PROCEEDINGS
OF
THE ROYAL
SOCIETY B

Proc. R. Soc. B (2012) **279**, 715–721
doi:10.1098/rspb.2011.1311

Dietary quality and encephalization in platyrrhine primates

Kari L. Allen* **and Richard F. Kay**

Department of Evolutionary Anthropology, Duke University, Durham, NC 27708, USA

The high energetic costs of building and maintaining large brains are thought to constrain encephalization. The 'expensive-tissue hypothesis' (ETH) proposes that primates (especially humans) overcame this constraint through reduction of another metabolically expensive tissue, the gastrointestinal tract. Small guts characterize animals specializing on easily digestible diets. Thus, the hypothesis may be tested via the relationship between brain size and diet quality. Platyrrhine primates present an interesting test case, as they are more variably encephalized than other extant primate clades (excluding Hominoidea). We find a high degree of phylogenetic signal in the data for diet quality, endocranial volume and body size. Controlling for phylogenetic effects, we find no significant correlation between relative diet quality and relative endocranial volume. Thus, diet quality fails to account for differences in platyrrhine encephalization. One taxon, in particular, *Brachyteles*, violates predictions made by ETH in having a large brain and low-quality diet. Dietary reconstructions of stem platyrrhines further indicate that a relatively high-quality diet was probably in place prior to increases in encephalization. Therefore, it is unlikely that a shift in diet quality was a primary constraint release for encephalization in platyrrhines and, by extrapolation, humans.

Keywords: expensive tissue; New World monkeys; human brain size evolution; phylogenetic comparative methods

1. INTRODUCTION

Primates are notable among mammals for having relatively large brains. A number of selective mechanisms have been proposed to explain primate encephalization and to account for variation in encephalization within the order. These hypotheses centre upon benefits for cognitive and social strategies [1–7], or on the demands of obtaining various dietary components [8–14]. More proximate adaptive scenarios involve diurnal living [3] and accompanying changes in visual acuity [15,16]. Diet quality has long been suspected to play a role in brain size evolution, as species consuming higher levels of fruit or animal matter often have larger brains than those whose diets require more digestive processing (e.g. diets high in structural carbohydrates) [9,17,18]. While many researchers have focused on the challenges of locating, choosing and extracting food as driving selective mechanisms for encephalization [8,19], others have focused on mechanisms that have ameliorated metabolic constraints on brain size [20–26]. Aiello & Wheeler's 'expensive-tissue hypothesis' (ETH) proposes that encephalization was enabled via the release of energetic constraints on brain tissue growth [20–22].

Large brains are metabolically expensive, and primates expend a larger percentage of their energy budget in growing and maintaining brain function than do most other mammals [13,22,27,28]. Paradoxically, this incremental metabolic cost has not resulted in a markedly higher resting metabolic rate (BMR) [13]. ETH was proposed to explain the marked encephalization of humans in the absence of elevated BMRs. Aiello & Wheeler [22] propose that an increase in brain tissue is compensated for by the reduction of another metabolically expensive tissue, the digestive tract [20–22]. It has recently been emphasized that tissue reduction is just one possible energy trade-off mechanism for encephalization. The broader 'expensive brain hypothesis' emphasizes that the energetic costs of encephalization may be offset by energy allocation to 'maintenance' (expensive tissues including the gut but also of musculature) or 'production' (growth and reproduction) [23–25].

Gut size reduction appears to have been a plausible constraint release in human encephalization, especially when coupled with the use of cooking to enhance digestibility [20–22,29], however, the extent to which it explains interspecific variation in primate brain size has not been widely explored. Direct testing of the hypothesis in nonhuman primates has been hampered by a paucity of high-quality data on gut mass. The predictions of ETH may be tested in another way by analysing the relationship between diet quality and brain size [18]. The hypothesis posits that a small gastrointestinal tract is a proxy for a relatively high diet quality ([22], p. 207). Small guts are characteristic of animals with a high-energy diet, one low in structural carbohydrates and high in fat, protein, and simple carbohydrates [30–32]. ETH predicts that a high-quality diet releases metabolic constraints on brain size, when encephalization is selected by other factors. The predictions of ETH across primates would be supported if the following criteria are met: (i) relatively large-brained species should exhibit correspondingly high-quality diets and (ii) species with low-quality diets should be energetically constrained from marked encephalization. Notably, however, a species with a high-quality diet need not necessarily be encephalized,

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* Author for correspondence (kari.allen@duke.edu).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2011.1311 or via http://rspb.royalsocietypublishing.org.

Received 22 June 2011
Accepted 21 July 2011

because ETH is formulated as a releasing mechanism, not a driving factor in encephalization.

Sailer *et al.* [33] devised a method for quantification of dietary quality (DQ) by weighting percentages of dietary composition by their relative volume, nutrient density and digestibility. Conversion of categorical percentages (per cent of consumed leaves, fruit and animal matter) from the comparative literature of primate ecology into a measure of energy input allows broad comparisons of diet quality with body size and brain size. Fish & Lockwood [18] report a significant positive correlation between relative brain size and DQ in a broad sample of primates after controlling for allometric and phylogenetic effects. Their results broadly support ETH, but their dataset crosses several clades of differing overall encephalization. It remains to be seen whether the correlation is significant within a densely sampled taxon—a limitation we address here with a more phylogenetically constrained and extensively documented clade, the New World monkeys (Platyrrhini).

Extant platyrrhines are an ideal focus group for such a study. Platyrrhini is a diverse group of 16 genera and more than 100 species. The phylogeny is tightly constrained by molecular data at the genus and in most cases, species level. Moreover, the range of relative endocranial volume (ECV) exceeds that of any other clade of extant primates, excluding Hominoidea [34]. Finally, platyrrhine diets are extensively documented from long-term field studies in a variety of habitats and seasons.

2. MATERIAL AND METHODS

(a) *Variables*

Species mean brain size is taken from published ECVs from Isler *et al.* [34]. The Isler *et al.* dataset include associated body masses (BM1) for many of the measured crania. For those species that did not have associated body weights, published mass estimates were supplemented from other sources [35–37]. A second independent source for platyrrhine body masses (BM2) was taken from Smith & Jungers [38]. Species body mass estimates were calculated as the average between the reported male and female weights (data in the electronic supplementary material). The raw data for DQ calculations were gathered from diet composition, reported in the literature. DQ was calculated following the equation proposed by Sailer *et al.* [33]:

$$\mathrm{DQ} = s + 2r + 3.5a,$$

where s is the percentage of structural plant parts (leaves and stems), r is the percentage of reproductive plant parts (fruits, seeds, flowers, nectar and gums) and a is the percentage of animal matter in the diet, and $s + r + a = 100\%$. The constants 2 and 3.5 reflect the assumed relative energetic values per unit mass of these three dietary categories. Measured in this way, DQ scores range from 100 to 350. Higher DQ values represent a higher 'quality' (e.g. more energetically rich and more easily digestible) diet. DQ was calculated for 16 genera and 37 species of platyrrhines, from 67 published sources (see electronic supplementary material). The mean DQ for each species was calculated as the average of reported scores from all sites recorded in the literature.

(b) *Analysis*

All raw variables were log transformed (base 10) prior to analysis. Previous studies suggest that DQ is correlated to body size, such that larger bodied primates tend to be folivorous (low-quality diet), while small-bodied primates gain their protein from insectivory (higher diet quality) [18,33,39]. ECV is known to scale with negative allometry [34,40–43]. Both ECV and DQ were size-adjusted through the use of residuals. Statistics computed on biological data run the risk of non-independence of data points, owing to the similarity in species characteristics as a result of common ancestry [44,45]. The parameter λ is a measure of phylogenetic signal in the data, where λ ranges from 0 to 1, with 1 indicating a strong phylogenetic signal [46]. A phylogenetic generalized least-squares (PGLS) analysis where $\lambda = 0$ is analogous to a non-phylogenetic least-squares regression. Raw variables used in this analysis (logECV, logBM1, logBM2 and logDQ) produce λ values that do not differ significantly from 1, indicating a strong underlying phylogenetic signal in the data. Thus, to control for the effects of phylogenetic signal in the data, residual ECV and residual DQ are calculated from PGLS regressions of each variable on BM1 or BM2, in the 'caper' package of the software program 'R' [47,48]. Residuals themselves also contain phylogenetic signal, and as such the relationship between residual ECV and residual DQ was subsequently examined using PGLS. For comparison of our results, we also present non-phylogenetic least-squares regression analyses in the electronic supplementary material. When performing a correlation analysis of two residuals, the use of the same control variable in the calculation of both residuals may lead to an increase in type I error rates [49,50]. One way to account for this problem is to use independent sources for the control variable, in this case body mass [51]. For this analysis, we used species average body mass estimates from the Isler *et al.* [34] database (BM1) to calculate ECV residuals, and mean body masses from the Smith & Jungers [38] (BM2) database to calculate the DQ residuals. Independent estimates of body mass were not available for two species (*Cacajao calvus* and *Brachyteles arachnoides*). The Smith & Jungers [38] estimate was used in both residuals for these species. We also calculated ECV residuals using the Smith & Jungers dataset, and compared the results with those obtained from the independent body mass estimates.

Published molecular phylogenies of platyrrhines are in general agreement. They differ, however, in the phylogenetic placement of Pitheciidae (sister to all other platyrrhines versus sister to Atelidae) and the genus *Aotus* (sister to *Cebus*/*Saimiri* versus sister to Callitrichinae) [52–56]. To test the effects of these phylogenetic uncertainties on the results of the PGLS analysis, all analyses were run on three separate trees, reflecting variation in opinions about pitheciid and *Aotus* affinities (electronic supplementary material, figure 1). Trees 1 and 2 use genus-level divergence dates from Opazo *et al.*'s [53] maximum-parsimony tree and maximum-likelihood tree, respectively. Resolution of the tree at the species level was achieved from a consensus view of evidence from morphological intrageneric studies [54,57–61]. Tree 3 is taken directly from Perelman *et al.* [54], which is resolved to the species level with associated branch lengths. The availability of diet composition data has resulted in over-representation of some genera (in terms of number of species) and under-representation of others. As such, data were analysed at both the species and genus levels. Maximum-likelihood-based ancestral character states were reconstructed for non-phylogenetically derived relative ECV and raw DQ values, using the 'APE' package in 'R' [62].

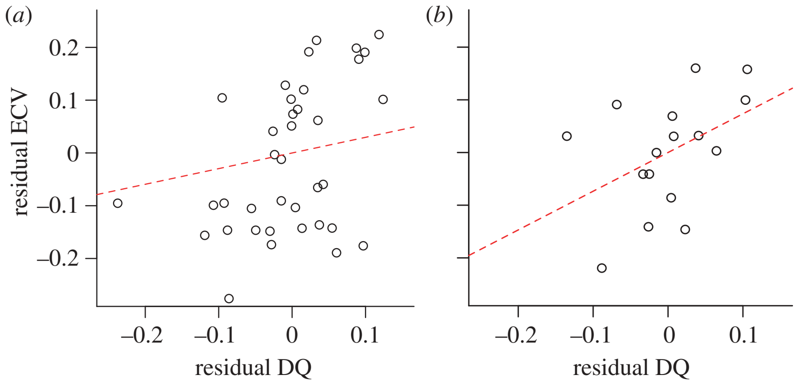

Figure 1. Phylogenetic generalized least-squares (PGLS) regression of residual endocranial volume (ECV) versus residual diet quality (DQ) at the (*a*) species and (*b*) genus level.

Table 1. Results for phylogenetic generalized least-squares (PGLS) regressions of brain size, body size and diet quality.

	level of analysis	slope	intercept	r^2	p-value
logECV versus logBM1	species ($n = 37$)	0.66	−0.65	0.74	<0.01
	genus ($n = 16$)	0.75	−0.91	0.94	<0.01
logDQ versus logBM2	species ($n = 37$)	−0.06	2.47	0.05	0.19
	genus ($n = 16$)	−0.10	2.62	0.44	<0.01
residual ECV versus residual DQ	species ($n = 37$)	0.29	0	0.03	0.26
	genus ($n = 16$)	0.73	0	0.02	0.08

3. RESULTS

Results for the PGLS analyses are the same irrespective of which among the three platyrrhine phylogenies is used. Therefore, we present the results from tree 1 only, which places pitheciids as sister to other platyrrhine families and *Aotus* as sister to *Cebus*/*Saimiri*. Preference is given to this phylogeny owing to its concordance with genetic ‘Alu’ data, which demonstrate low risk of homoplasy [63]. Results for trees 2 and 3, as well as the raw data and residuals are presented in the electronic supplementary material.

PGLS regression results are presented in table 1 and figure 1. As expected from previous work, logECV and logBM1 are strongly correlated with a negatively allometric slope of 0.66 for the species-level and 0.75 for the genus-level data. In general, diet quality declines with increasing body mass, however, a significant but weak correlation between logDQ and logBM2 occurs only at the genus level (slope $= -0.10$, $p = 0.0048$, $r^2 = 0.44$). Notably, we do not find a significant correlation between residual ECV and residual DQ at either the genus ($p = 0.08$) or species level ($p = 0.26$). Use of residuals for ECV and DQ computed from the same control variable (BM2 from Smith & Jungers [38]) resulted in slightly different p-values, but did not create any ‘false positives’ when compared with analyses using independent control variables.

Maximum-likelihood-based ancestral character state reconstructions for raw DQ values and non-phylogenetically calculated relative ECV values for tree 1 are depicted in figure 2. The root node for crown platyrrhines was reconstructed as having a diet quality of 197 (95% confidence interval = 181.8–213.2), and a relative ECV that is 0.2 per cent greater than that predicted by an ordinary least-square regression of extant platyrrhine species (95% confidence interval = −13.2 to 13.6%). These values are comparable with those of moderately encephalized extant frugivores *Pithecia* and *Ateles*.

4. DISCUSSION

We acknowledge that DQ, as calculated by the formula of Sailer *et al.* [33] is a crude measure of the energetic resources ingested by platyrrhines. For example, within the category of structural plant parts, resources differ in energy content and digestibility: considerable variation occurs in the proportions and kinds of structural carbohydrates (some of which are indigestible) and the types and concentrations of secondary compounds that might depress digestibility. Furthermore, even if the diet quality index is a useful measure for broad comparative studies, it may obscure the finer details of short-term fluctuations in resource availability that may in turn affect development and maintenance of brain function. For example, *Cacajao* feeds almost exclusively on reproductive plant parts throughout the year, yielding a stable diet quality value for this species; however, this masks marked fluctuations in the contribution of soft fruit, hard fruit, seeds and flowers, according to seasonal availability [64]. By contrast, *Alouatta* exhibits high seasonal variation in DQ, at least in some environments [65–67]. In spite of the above caveats, the availability of data on diet composition and the persistent and widespread categorization of food types as fruit, leaf and animal matter in the literature make DQ the only currently feasible comparative measure for capturing the broad strokes of relative diet quality.

(a) *Diet quality and body size*

Diet quality tends to decrease with increased body size among platyrrhines, although the variance explained is very low when using phylogenetically corrected regressions

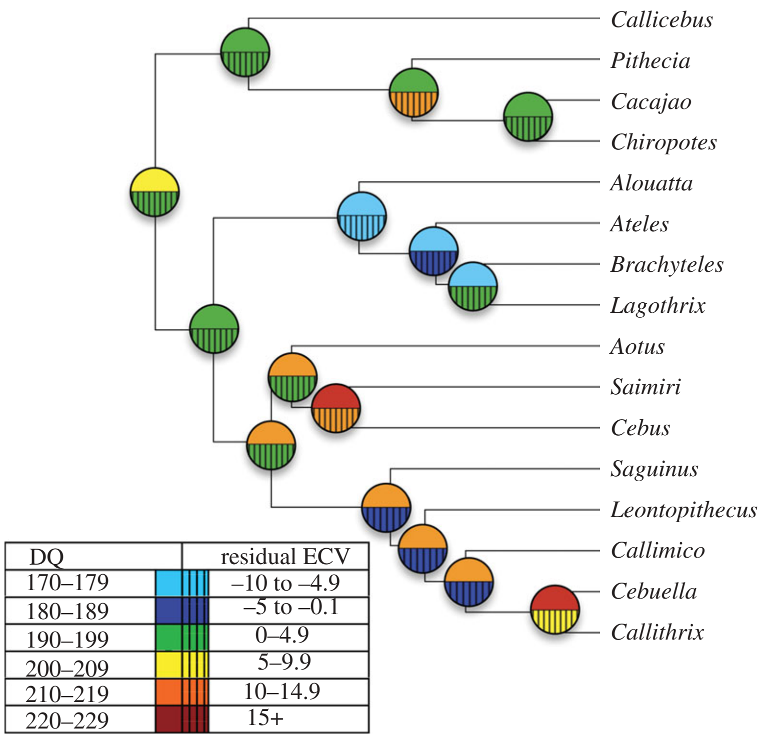

Figure 2. Phylogenetic tree of New World monkeys with a heat map of maximum-likelihood-based ancestral root node reconstructions for DQ and residual ECV. The magnitude of the DQ reconstruction is depicted in solid colours on the upper hemisphere, while the residual ECV is coloured in stripes in the bottom hemisphere of each node.

and conceals more than it reveals: several taxa of fairly uniform size, like the atelids (spider, woolly, woolly spider and howling monkeys) and callitrichines (marmosets and tamarins) evince considerable variance in diet quality. This may reflect the lability of this behavioural trait and/or a range of adaptive options available to animals of small to moderate body size. Among platyrrhines, the inclusion of animal and insect matter into the diet tends to decrease with increasing body size [33,68,69]. The protein demands of animals below 500 g require the inclusion of insects into the diet, while those platyrrhines above 500 g more often obtain their protein from plants [70]; however, even those in the below 500 g range include varying rates of insectivory. For example, animal matter comprises only 11 per cent of the diet in the small-bodied *Cebuella*, but 74 per cent in *Saguinus tripartitus*, an animal nearly four times larger with a relatively smaller brain [71]. The relative low use of faunal resources reported for *Cebuella* results in its placement as a slight outlier in the regression of relative brain size and relative diet quality. Platyrrhines have been previously noted to display a broad variability in diet quality within body size categories [37,72]. Ford & Davis [37] hypothesize that this diversity could be the result of body size convergence among groups with differing adaptive histories.

(**b**) ***Tests of the ETH***

The principal prediction of ETH is that species with relatively large brains also have correspondingly high diet quality in the absence of some other energetic compensatory mechanism. Our findings do not conform to this expectation. Instead, we find no significant correlation between diet quality and relative brain size in extant platyrrhines, when phylogenetic effects are controlled for. This indicates that any association which may exist between these two variables is overshadowed by the pervasive effects of similarity owing to common descent.

When phylogeny is *not* taken into account, it is apparent that the most encephalized platyrrhines tend to have high-quality diets (e.g. *Cebus*, *Saimiri*), while those with relatively small brains have the lowest quality diets (e.g. *Alouatta*), consistent with the traditional perceptions that diet and brain size are linked in these animals [11,18,20,32]; however, these extremes appear to drive the correlation and the overall explained variance is quite low (see the electronic supplementary material). At this level of explanatory power, DQ is not highly predictive of encephalization. Any predictive power that may exist is lost when phylogenetic controls are applied. This result emphasizes the importance of using phylogenetic control in analysing these traits.

ETH proposes gut reduction as a release mechanism on the metabolic constraints limiting encephalization, rather than a prime selective force for brain enlargement [20–22]. Consequently, brain size and diet quality may be asymmetrically associated. On the one hand, the presence of a relatively small-brained species with a high diet quality should not be considered as evidence against the hypothesis. For example, while tamarins (*Saguinus*) have a relative brain size on par with the empirical platyrrhine average, this group has a diet quality above that expected by the model, owing to the large contribution of insects to its diet. Under ETH, tamarins do not count as an exception: they may have the potential resources to invest in a large brain but may not have been selected to do so.

On the other hand, energetic constraints should mitigate against increased encephalization in species with low-quality diets and lacking some other compensatory mechanism [23,25]. ETH is inconsistent with our finding of highly encephalized species with low diet quality. *Brachyteles arachnoides* is one such species that presents a significant problem for the hypothesis. *Brachyteles* is a large-bodied platyrrhine that has dental and gastric adaptations for folivory [69,73,74]. Ecological studies have confirmed this species as predominantly folivorous [75,76] and it is aligned with the howling monkey, *Alouatta*, in possessing one of the lowest diet qualities within the Platyrrhini. Contrary to the expectations of ETH, *Brachyteles* possesses a relatively large brain, comparable to its more frugivorous and phylogenetically closer relatives *Ateles* and *Lagothrix*. It is possible that *Brachyteles* supports its large brain by reducing energy costs through the reduction of other expensive tissues rather than those associated with the gastrointestinal tract, i.e. via the 'expensive brain hypothesis', which emphasizes energy offsets by allocation to 'maintenance' or 'production'. *Brachyteles* does not appear to have a reduction in limb musculature when compared with *Ateles* and *Lagothrix* [77]. However, *Brachyteles* does demonstrate a 'slower' reproductive pace, at least compared with the equally folivorous *Alouatta* [19,78–84]. Thus, it is possible that increased interbirth intervals and slowed maturational processes are the trade-offs being used by this animal to 'afford' such a metabolically expensive brain. Its reproductive similarities to frugivorous atelines may indicate that *Brachyteles* evolved from a 'brainy' frugivorous ancestor, or alternatively, that the driving mechanisms for encephalization were strong enough to force the exploration of alternative avenues for constraint release. Interestingly, *Brachyteles* has been found to display dramatic intrageneric variation in diet composition, day ranges and activity levels. In areas with greater fruit availability, *Brachyteles* is more frugivorous, with larger day ranges compared with groups living in fruit-scarce regions [85].

(c) *Diet quality and the evolution of anthropoid encephalization*

Our ancestral character state reconstructions suggest the last common ancestor of crown platyrrhines had a degree of encephalization on par with that of modern *Pithecia* or *Ateles*, both frugivorous, moderately encephalized platyrrhines. Stem platyrrhine taxa from the Early Miocene of South America (*Homunculus*, *Dolichocebus* and *Tremacebus*) had diets very similar to those of extant platyrrhines—mixed frugivorory/insectivory or frugivory/folivory, not unlike the extant medium-sized platyrrhine *Callicebus* [86]. However, these stem taxa were substantially less encephalized than living platyrrhines [87–89]. Thus, the modern level of encephalization in platyrrhines appears to have been achieved without any shift to a more energy-rich diet. Given the relatively high-quality diets of extant and fossil platyrrhines, it is unlikely that diet quality constrained encephalization in the presence of a persistent selective pressure; instead, it is more likely that the abundance of high-quality diet niches available to Neotropical primates allowed encephalization to occur freely, once initiated later by other driving mechanisms.

We thank C. L. Nunn, R. Mundy, L. C. Aiello, E. C. Kirk, A. Barr and E. L. MacLean for helpful discussions. For training in phylogenetic comparative methods, we thank the AnthroTree Workshop which is supported by the NSF (BCS-0923791) and the National Evolutionary Synthesis Center (NSF grant EF-0905606). Further funding was provided from NSF BNS 0824546 to R.F.K.

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