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Evolutionary modeling and correcting for observation error support a 3/5 brain-body allometry for primates

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ABSTRACT

The tight brain-body allometry across mammals and primates has motivated and informed many hypotheses about brain evolution in humans and other taxa. While a 2/3 or a 3/4 scaling is often at the core of such research, such exponents are derived from estimates based on particular statistical and evolutionary assumptions without careful consideration of how either may influence findings. Here we quantify primate brain-body allometry using phylogenetic comparative methods based on models of both adaptive and constrained evolution, and estimate and account for observational error in both response and predictor variables. Our results supported an evolutionary model in which brain size is directly constrained to evolve in unison with body size, rather than adapting to changes in the latter. The effects of controlling for phylogeny and observation error were substantial, and our analysis yielded a novel 3/5 scaling exponent for primate brain-body evolutionary allometry. Using this exponent with the latest brain- and body-size estimates to calculate new encephalization quotients for apes, humans, and fossil hominins, we found early hominins were substantially more encephalized than previously thought.

1. Introduction

The size of the brain scales hypoallometrically with the size of the body across mammals (Snell, 1891), including primates (Striedter, 2005). Modern humans and our recent fossil ancestors deviate considerably from this relationship—our brains are many times larger than expected for a mammal or primate of our body size (Striedter, 2005). Some researchers hypothesized that this increase in relative brain size explains the enhanced cognitive abilities of modern humans when compared to species with absolutely larger brains but much larger bodies such as whales and dolphins (Jerison, 1973; but see Deaner et al., 2007; Herculano-Houzel, 2011). Though different scaling exponents were obtained with different data and approaches (Snell, 1891; Jerison, 1973; Martin, 1981; Isler et al., 2008; see Table 1), the regularity of brain-body allometry among species of vastly different adaptive grades, environments, and evolutionary histories (Striedter, 2005) is striking and has prompted numerous attempts to understand its causes and biological significance.

Early works suggested that brain size scales with a 2/3 power of body size, and this motivated the hypothesis that brain size is fundamentally related to body surface area (Snell, 1891; Jerison, 1973; Gould, 1975). Later analyses using larger datasets and different statistical methods found a higher slope, around 3/4 (Martin, 1981; Martin and Harvey, 1985), suggesting to some that brain size was constrained by maternal basal metabolic rate (Martin, 1981), which also scales to a 3/4 power with body size according to Kleiber's law (Kleiber, 1947; Capellini et al. 2010). Such differences in scaling exponents not only inspire different biological explanations, but also impact upon assessments of relative brain size. Quantifying relative brain size with the encephalization quotient (Jerison, 1973), the ratio between observed and allometrically-predicted brain size for the given body-mass, a 2/3 exponent gives modern humans a brain that is eight times as large as expected for our body size, while a 3/4 exponent gives a brain that is six times as large (e.g., Aiello and Dean, 1990).

Whether the goal is to understand the causes of brain-body scaling or simply to calculate relative brain sizes, it is clear that accurate estimates of allometric parameters are vital. Accurate

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Table 1
Compilation of brain-body allometry studies.[a]

Study	Method	Slope	95% CI	R^2	*N*
von Bonin (1937)	Ordinary least squares	0.66		69%	115 mammalian species
Jerison (1955)	Ordinary least squares	0.67	–	85%	163 mammalian species
Hofman (1981)	Reduced major axis	0.73	–	–	249 mammalian species
Martin (1981)	Major axis	0.76	0.73–0.78	86%	309 mammalian species
Armstrong (1982)	Ordinary least squares	0.72	0.62–0.82	90%	16 mammalian orders
Armstrong (1983)	Ordinary least squares	0.76	0.74–0.78	95%	93 mammalian species
Armstrong (1983)	Ordinary least squares	0.81	0.69–0.93	95%	15 primate species
Harvey and Clutton-Brock (1985)[b]	Major axis	0.86	0.74–0.99	–	135 primate species
Martin and Harvey (1985)	Major axis	0.72	0.68–0.77	–	15 mammalian orders
Harvey and Krebs (1990)	Independent contrasts	0.69	–	–	917 mammalian species
Pagel (1999)	Generalized least squares	0.48	0.39–0.57	92%	59 primate species
Martin (1996)	Ordinary least squares	0.77	–	96%	477 mammalian species
Barton (2001)	Independent contrasts	0.55	0.49–0.60	81%	106 primate species
Isler et al. (2008)	Ordinary least squares	0.77	0.75–0.80	95%	176 primate species
Isler et al. (2008)	Independent contrasts	0.57	0.52–0.61	77%	176 primate species
This study	Generalized least squares	0.60	0.56–0.64	81%	161 primate species

[a] Shown is statistical method employed, slope, 95% confidence interval (CI) around slope, coefficient of determination (R^2), and sample size and composition. Slope and confidence intervals are left in significant digits as originally reported. Correlation coefficients were converted to coefficient of determination where warranted.
[b] Adult female body mass used.

parameter estimates depend on the methods used for analysis, and on the quality and quantity of the data used in their calculation, a standard for which many early analyses fell short (as discussed in Smith and Jungers, 1997; Isler et al., 2008). While later studies were based on progressively more and better quality data, the statistical assumptions often remained biologically simplistic. Some studies assumed that all species are independent of each other and that there is no effect of evolutionary history. Other studies attempted to control for phylogenetic effects by use of independent contrasts (Felsenstein, 1985) and related methods, but this also entails strong assumptions about the evolutionary process that may not be fulfilled (Hansen, 2014). In particular, these methods assume patterns of phylogenetic residual correlations that are incompatible with adaptive evolution, and will yield inaccurate estimates if brain size adapts to body size rather than following along as a correlated response. It is essential that phylogenetic residual correlations are estimated and not assumed, and also that they are not confused with species correlations. Correcting for species correlations (i.e. correlations in response variables like brain size) in lieu of residual correlations is a common error that can seriously distort the evolutionary relationship between traits (Hansen and Orzack, 2005; Labra et al., 2009; Revell, 2010; Hansen, 2014).

The choice of phylogenetic comparative method is not merely cosmetic, as radically different outcomes may result (see Table 1). For example, Isler et al. (2008) obtained a brain-body scaling exponent as low as 0.565 among primate species using independent contrasts, compared to 0.773 in a non-phylogenetic analysis of the same data. Non-parametric line-fitting methods such as major-axis or reduced-major-axis regression were also frequently used (e.g., Martin, 1981), but these lack both biological and statistical justification, and may yield "estimates" of allometric exponents that are far from reality (Kelly and Price, 2004; Hansen and Bartoszek, 2012; Voje et al., 2014). These methods are sometimes said to correct for "error" in predictor variables, but fail to distinguish between biological and observational error (e.g., Riska, 1991), and do not yield reasonable estimates of allometric exponents except under certain special circumstances (Hansen and Bartoszek, 2012). Correction for observational error is important, but must be done jointly with, and not as a replacement for, modeling of biological residual variation in a least-squares or likelihood framework (Riska, 1991; Felsenstein, 2008; Hansen and Bartoszek, 2012; Garamszegi, 2014).

Here, we reanalyze data from Isler et al. (2008) on brain and body size in 161 primate species with two major methodological improvements. The first is that we use a more general phylogenetic comparative approach that allows us to assess which of several different evolutionary models best fits the data. The models include adaptation of the brain to the body, which can happen instantaneously or with lag, and one where brain size is constrained to change immediately with changes in body size (see below for an extended explanation of the models). Whether the adaptation or the constraint model show the best fit to the data will provide important information about the possible evolutionary processes that generated the data, and aid in interpretation of the allometric exponent. Our overall approach estimates phylogenetic signal in model residuals jointly with model fitting, and uses the best estimate rather than relying on a priori assumptions about phylogenetic effects. The second improvement is that we estimate and include observation error in the statistical model, which can bias regressions and lead to inaccurate parameter estimates. Hansen and Bartoszek (2012) showed how known "measurement" variance in both response and predictor variables can be included in a generalized least-squares (GLS) framework to obtain unbiased minimum-variance estimators of regression parameters (see also Lynch, 1991; Martins and Hansen, 1997; Ives et al., 2007; Felsenstein, 2008; Hadfield and Nakagawa, 2010; Garamszegi, 2014). Here we use this approach, together with a new method to estimate species-specific observation variances for use with small sample sizes, to obtain more accurate estimates of brain-body allometric scaling. Finally, we use our allometric parameters to calculate new encephalization quotients for various fossil hominin species using the latest estimates of brain and body sizes.

2. Materials and methods

Data on primate endocranial volume and body-mass come from Isler et al. (2008). This dataset is nearly unique in that it contains not only species means broken up by sex, but also sample sizes, complete references, and in some cases data from individuals. Because we need species sample sizes to estimate observation variances, we could not use data on endocranial volume of *Saguinus nigricollis Trachypithecus geei, Trachypithecus johnii, Macaca silenus*, and *Presbytis comata* and body masses of *Arctocebus aureus*, *Cercopithecus erythrotis*, *Euoticus pallidus, Lepilemur mustelinus*, *Nycticebus pygmaeus*, and *Propithecus edwardsi*, as sample sizes for these were not