with home range size, ( $\lambda=0.99$ ,  $t_{6,97}=2.8$ ,  $p$   
189  $< 0.01$ ), but the partial correlations with activity period did not reach significance ( $p=0.06$ ), and  
190 no other behavioural-ecological variables were significantly correlated with brain size while  
191 accounting for these effects.

## 192 (Table 2)

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

197 We next performed PGLS analyses on the datasets (i) after they had been made completely  
198 independent from each other, and (ii) after they had been reduced to include only species that  
199 appeared in Stephan et al.'s 1981 brain component volumes dataset (76). Again, results  
200 differed between the datasets and from the results reported above (see ESM1, tables S4 and  
201 S9 for full results). Folivory showed a significant negative association with brain size in  
202 independent dataset 1, whereas there were no significant predictors after accounting for body  
203 mass in independent dataset 2. Similarly, no significant associations were found in the full  
204 multiple regressions on either dataset when they were matched to the Stephan et al. (76)  
205 species list. However, because the sample sizes in these analyses were small relative to the  
206 number of predictors, we used model comparisons to determine which combinations of  
207 predictors are best supported (see below).

## 208 Model Comparison

209 To establish which combination of variables model endocranial volume best in each dataset,  
210 we employed a model comparison approach using Akaike's Information Criterion (69) and log

211 likelihood ratio tests (70). We first subjected the full datasets to model comparison (ESM1,  
212 Tables S2 & S3).

213 AIC values indicate that the model offering the best and most parsimonious explanation of  
214 dataset 1 was one which included activity period, home range size, diet and group size. (model  
215 ix, Table S2). Following Burnham and Anderson (2002) (70), an AIC difference ( $\Delta_i$ ) of less than  
216 2 was considered to indicate substantial empirical support (p. 70). The best model was  
217 therefore not a significantly better fit to the data than models vii, viii and x ( $\Delta_i < 2$ ). AIC  
218 differences between the models fitted to dataset 2 (Table S3) showed that a model containing  
219 home range size and activity period was the best fit to the data, but model vi which included  
220 only body size (the covariate) and home range size provided a comparable fit ( $\Delta_i < 2$ ). Model  
221 viii (home range size, activity period and terrestriality) also gave a comparable fit according to  
222 the  $\Delta_i < 2$  rule, but a log likelihood ratio test showed that this addition of terrestriality did not  
223 significantly improve the fit (Table S3). In summary, these results show that endocranial volume  
224 is best modelled by different combinations of variables in the two datasets. Home Range Size  
225 was consistently present in the best models ( $\Delta_i < 2$ ) across the two datasets, appearing in all  
226 seven of the best models. Group size appeared in only two of the seven best models and only  
227 when accompanied by home range size, folivory and activity period.

228 As described above, the inclusion of different species in each dataset may result in the  
229 composition of the best models varying between datasets. We therefore also subjected the  
230 species matched datasets to model comparison, as detailed in Tables S5 and S6 in ESM1.

231 The model comparisons for the species matched datasets show broad agreement with those  
232 of the non-matched, full datasets in Tables S2 and S3. The best models still consistently included  
233 home range size, appearing in every model with substantial support (i.e. where  $\Delta_i < 2$ ) save one

234 (model viii, Table S5). Group size appeared in only one of the best models, again together with  
235 home range size, folivory and activity period.

236  
237 PGLS model comparisons for the Stephan et al.(76) sample of species identified social group  
238 size as a significant predictor: in both datasets, group size and folivory were included in the best  
239 model. The addition of home range size was found not to improve the fit in either dataset  
240 (Tables S10 and S11, ESM1).

241

#### 242 [Accounting for phylogenetic uncertainty](#)

243 A Bayesian phylogenetic regression of the full datasets replicated the qualitative results of the  
244 PGLS analyses. In dataset 1, Home range size (posterior mean = 0.0247, 95%CI = 0.0241 to  
245 0.0253, pMCMC=0.0066) and activity period (posterior mean=0.1327, 95%CI = 0.1293 to  
246 0.262, pMCMC=0.0154) both had pMCMC values of less than 0.05 (Table S14), indicating that  
247 these traits are well supported (73). Home range size was the only predictor with strong  
248 support in dataset 2 (posterior mean=0.0426, 95%CI = 0.0416 to 0.0436, pMCMC = 0.0007,  
249 Table S15). Figures S14a, S14b and S15 in ESM1 show the posterior distributions of estimates  
250 of those traits that had pMCMC < 0.05.

#### 251 [Discussion](#)

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

258 This lack of robustness raises doubts about inferences from behavioural-ecological correlates  
259 of brain size based on analyses of single datasets, and may help to explain divergent results  
260 between studies. To the extent that we find stability, there is stronger evidence for correlations  
261 with ecological factors, notably home range size, than for social group size, as found in Clutton-  
262 Brock and Harvey's pioneering study (17). Our results are also broadly in line with the more  
263 recent study of DeCasien et al. (20), in finding stronger and more robust associations with  
264 ecological factors related to foraging than with social group. However, our inclusion of  
265 additional variables and datasets also reveals differences. DeCasien et al. identified frugivorous  
266 diets as the key correlate of large brain size, but did not examine home range size. In contrast,  
267 we found home range size rather than diet to be the most consistent correlate of brain size,  
268 but note that this varied between datasets, suggesting their effects are hard to separate,  
269 perhaps because diet and ranging together form an adaptive 'syndrome': more frugivorous  
270 and (less folivorous) diets are strongly associated with more patchily distributed resources and  
271 larger home ranges (44) . The manner in which diet is categorised also appears to have an  
272 impact; when only species with biological adaptations to leaf processing are classified as  
273 folivorous, diet additionally becomes a significant predictor of brain size (ESM1; S16a&b). We  
274 also found some evidence for an association between activity period and large brain size,  
275 though this effect was small and variable across datasets, the potential reasons for which we  
276 discuss below.

277 Evidence for a correlation between brain size and social group size after accounting for effects  
278 of other variables was weak. We found that this well-known correlation appears largely  
279 dependent on the particular sample of species in the Stephan dataset (76). One elaboration of  
280 the Social Brain Hypothesis accounts for dietary correlates of brain size in primates as a  
281 reflection of energetic constraints (31,34,43) . In this view, sociality selects for bigger brains

282 and diet must become more frugivorous to provide the additional energy required to meet the  
283 costs. However, this hypothesis would presumably predict stronger correlations with diet than  
284 with home range size, which we do not find. In addition, we do not find support for the claim  
285 that social group size and brain size are robustly correlated after accounting for the effects of  
286 ecological variables (34,43). We agree with Dunbar & Shultz (43) that, in principle, comparative  
287 analysis should differentiate between selection pressures and constraints, but it remains  
288 unclear how this can be achieved in practice. While path analysis has been suggested as a  
289 possible solution (31,43), it is essentially a protocol for arranging a set of regression coefficients  
290 according to some causal hypotheses; it cannot be used to discover causality from correlational  
291 data (77), it cannot solve the problem of instability across datasets, and it is as vulnerable to  
292 underlying issues with the data as are the regression analyses on which it is based. In summary,  
293 while it remains plausible that sociality is related to cognitive evolution in primates, we suggest  
294 that this can no longer be claimed on the basis of a strong or robust correlation between brain  
295 size and group size that remains after controlling for other variables.

296 Why are results unstable, and what implications does this have for using them to infer selection  
297 on cognitive abilities? We highlight three empirical issues (data quality, statistical power and  
298 intrinsic intra-specific variability) as well as theoretical difficulties with brain size as a global  
299 measure of cognitive capacities. Data quality and replicability are major issues for comparative  
300 studies because of the diversity of sources and of the methods used by different researchers  
301 to collect the primary data (78–80). Furthermore, many behaviours vary extensively within and  
302 between populations of the same species, and comparative studies routinely collapse this intra-  
303 specific variation into species-specific means. The validity of these mean values depends on  
304 the extent to which the variation has been sampled to a comparable extent across species, and  
305 on the assumption that inter-specific variation is substantial by comparison. For example, group

306 size in different populations of terrestrial or semi-terrestrial cercopithecine species varies  
307 widely, depending on habitat, reflecting facultative adjustment of behaviour to local ecological  
308 conditions. Group size in yellow baboons (*Papio cynocephalus*) was found to vary between 8  
309 and 44 within one study population (81); the contrasts between *Papio* populations or sub-  
310 species is even more marked, with estimates of group size varying approximately 20-fold (82)  
311 and of home range size approximately 100-fold (83). Phylogenetic methods which control for  
312 intra-specific variation by incorporating the uncertainty in to the error term are now available  
313 (84). Future work could exploit this development, if and when sufficient reliable data for  
314 sampling intraspecific variance become available for a large sample of species. However, this  
315 would in one sense only make the problem we have highlighted worse: the inflation of error  
316 terms that inevitably result can be expected to reduce the likelihood of finding significant  
317 correlations. The point we wish to emphasise here, however, is that current inferences in the  
318 literature about the selection pressures driving the evolution of brain size made using the  
319 standard approach of analysing single datasets appear to be unreliable. This point has  
320 important implications both for interpreting the existing literature, and for the design of future  
321 studies. Where variables are prone to measurement error and/or extensive intraspecific  
322 variation, such as is particularly likely to be the case with many behavioural variables, we  
323 recommend careful attention to data quality, testing the stability of results across datasets  
324 and/or incorporation of uncertainty in estimation of species-typical mean values.

325 In addition, statistical power is a serious issue where a range of predictors are considered with  
326 moderate or small numbers of species, as is not uncommonly the case in published  
327 comparative studies. In this situation (model overfitting) we can expect models with high  
328 coefficients of determination but poor generalizability from one dataset to another. This is a  
329 particular issue with the relatively small dataset of Stephan et al. (76), which has been the main

330 empirical foundation for the claim that social group size is the strongest predictor of brain  
331 and/or neocortex size (30,31,85,43). When datasets 1 and 2 were matched to the species in  
332 the Stephan et al. data, the best models identified by our model comparisons did include group  
333 size (ESM1, Tables S10a – S11b), in contrast with our results for the larger datasets. Hence, in  
334 accord with the suggestion of Parker that this dataset may be biased in favour of the SBH (13),  
335 we recover a clear correlation with group size only when analysis is restricted to these species.  
336 It therefore seems that the differences in patterns of correlations between studies (20,31) are  
337 at least partly due to different species sampling and/or different predictor variables, rather  
338 than simply to use of different brain measures (overall brain size versus neocortex size).

339 The fact that an effect of home range size emerges through two different types of analysis and  
340 two different (albeit not independent) datasets may make it tempting to interpret ranging as  
341 the “true” correlate of primate brain size, and to suggest, as others have done, that large brains  
342 reflect selection on spatial memory (33,86). We, however, urge caution in this respect. First, we  
343 cannot unambiguously separate the effects of home range size, diet and activity period.  
344 Second, and in our view more importantly, overall brain size does not necessarily reflect the  
345 ways in which different selection pressures acted on different neural systems (3,23,87). For  
346 example, we found evidence that diurnality is associated with larger brains, but this result was  
347 weak and lacking consistency across datasets. Evolutionary transitions between nocturnal and  
348 diurnal niches are known to correlate with the relative size of visual and olfactory brain regions  
349 (23). Crucially, visual and olfactory regions show opposite evolutionary patterns (the former  
350 being relatively large and the latter relatively small in diurnal species) , so that overall brain size  
351 fails to adequately capture the influence of sensory niche on information-processing capacities  
352 (23). In this case, the relatively weak and variable effects of activity period on overall brain size  
353 can only be interpreted by understanding the divergent responses of underlying neural

354 systems. Similarly, recent evidence reveals a striking difference in the pattern of brain  
355 component evolution in apes compared to other anthropoid primates, with increased  
356 cerebellar relative to cortical expansion in the former (75). These different neural causes of  
357 brain size variation in different clades can be presumed to have different cognitive implications,  
358 presenting a difficulty for the attempt to relate overall brain size to individual selection  
359 pressures (3) or to some general cognitive ability. While large brain regions such as the  
360 mammalian neocortex and avian pallium inevitably have a relatively strong impact on overall  
361 brain size (88), these components themselves consist of multiple functional systems that evolve  
362 in a mosaic fashion in response to different selection pressures (23,88–93). Making sense of  
363 the behavioural and ecological correlates of brain size will therefore depend on the difficult  
364 task of understanding the complex and clade-specific ways in which brain size reflects variation  
365 in specific neural systems.

366

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371 methods for LP.

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## 570 Tables

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572 Table 1: Phylogenetic Least Squares (PGLS) regressions examining the effects of five  
573 behavioural-ecological variables on endocranial volume.

Predictor	Dataset 1 (n=144)		Dataset 2 (n=104)	
	$t_{137}$	$p$	$t_{97}$	$p$
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:				
$\lambda$		.988		.997
$R^2$		.8		.75

574 Table 2: Phylogenetic Least Squares (PGLS) regressions examining the effects of five  
575 behavioural-ecological variables on endocranial volume with datasets matched for  
576 species.

Predictor	Dataset 1 (n=99)		Dataset 2 (n=99)	
	$t_{92}$	$p$	$t_{92}$	$p$
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:				
$\lambda$		.99		1
$R^2$		.81		.75

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582 **AUTHOR CONTRIBUTIONS**

583 RB and LP conceived of the project and wrote the manuscript; LP and KI collected the data; LP and RB analysed  
584 the data. All authors gave final approval for publication.

585 **DATA ACCESSIBILITY**

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

588 **COMPETING INTERESTS**

589 We declare no competing interests.

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592 **ETHICS STATEMENT**

593 Ethical approval was not required.

594