Significance of Evolutionary Lags in the Primate Brain Size/Body Size Relationship

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Abstract

Although brain size and body size co-evolves in primates, the correlation is far from perfect. This was originally interpreted as implying that evolutionary changes in brain size lag behind evolutionary changes in body size. Subsequent tests of the hypothesis, however, concluded that there is no meaningful lag. I reanalyse the original data taking socio-cognitive grades into account and show that there is, in fact, a very strong lag effect, but that the original "catch-up" hypothesis is not the explanation. Rather, the "lag" is part of an adaptive response to predation risk in which species initially respond by increasing body size, but later switch to increasing group size (with the latter made possible by a correlated increase in brain size). This adaptive response takes between 2 and 8 million years to fully implement, and is dependent on a switch to a more energy-rich diet. This trajectory can be clearly documented in the evolutionary history of fossil hominins over the past 5 My.

Key words: brain mass, body mass, group size, allometry, diet, *Homo*

Introduction

Ever since Jerison's (1973) seminal analyses, it has been known that, across mammals in general and primates in particular, brain size is correlated with body mass in an allometric power relationship. Nevertheless, there is considerable variation around the common regression line, and it was suggested that this is a consequence of a lag effect in which brain mass takes time to catch up with changes in body mass (Jerison 1973; Lande 1979; Martin & Harvey 1985; Willner & Martin 1985; Deacon 1990, 1997; Aboitiz 1996). This assumption was based mainly on the fact that body size is relatively labile, and can vary considerably even within species as a function of local environmental conditions (see for example Dunbar 1990; Bettridge et al. 2010), whereas the complex interconnectivity of brain systems means that it is likely to take longer to bring together the necessary genetic changes without disrupting functional neural systems. The fact that changes in body size clearly outstripped changes in brain size during domestication (Hemmer 1990) seemed to provide confirmation. Given this, it was assumed that, over time, brain and body size would converge back on the common allometric relationship as brain size expanded to absorb the additional energy made available by a larger body mass through the efficiencies of provided by Kleiber's Law (Kleiber 1961; Martin 1981; Schmidt-Nielson 1984).

Deaner & Nunn (1999) developed a novel method for testing the brain lag hypothesis that involved plotting the residuals of the phylogenetic contrast in brain mass regressed on the contrast in body mass against estimated date of divergence. Since body mass would always change first, and the lag would hence be directional, they predicted that the magnitude of the signed residual from the brain-to-body size allometric relationship should be positively correlated with divergence date: when body mass contrasts are constrained to be positive, 'young' nodes (i.e. recent speciation

events) would consist of species pairs with strongly negative residuals (smaller brains relative to body size), whereas older nodes (that have had more time to readjust) will approximate the allometric line. They found that, for a sample of primates, there was in fact no correlation between the two variables, either for males or for females, or when controlling for circadian rhythm, and hence concluded that there was no evidence for the lag hypothesis.

There are three problems with their analysis, however. First, it assumed that brain size is largely a function of body size, with the two being genetically linked. But if brain size and body size are genetically uncoupled, as they appear to be in primates (Lande 1979), there is no principled reason why body size should always have to change first or why brain size should subsequently to have to "catch up" with body size. That brain and body mass are not yoked in close genetic linkage is confirmed by breeding experiments showing that they can undergo independent selection, at least in the short term (Riska & Atchley 1985).

Second, it was not widely appreciated at the time that the social brain data do not in fact form an homogenous set; instead, it consists of four separate, and very distinctive, socio-cognitive (as opposed to taxonomic) grades (Dunbar 1993; Dunbar & Shultz 2021, 2023). Setting conventional regressions through data that have grades falls foul of the Simpson-Yule Paradox (a version of the Ecological Fallacy) (Simpson 1951; Dunbar & Shultz 2023). Because grades increase the error variance in the data, this has the effect of dramatically lowering the slope of conventional least squares regression – a problem that was discussed at some length during the early days of comparative analyses (Mace et al. 1981; Harvey & Clutton-Brock 1985; Harvey & Pagel 1988, 1991). Partitioning the data by grades may thus yield very different results (Dunbar & Shultz 2023).

Third, although Deaner & Nunn (1999) reported that there was no correlation between their index of residual brain size and social group size, one plausible explanation for the variability in the residuals of brain size regressed on body size is that they in fact reflect different species pursuing alternative anti-predator strategies. Large body size and large group size have long been known to be alternative strategies that primates use to reduce predation risk in order to occupy habitats subject to high predator densities (Dunbar 1988; Shultz et al. 2004; Shultz & Dunbar 2006; Shultz & Finlayson 2010). In primates at least, group size has been shown to correlate strongly with brain size, both within (humans: Bickart et al. 2011; Powell et al., 2012; Kanai et al., 2012; Kwak et al., 2018; Noonan et al., 2018; Spagna et al., 2018; Peer et al., 2021; Hyon et al., 2022; monkeys: Sallet et al., 2011; Meguerditchian et al., 2020; Testard et al., 2022) and between species (Dunbar 1998; Pérez-Barbería et al. 2007; Dunbar & Shultz 2007, 2010, 2017, 2021, 2023; Shultz & Dunbar 2007, 2010, 2022), because the cognitive demands imposed by increasing social group size in the kind of bonded societies characteristic of primates are neurally very demanding (Lewis et al. 2017; Dunbar 2018; Kiesow et al. 2020; Dunbar & Shultz 2021). (Note: the few cases claiming that brain size and group size are uncorrelated all turn out to be statistically flawed: they inadvertently tested hypotheses about constraints, not hypotheses about selection effects. For details see Dunbar & Shultz 2023.)

Here, I reanalyse the Deaner & Nunn data to determine whether a brain lag is evident if we take grades into account. I then test the hypotheses that (1) deviations in either direction from the allometric regression line are a response to high predation risk and (2) opting for larger brains (but not larger bodies) required dietary changes to meet the additional energetic costs of the additional neural tissue. Finally, I use the excellent fossil record for hominins to test this evolutionary trajectory.

Methods

It is essential to use exactly the same dataset and statistical methods as Deaner & Nunn (1999) in order to be sure that any differences in findings are due to the analysis and not to differences in the data or methods. Deaner & Nunn used the Stephan et al. (1981) primate brain dataset. Although much larger datasets are available for endocranial volume (e.g. Isler et al. 2008), Deaner & Nunn (1999) themselves rejected these, arguing (rightly) that using endocranial volume (ECV) as a proxy for brain size introduces unnecessary error variance: though well correlated, endocranial volumes are ~5% larger than actual brain size because they include space not occupied by brain tissue (Martin 1990). More importantly, their main concern was that the body mass and cranial volume data should derive from the same individuals, and only Stephan's dataset provides this. In the Isler et al. (2006) datasets, and its earlier predecessors (e.g. Clutton-Brock & Harvey 1979), ECV estimates are based on museum crania from individuals of unknown body mass, with body weights based on a mix of zoo and wild-caught specimens. Residual contrast in brain size was calculated (as Deaner & Nunn did) from the common ordinary least squares (OLS) regression of the contrast in $\log_{10}$ brain volume regressed against the contrast in $\log_{10}$ body mass (with these values as given in Deaner & Nunn 1999). The equation is:

$$\text{contrast in } \log_{10} \text{ brain} = 0.011 + 0.614 * \text{contrast in } \log_{10} \text{ body mass}$$

($r^2=0.532$, $F_{1,29}=32.9$, $p<0.001$).

Deaner & Nunn used CAIC contrasts without reference to divergence times on the grounds that they wanted to use divergence time as the independent variable in their analysis. In addition, they explicitly used only nodes that were tip comparisons (i.e. comparisons between living species); they avoided ancestral nodes at higher levels in

the phylogeny because these have to be estimated rather than being known directly. The Stephan et al. (1981) primate brain dataset yields 31 nodes for which contrasts in brain mass and contrasts in body mass are available. I therefore use the contrasts as given by Deaner & Nunn (1999). For the analysis of fossil hominin contrasts, I use ECV volumes and earliest appearance dates from De Miguel & Henneberg (2001) and body sizes from Will et al. (2017).

Deaner & Nunn (1999) used the divergence times given by Purvis (1995), which were based largely on anatomical traits and fossil dates. Since then, more accurate genetic phylogenies have become available, and I here use the genetic divergence times provided by Perelman et al. (2011). Although the two divergence estimates correlate significantly ($r=0.732$, $N=25$, $p<0.0001$), the agreement on some comparisons between taxonomically very different species (e.g. lemurines versus Old World monkeys) is poor. I did, however, also run the analysis with the Purvis dates to check whether using these made a significance difference. In the case of the hominin fossils, we are interested in the changes that have occurred since the hominin/*Pan* split (~7.0 Ma); I therefore calculated the time elapsed from 7 Ma to the appearance of the earliest member of each subsequent species in the lineage.

Group size and dietary data for individual species are from Dunbar et al. (2018) and Powell et al. (2017), respectively. Powell et al. provide an implausibly low value for the proportion of fruit in the diet for *Macaca mulatta*; I therefore substituted the corrected value given by Dunbar & Shultz (2024). To test whether predation risk is a likely driver for the brain residuals, I use terrestriality (a proxy for predation risk since terrestriality exposes primates to higher predation risk: Shultz et al. 2004; Shultz & Dunbar 2004). Contrasts were defined simply as being the same or different in terms of terrestriality score using Heldstab et al.'s (2016) 3-point categorical classification, with

further reference to the primary literature for more nuanced interpretation in cases where both species fell into the same broad category.

To determine whether the data form natural clusters, I used *k*-means cluster analysis. Inspection of the data suggests that within-genus contrasts form a distinct cluster on the left of the graph, whereas contrasts formed by comparisons of species belonging to different genera (in many cases, different families and even sub-orders) form a scatter of datapoints to the right of the graph (corresponding to deeper divergence times). To avoid confounding grade with taxonomic effects, I used as the baseline from which to calculate residuals for the cluster analysis the RMA regression for within-genus contrasts only. The RMA regression for the residual of brain size contrast regressed on body mass contrast as a function of divergence time (based on the Perelman estimates) is:

$$\text{Residual of } \log_{10} \text{ brain volume regressed on } \log_{10} \text{ body mass} =$$

$$-0.14106 + 0.017439 * \text{DivergenceDate}$$

(Spearman r=0.508, p=0.032 1-tailed).

Where a directional prediction is being tested, 1-tailed p-values are given and so indicated; all other statistical tests are 2-tailed.

Results

Fig. 1 plots the residuals for the contrast in brain mass regressed on body mass against the Perelman et al. (2011) divergence times. Essentially, these are the data as presented by Deaner & Nunn (1999). A *k*-means cluster analysis of the residuals from the RMA regression line for within-genus contrasts with $2 \leq k \leq 7$ identifies $k=5$ clusters as the optimal way to partition the data (Fig. S1). The clusters are indicated by different symbols. One cluster (the *Homo-Pan* contrast) contains just a single member. All but

two of the datapoints in the two leftmost grades (labelled II and III) are congeneric species; and all but one of the datapoints in the two rightmost grades (labelled IV and V) are comparisons between species that belong to different genera, families or suborders.

Deaner & Nunn (1999) tested for a positive relationship with time in these data. Since the regression slope did not differ significantly from b=0, they concluded that there was no evidence for any lag effect. With the Purvis divergence dates, the regression is positive but not significant (standardised β=0.101, r^2=0.010, $F_{1,23}$=0.23, p=0.316 1-tailed). However, with the updated Perelman divergence dates (shown in Fig. 1), the overall regression is in fact significant (β=0.445, r^2=0.198, $F_{1,23}$=5.68, p=0.013 1-tailed). More importantly, grades II-V have individually positive and significant or near-significant regressions. The mean correlation across the four grades is r=0.933 (r^2=0.892, β=0.936: Fisher's procedure for combining independent tests: χ^2=19.2, df=2*4=8, p=0.013, indicating a consistent underlying positive trend). Failing to take grades into account clearly results in a significant underestimate of the true regression slope, as well as the goodness-of-fit.

Two points may be noted about the distributions in Fig. 1. First, in each case, the more recent contrasts in each grade have a negative residual, while the older ones have a positive value. This suggests that species opt first for an increase in body size, and later switch to favour an increase in brain size. Second, for the two within-genus grades (II and III), the distribution of datapoints in grade II is displaced upwards compared to the distribution in grade III: in grade II, only 1/7 datapoints falls below the zero line (where brain size is what would be expected for body size), but 6/8 do so in grade III. In effect, the latter group of genera prefer the body size option whereas the former prefer the brain size option (in effect, increasing group size). The time lapse to

converge on the main diagonal is 2.0 million years for grade II and 8.6 million years for grade III. Notice the high value for the *Homo/Pan* contrast (which Deaner & Nunn chose to discount from their analysis). Its location suggests that it might represent the end-point of a separate grade whose starting point is higher than that for grade II; projecting a parallel grade line down from this datapoint would suggest a start point on the common regression line.

Note that the datapoints for grade IV typically cluster around the zero line. Given that the divergence times for these species are far older, it may be that they also initially opted for an increase in body size, but they have had more time to converge without extending beyond the common regression line. All but two of the contrasts in this grade are strepsirrhines (the other two being New World monkeys and a great ape pair, both with unusually deep divergence times). This might suggest that, unlike the anthropoids, the strepsirrhines are more likely to be constrained by a classic brain lag effect. Unfortunately, no strepsirrhines with more recent divergent dates were sampled, so it is not possible to determine how these species might have responded initially.

An increase in brain size above the common allometric regression line necessarily creates an energetic demand to fuel the additional brain growth. One solution to this is to switch to a more nutrient rich diet. Primates broadly divide into folivores and frugivores, with frugivory considered the richer diet. To test whether the switch from a body size solution to a brain size solution, Fig. 2 plots contrasts in percent of fruit in the diet against residual brain size. The regression is positive and significant ($F_{1,22}$=4.59, p=0.022 1-tailed): species with larger than expected brains were more likely to be frugivorous. I then compared the percentage of fruit in the diet for species contrasts whose brain size residuals were positive or negative (Fig. S2). Overall, the difference is not significant (t_{22}=1.06, p=0.151 1-tailed). However, most strepsirrhines

are insectivorous and belong to a smaller-brained sub-order than haplorrhines. Excluding these yields a significant difference (t_{16}=2.05, p=0.029 1-tailed). Thus, when anthropoids opted for an increase in brain size, a change in diet to a more nutrient-rich regime was required.

Deaner & Nunn (1999) tested for a relationship between social group size and residual brain size, but found none. However, using more up-to-date data on species mean group sizes from Dunbar & Shultz (2018) yields a highly significant positive correlation (Fig. 3: r=0.612, p=0.005). All three grades with N>3 exhibit individual positive slopes (r=0.806, p=0.015; r=0.410, p=0.312; r=0.724, p=0.052; Fisher's procedure: χ^2=16.64, df=6, p=0.011, indicating a consistent positive trend across all three samples). Note that two of the squares (grade V) lie well off-diagonal, which usually indicates a grade shift. The higher one (datapoint 2) represents a contrast between *Piliocolobus* (an Old World monkey) and *Leontopithecus* (a New World monkey) and indicates a shift between a highly social and a much less social grade (*sensu* Dunbar & Shultz 2021) as well as a distant taxonomic separation. The lower datapoint 3 is a contrast between two very distantly related strepirrhines (*Daubentonia* and *Avahi*). For present purposes, and to be conservative, I followed Deaner & Nunn in assigning a group size of N=1 to *Daubentonia*. However, there are good grounds for believing that this species actually lives in dispersed communities of N≈8 (Dunbar & Shultz 2023). If their correct group size is anywhere close to 8, this would place this contrast very close to the star (*Homo-Pan* contrast), yielding an improved overall linear fit (r^2=0.622, p=0.004).

Fig. 4 tests the hypothesis that the underlying driver for this effect is predation pressure, using terrestriality as a proxy for predation risk. For contrasts where there is no difference in terrestriality, residual brain size values cluster around 0 (brain size in

line with body size), but where one species is more terrestrial residual brain size is positive (larger brains) for the large-bodied species and negative (larger bodies) for the small-bodied species, with the latter difference being significant (t_{21}=2.61, p=0.016). This suggests a divergence in strategies as a function of body size.

Deaner & Nunn (1997) implicitly assumed a causal relationship in which changes in body size drive changes in brain size, with changes in group size implicitly being a default by-product of changes in brain size. A path analysis of the relationships between the three variables (based on significant standardised slopes in multiple regressions with each variable in turn as the dependent) yields a best fit model in which brain size is correlated independently with body size and group size, and no relationship between body size and group size (Fig. 5). Importantly, mediation analyses for the six possible threeway causal pathways indicate that the only significant pathway is group size predicting brain size, and brain size predicting body size (Sobel test: p=0.028); none of the other alternatives are significant (p≥0.103).

The hominin lineage is one of the few cases where the fossil record allows us to trace this evolutionary pathway. *Homo* derives from an ape-like australopithecine root with a body size indistinguishable from that of modern *Pan* (Fleagle 2013). Fig. 6 shows that, early on, australopithecines undertook an initial move towards relatively larger body size (with residuals at or below the common primate regression line), and then, once the more nomadic early *Homo* began to occupy increasingly open (high risk) environments from around 2 Ma, they underwent an increasingly rapid increase in relative brain size towards the position modern humans now occupy (the star symbol on Fig. 1). This correlates closely with a dietary shift towards a more nutrient rich meat-based diet from ~2.0 Ma, initially as scavenging in early *Homo* and later in the form of active hunting among archaic and modern humans from ~0.5 Ma. Notice that the

earliest australopithecines, representing the earliest phase of grade I, sit on the common regression line, just as Fig. 1 predicts they should.

Discussion

Although the data do not support the original brain lag hypothesis, thus confirming Deaner & Nunn (1999, nonetheless changes in body size do seem to precede changes in brain size. However, the subsequent increase in brain size does not involve simple convergence on equilibrium brain/body ratios in the way the brain lag hypothesis implied. Instead, at least in anthropoid primates, it involves continued increases in brain size beyond the main diagonal to a point where brain size is stably larger than expected for body size. There are grades present in this relationship that seem to represent a ratcheted shift towards increasingly large brains. These grades are not taxonomic in origin; they do, however, map closely onto the socio-cognitive grades identified by Dunbar & Shultz (2021). This result thus confirms the earlier finding that grades within the social brain dataset represent increasing stepwise emphasis on neurally expensive socio-cognitive skills.

These trends in the brain/body relationship seem to be driven by a response to heightened predation risk. Although primates exploit both large body size and large group size as anti-predator strategies (Shultz et al. 2004; Shultz & Dunbar 2006; Shultz & Finlayson 2010), they face a particular problem in the latter respect: the bonded nature of primate social groups (Dunbar & Shultz 2011, 2021; Dunbar 2024) means that stable changes in group size are difficult to effect because the personalised relationships that underpin these groups involve complex neural pathways (Dunbar 2024). In other words, increases in body size are easier to effect, and hence invariably appear first. Once in place, however, they seem to provide an energetic platform that

generates enough spare capacity derived from savings of scale via Kleiber's Law to allow species to invest in larger brains. When combined with switches to a more nutrient-dense diet, this allows brain size to break through the brain/body size equilibrium threshold, allowing larger much groups to evolve. This trajectory is well illustrated by the historical changes in relative brain size in fossil hominins (Fig. 6).

Two important features of this process are worthy of note. First, the way the grades in Fig. 1 are staggered suggests a ratcheted effect in which the earliest transitions were largely forced to emphasise body size over brain size, whereas later transitions were able to build on changes already in place to catapult themselves onto a higher cognitive plane in which group size replaces body size as the main anti-predator strategy. Second, the switch from large body size to large brain size appears to take place over a much longer time period than we might expect for most anatomical changes. In the two within-genus grades (II and III), this switch is distributed over periods of 2 and 8 My (Fig. 1). This suggests that, as species sought to extend the range of ecological niches they could occupy, there was a form of directed evolution in response to specific selection pressures which had to act against considerable evolutionary inertia (represented by the costs involved in both the energetic demand of larger brains and the need for considerable internal neural restructuring). Fig. 1 perhaps suggests that each later grade shift was able to achieve a higher by exploiting the progressive reorganisation achieved in the preceding grade. Note that these did not, however, necessarily involve conventional taxonomic divisions. Rather, there seems to have been independent, parallel advances in several taxonomic lineages.

Thus, contrary to Deaner & Nunn's (1997) claim that there is no brain lag effect, there was in fact a positive direction of change over time. However, this is not due to brain size "catching up" with body size. Instead, it reflects a continuum in which species

initially increase body size in order to manage increasing predation risk, and then switch to exploiting the benefits of group size once they can increase brain size sufficiently to exploit the cognitive mechanisms needed to enable cohesion in large, bonded social groups. The mediation analyses in Fig. 5 seem to suggest that, if anything, once the brain size/group size regime takes over, it drags body size along with it – presumably as a partial solution to the problem of fuelling the energetic cost of a larger brain. This would not be evident in Fig. 1 because body size is held constant by the use of residuals: we can only gauge relative body size, not absolute body size. One implication of this decoupling of brain and body size, especially among the larger-bodied species (as Lande 1979 noted), means that the conventional use of relative brain size in many analyses may be seriously misleading (see also Kronmal 1993; Friedman & Wall 2005; Rogell et al. 2020; Smeele 2023).

Lande (1979) examined the brain-to-body size relationship across mammals in order to evaluate the evolutionary coupling between these traits. He argued that the genetic correlation between brain and body size in primates is unusually weak compared to other mammalian orders. More importantly, he found that the variance in the primate allometric relationship increases with body size, suggesting that the two become progressively decoupled as body size increases (see also Gonzalez-Voyer et al. 2009; Hager et al. 2012; Smaers et al. 2012). This might explain how brain size escapes from the energetic constraint imposed by body size in species with large body sizes (mainly those in grades I and II in Fig. 1). What may have been critical in facilitating this seems to have been a shift to more nutrient-rich (i.e. frugivorous) diets, itself dependent on being able to cope with longer day journeys since edible fruits are more sparsely distributed than leaves (Dunbar 1988; Dunbar et al. 2009).

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Legends to Figures

Fig. 1. Residuals of the contrasts in $\log_{10}$ brain mass regressed on contrasts in $\log_{10}$ body mass, plotted against time of divergence for the species pairs. A *k*-means cluster analysis indicates that the data form five distinct grades (indicated by the different symbols and Roman numerals by their respective OLS regression lines). Star: grade 1 (*Homo-Pan*); filled circles: grade 2 (within-genus contrasts); grey circles: grade (within-genus contrasts); unfilled circles: grade 4 (between-genus contrasts); squares: grade 5 (between-family contrasts) (1: *Aloutta/Lagothrix*; 2: *Piliocolobus/Leontopithecus*; 3: *Daubentonia/Avahi*).

Fig. 2. Contrast in percent fruit in diet plotted against residual of contrast in $\log_{10}$ brain volume from contrast in $\log_{10}$ body mass. Dashed line (OLS): ordinary least squares regression; solid line (RMA): reduced major axis regression. Symbols as for Fig. 1.

Fig. 3. Contrasts in $\log_{10}$ mean group size plotted against residual of contrast in $\log_{10}$ brain mass regressed on contrast in $\log_{10}$ body mass. Symbols as for Fig. 1. Regression lines are for grades II (solid line), III (dashed line) and IV (dotted line), as defined in Fig. 1.

Fig. 4. Residuals in the contrasts in $\log_{10}$ brain size regressed on $\log_{10}$ body size as a function of the relative degree of terrestriality. Dashed horizontal line indicates residual = 0 (brain size is directly proportional to body size). Symbols as for Fig. 1.

Fig. 5. (a) Path analysis of the functional relationships between contrasts in $\log_{10}$ brain mass, contrasts in $\log_{10}$ body mass and contrasts in $\log_{10}$ social group size, based on multiple regressions for each in turn as the dependent variable. The numbers adjacent to the arrow heads are the standardised slopes (ßs) in each direction (where the adjacent arrowhead specifies the dependent variable). Solid lines indicate significant predictors; dotted lines indicate non-significant predictors. (b) Sobel tests of mediation analyses for all six possible causal (i.e. directional) sequences, and for bivariate regression between contrasts in brain size and contrasts in group size.

Fig. 6. Residual of hominin/*Pan* Log_{10} contrast in brain volume regressed on Log_{10} contrast in body mass for individual fossil hominin species, plotted against time since *Homo/Pan* divergence at ~7 Ma. The modern human datapoint is the *Homo/Pan* contrast from Fig. 1; the increase in residual brain size compared to fossil *Homo sapiens* is due to a marked reduction in human body size in modern populations. Dating is to midpoint of species time span. For this analysis, brain volume is ECV, which will overestimate actual brain volume by ~5%. Unfilled symbols: australopithecines; filled symbols: *Homo*. Solid line: grade II regression line, with the dashed line giving the upper 95% CI around the regression (from Fig. 1); dotted line: common primate regression. AMH: fossil anatomically modern humans, dating to ~100 ka.

Figure 1

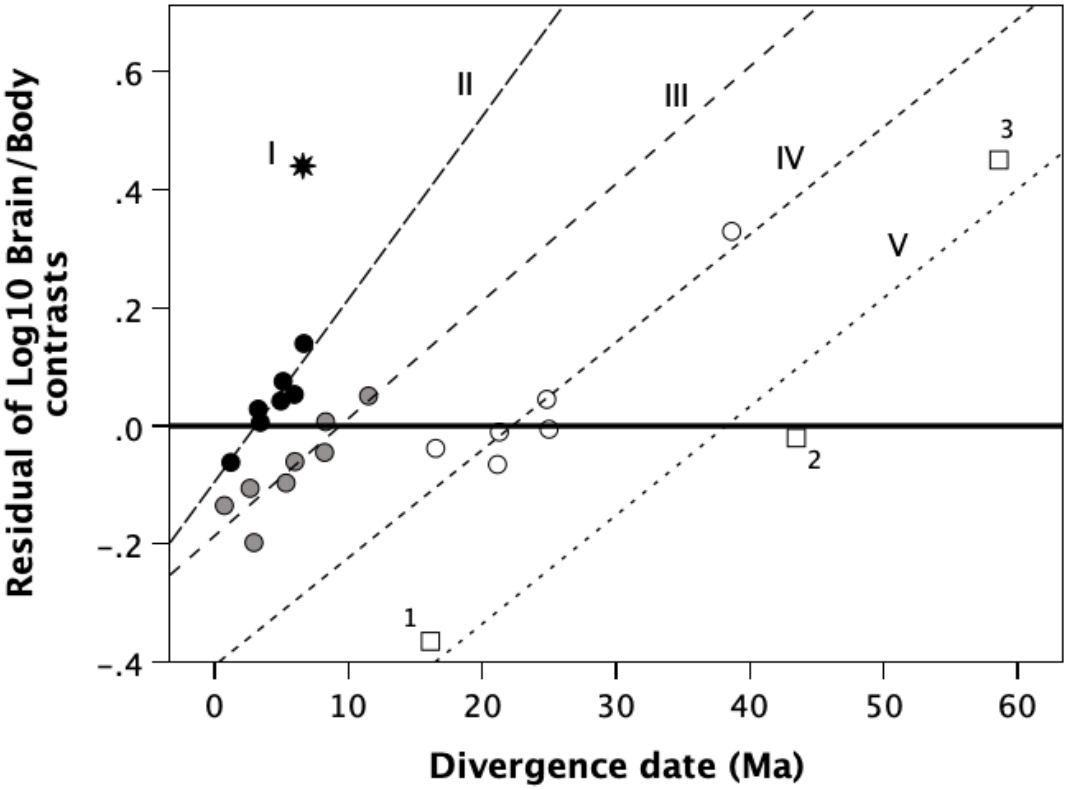

Residual of Log10 Brain/Body contrasts
.6
.4
.2
.0
−.2
−.4
0
10
20
30
40
50
60
Divergence date (Ma)
I
II
III
IV
V
1
2
3

Figure 2

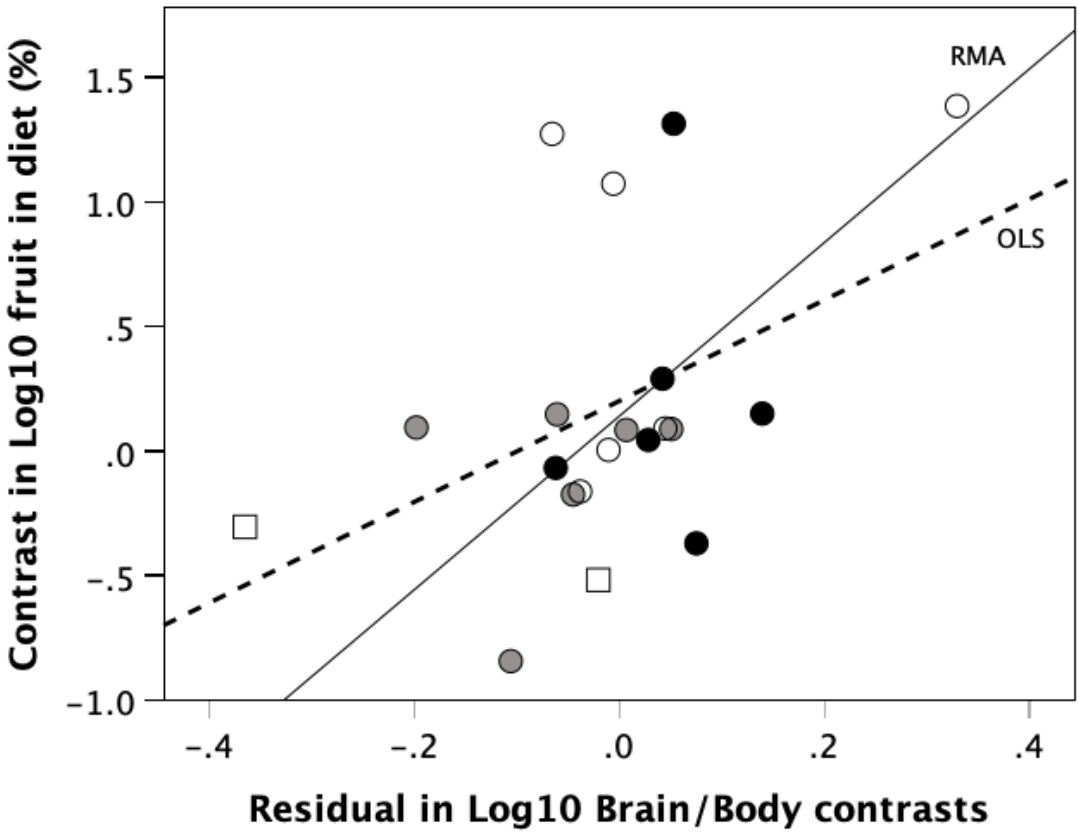

RMA
OLS
1.5
1.0
.5
.0
−.5
−1.0
−.4
−.2
.0
.2
.4
Contrast in Log10 fruit in diet (%)
Residual in Log10 Brain/Body contrasts

Figure 3

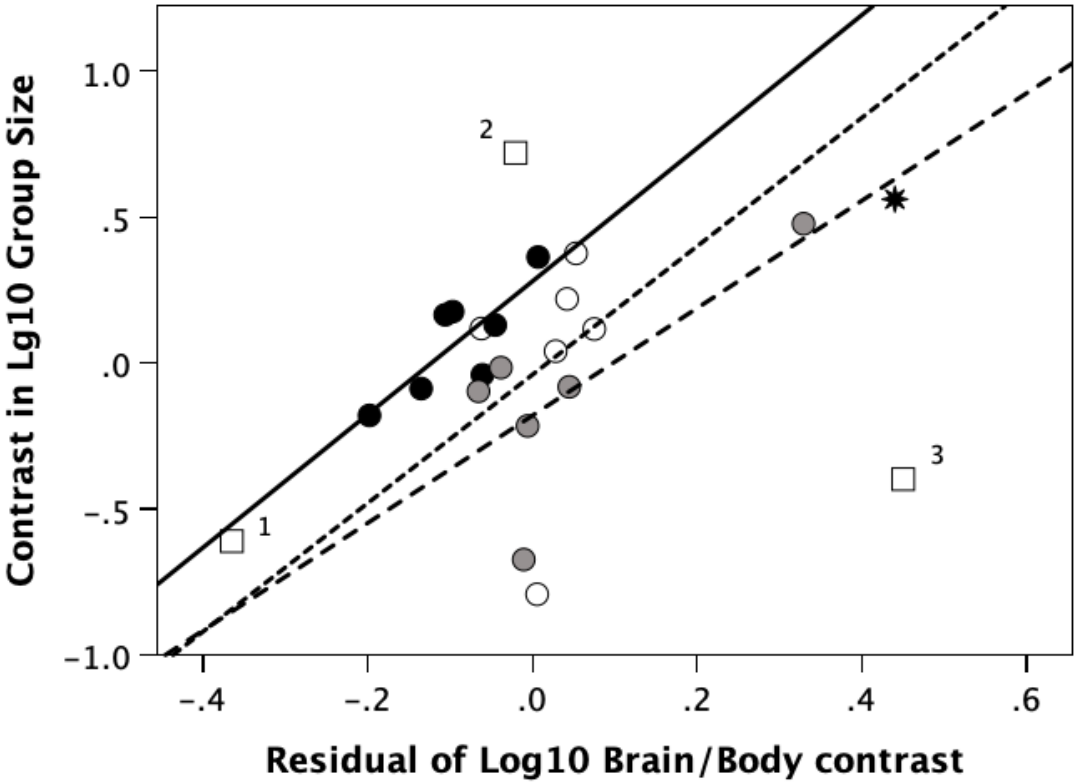

Contrast in Lg10 Group Size
1.0
.5
.0
-.5
-1.0
-.4
-.2
.0
.2
.4
.6
Residual of Log10 Brain/Body contrast
1
2
3

Figure 4

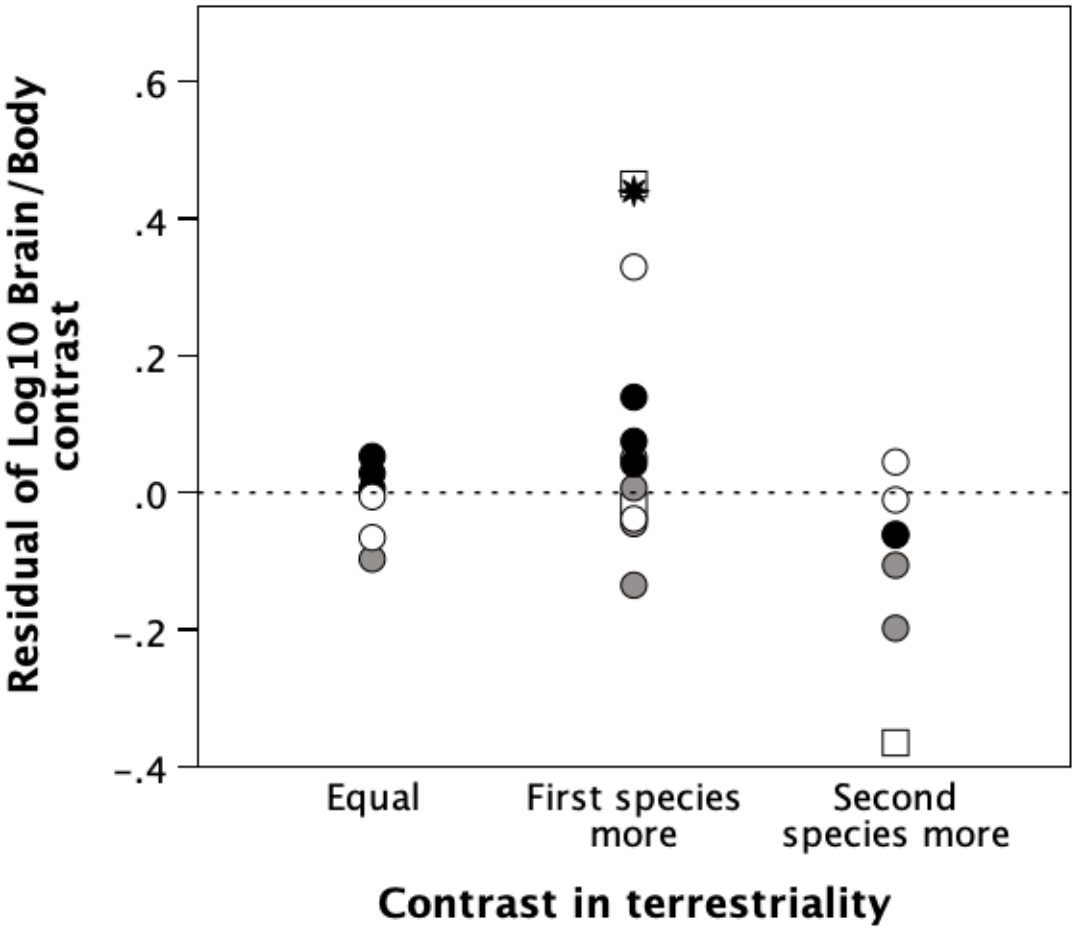
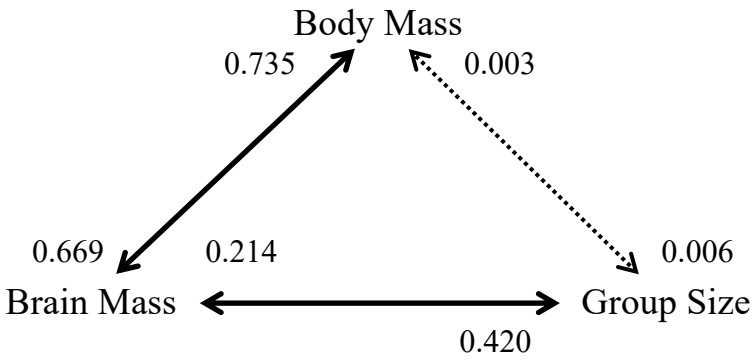

Residual of Log10 Brain/Body contrast
.6
.4
.2
.0
-.2
-.4
Equal
First species more
Second species more
Contrast in terrestriality

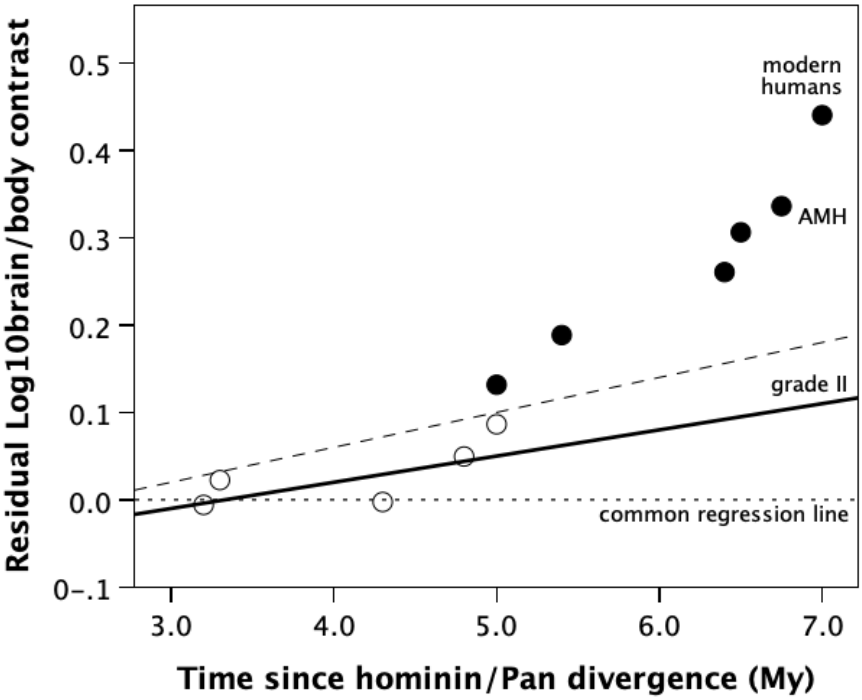
Figure 5



Sobel tests for Mediation Analyses:

Brain↔Group: p=0.022
Brain→Body→Group: p=0.984
Brain→Group→Body: p=0.981
Body→Brain→Group: p=0.123
Body→Group→Brain: p=0.282
Group→Brain→Body: p=0.028
Group→Body→Brain: p=0.103

Figure 6


Residual Log10brain/body contrast
0.5
0.4
0.3
0.2
0.1
0.0
0-.1
3.0
4.0
5.0
6.0
7.0
Time since hominin/Pan divergence (My)
modern humans
AMH
grade II
common regression line

Significance of Evolutionary Lags in the Primate Brain Size/Body Size Relationship

R.I.M. Dunbar

Supplementary Information

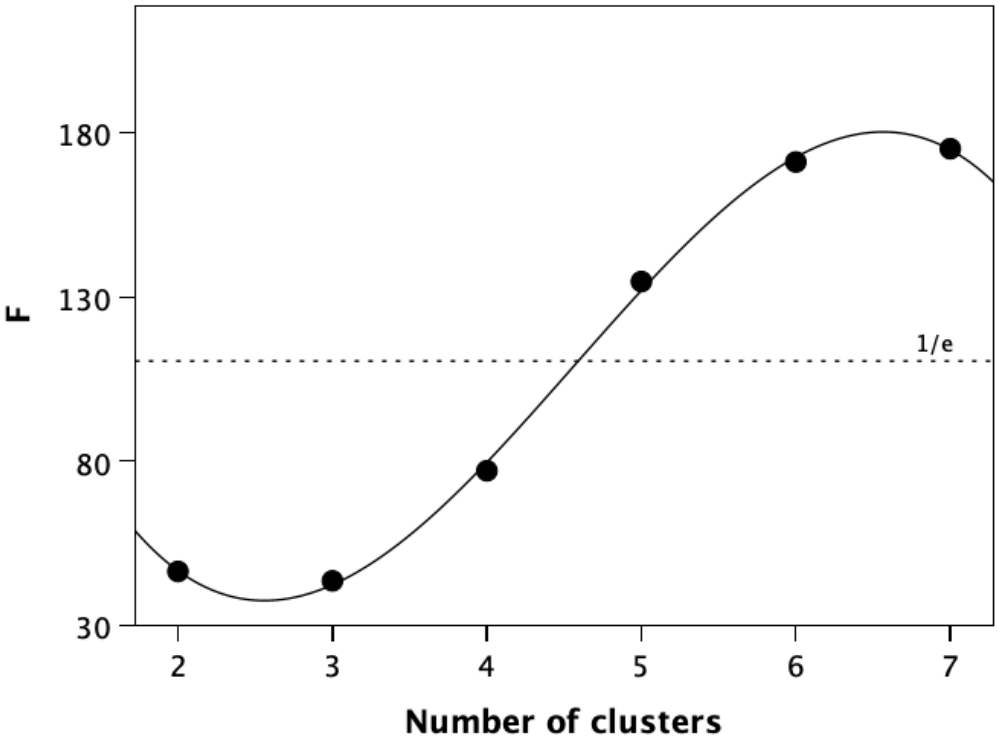


Figure S1. Goodness of fit (indexed by F-value) for number of clusters in a *k*-means cluster analysis. The dotted line demarcates the point of inflexion (1/eth down from the asymptote) that identifies the optimal number of clusters that maximises fit while minimising partitioning of the data.

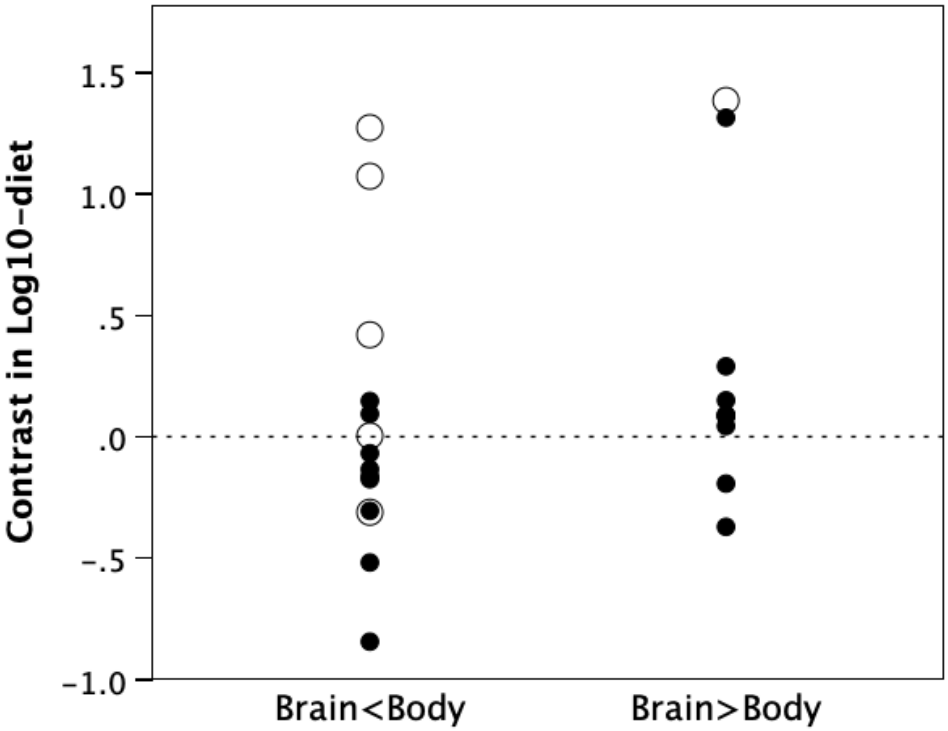


Figure S2. Contrast in $\log_{10}$ percentage of fruit in diet for species where residual brain size is negative (brains are smaller than predicted for body size) versus those where it is positive (brains are larger than predicted). Filled symbols are haplorrhines; unfilled symbols are strepsirrhines.