Journal of Mammalogy, 100(2):276–283, 2019
DOI:10.1093/jmammal/gyz043

Invited Paper

The allometry of brain size in mammals

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Why some animals have big brains and others do not has intrigued scholars for millennia. Yet, the taxonomic scope of brain size research is limited to a few mammal lineages. Here, we present a brain size dataset compiled from the literature for 1,552 species with representation from 28 extant taxonomic orders. The brain–body size allometry across all mammals is $(Brain) = -1.26\ (Body)^{0.75}$. This relationship shows strong phylogenetic signal. Thus, we conducted additional allometries using median species values for each order, family, and genus to ensure evolutionary independence. Slopes from these analyses at different taxonomic levels all approximate ~0.75 scaling. Why brain size scales to the 3/4 power to body size across mammals is to our knowledge unknown. Slopes within taxonomic orders, exhibiting smaller size ranges, are generally shallower than 0.75 and range from 0.24 to 0.81 with a median slope of 0.64. Published data on brain size are lacking for the majority of extant mammals (> 70% of species) with strong bias in representation from Primates, Carnivora, Perissodactyla, and Australidelphian marsupials (orders Dasyuromorphia, Diprotodontia, Peramelemorphia). Several orders are particularly underrepresented. For example, data on brain size are available for less than 20% of species in each of the following speciose lineages: Soricomorpha, Rodentia, Lagomorpha, Didelphimorphia, and Scandentia. Use of museum collections can decrease the current taxonomic bias in mammal brain size data and tests of hypothesis.

Key words: biodiversity, biological scaling, body size, cognition, comparative anatomy, comparative methods, macroecology, morphology, museum collections, neurobiology

Brain size in mammals has received attention from scholars for at least 3,500 years since Aristotle made the conjecture that humans have the largest brain in proportion to our size (Striedter 2005). Since Aristotle, brain size has continued to intrigue observers of the natural world including Darwin (1871), Snell (1891), Dubois (1898), Jerison (1973), Gould (1975), Lande (1979), and many studies and books in recent decades. The accumulation of years of inquiry shows Aristotle's conjecture is accurate only when considering allometric scaling effects of body size (Fig. 1; see residual values in Supplementary Data SD1). When allometry is accounted, *Homo sapiens* has the largest brain size of any mammal, and primates in general have relatively large brains compared to other mammals. However, understanding the evolutionary significance of brain size scaling and residual deviations across the diversity of mammals remains a challenge. This is in part because much research on brain size has focused on limited taxa with a bias towards understanding the evolution of big brains.

Studies of brain size variation in mammals include a number of hypotheses relating large brain size to various social (e.g., Dunbar and Shultz 2007), ecological (e.g., Sol et al. 2008), energetic (e.g., Isler and van Schaik 2006), life history (González-Lagos et al. 2010; Barton and Capellini 2011; Gonzalez-Voyer et al. 2016), and behavioral characteristics (e.g., Benson-Amram et al. 2016). However, the taxonomic scope for which hypotheses about brain size have been evaluated is limited and often shows mixed results. For example, the social brain hypothesis (Dunbar and Shultz 2007), which linked large brain size in primates to the challenges of social living, has been very popular. However, recent analysis with larger datasets, advanced statistical methods, and alternative hypothesis testing suggests that ecology, including diets of dispersed high-quality food items, is a better predictor of

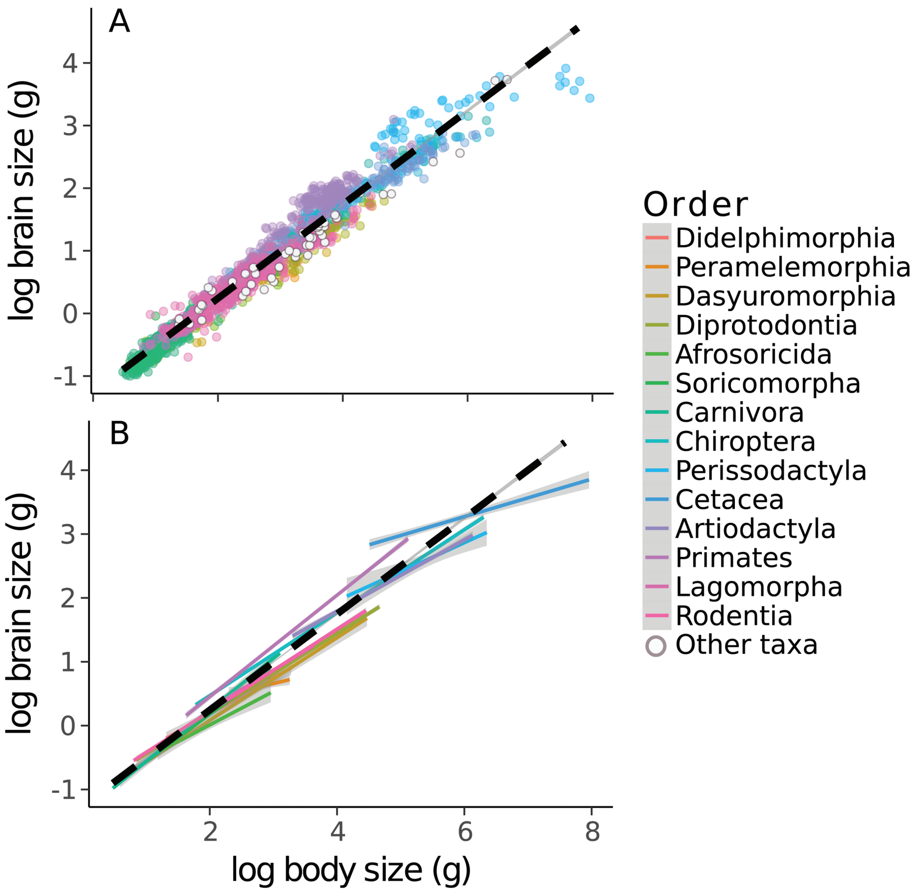

Fig. 1.—A) The allometry of brain size versus body size for 1,552 mammal species. Points are color coded based on orders with > 10 species; open circles are species in orders with ≤ 10 species. B) The allometries by taxonomic groups (> 10 species). Gray bands represent the 95% confidence intervals.

brain size among primates than sociality (DeCasien et al. 2017; González-Forero and Gardner 2018). There is no support for the social brain hypothesis in other diverse taxonomic groups such as marmots (Matějů et al. 2016), carnivorans (Benson-Amram et al. 2016), and bats (Pitnick et al. 2006). In contrast, it is well documented that toothed whales (Odontoceti) have relatively large brain sizes and complex socio-ecological systems (Marino 1998; Boddy et al. 2012; Montgomery et al. 2013; Fox et al. 2017). In contrast, the eusocial mole-rat (*Heterocephalus glaber*) has a relatively small brain (Kverková et al. 2018). Moreover, brain size among carnivorans (Carnivora) is related to puzzle-solving abilities and not sociality (Benson-Amram et al. 2016). These and other studies show that understanding the links between brain size, life histories, and socio-ecological lifestyles in mammals remains a challenge (Dunbar and Shultz 2007). Disentangling the multiple ecological and behavioral drivers and correlates of brain size is beyond the scope of this paper. Our point here is to emphasize that much research on brain size in mammals is focused on limited taxonomic scope with a bias towards explaining the evolution of large brain size. Any general theory and tests of brain size hypotheses should also provide insights into the evolution of small-brained species.

The use of brain size in comparative studies is certainly not void of contention, and Healy and Rowe (2007) and Logan et al. (2018) provide useful critiques. We suggest that brain size is still a useful biological trait in comparative and macroecological studies for several reasons. First, across species, brain size varies by more than an order of magnitude even after accounting for strong allometric scaling effects of body size (Figs. 1 and 2). So, this variation cannot simply be due to measurement error and therefore begs a biological explanation. Second, the brain is an energetically expensive organ, appropriating about ~20% of energy use in humans (or ~400 kcal per day) while only contributing to ~2% of human body mass (Herculano-Houzel 2011). Total brain size represents the aggregate cognitive costs of all of the brain parts, and thus variation in brain size is integral to understanding how animals allocate resources to various tradeoffs in life history traits that affect growth, survival, and reproduction. Third, brain size in mammals is unambiguous and easily quantified from museum specimens, allowing for large sample sizes spanning many taxa, which is required for macroecological and comparative studies. Moreover, these allometries from modern mammals are often used in studying fossil mammals (e.g., Finarelli and Flynn 2009; Smaers et al. 2012). So, quantifying the overall and taxon-specific allometries (Pagel and Harvey 1989) are important for inferring basic biology and natural history of modern and extinct mammals.

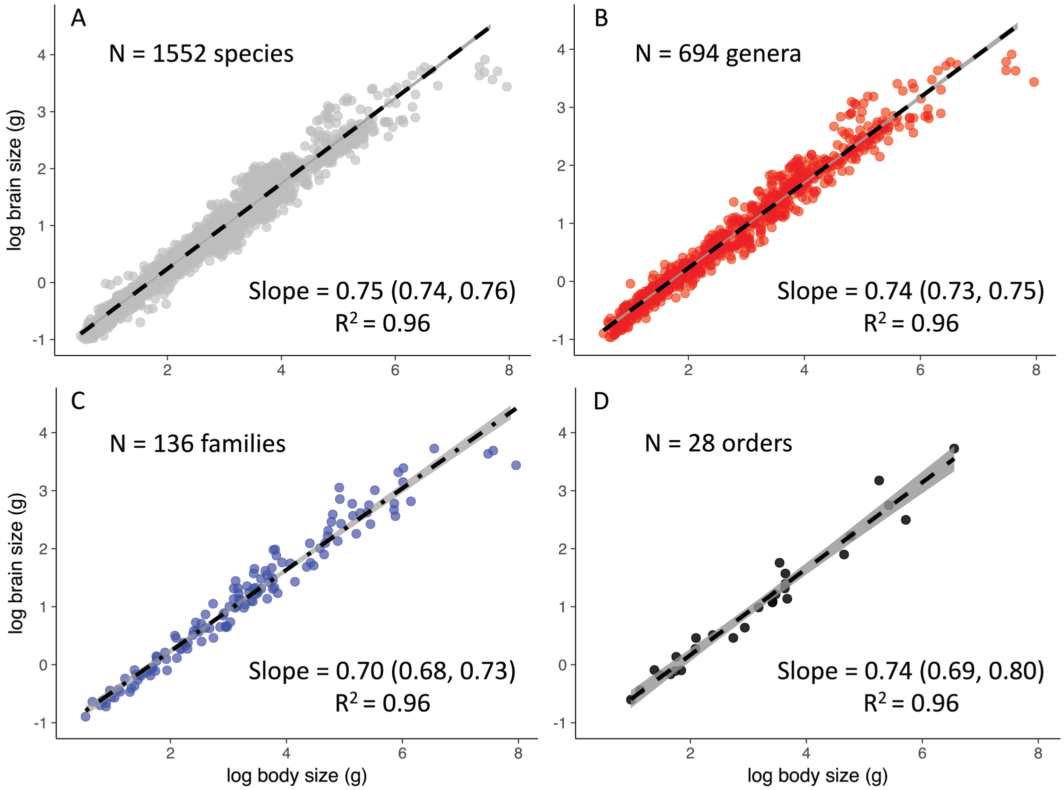

Fig. 2.—The allometry of brain size to body size across all species (A) and with median values by genera (B), families (C), and orders (D). Gray bands represent the 95% confidence intervals. Note that confidence intervals at all taxonomic scales are statistically indistinguishable from 0.75 with the exception of the family-level allometry. See the online version of this figure for color coding.

Here, we present a dataset on of brain sizes compiled from the literature for 1,552 species spanning 28 extant taxonomic orders. We analyze the allometry of brain size to body size across all mammals in our dataset and at multiple evolutionary scales. We summarize the general patterns in relative brain size variation among and within major evolutionary lineages and lifestyle groups. We end by highlighting some questions and gaps in the literature on brain size, offering future research opportunities.

Materials and Methods

Brain size data.—We conducted an extensive search using the key words "mammal brain size" in Google Scholar and datadryad.org for published datasets on brain size and other publications reporting brain size measurements. When these sources led to previously compiled datasets, we checked those references to confirm authenticity. We report both sources in Supplementary Data SD1. Data for each species were checked by at least two authors to confirm authenticity between the initial and second source encountered. We did not go beyond the second reference in checking data.

Data inclusion was based on the following criteria. We used brain and body size data from the same published source when possible. We referenced body size data when they were obtained from a different source than brain size. We report sex and sample sizes or ranges (e.g., $1 < n < 10$) of adult animals used in estimating brain size when reported. We used averages for adults of both sexes, and brain and body size of adult females for lineages known to exhibit sexual size dimorphism following (Isler and van Schaik 2012). For published datasets, we verified references for accuracy and merged data into a master file standardized by the taxonomy in Wilson and Reeder (2005) to be consistent with comparative databases of mammal life history and ecology (Jones et al. 2009; Myhrvold et al. 2015). When subspecies were reported, we took mean values for species weighted for sample sizes. We used a conversion of 1 g to 1 cm^3 when different units were reported following earlier studies (e.g., Isler and van Schaik 2009). The final dataset includes estimates of brain size and body size for 1,552 mammal species collated and verified from 54 published references. For each entry, we include taxonomy (order, family, genus, and Latin binomial), mean brain size in grams (g), mean body size in grams (g), brain size residuals from the overall allometry (e.g., *H. sapiens* compared to all other mammals), and order-specific residuals (e.g., *H. sapiens* compared to other primates; see Supplementary Data SD1).

Analysis.—The scaling of brain size with body size has typically been characterized by a power law (Snell 1891; Dubois 1898; Jerison 1973), where $(Brain\ Size) = \alpha\ (Body\ Size)^{\beta}$ and α and β are constants representing the intercept and slope, respectively. This relationship becomes linear by log transforming both sides of the equation: $\log(Brain\ Size) = \log(\alpha) + \beta\log(Body\ Size)$. Ordinary least squares (OLS) regressions were fitted to data to allow comparisons of parameter estimates (intercept and slope) across species and taxonomic and lifestyle groups.

We first evaluate the power law scaling of brain size to body size across all species (n = 1,552) in the dataset using OLS. We then conducted a phylogenetic generalized least squares (PGLS) by incorporating the mammal supertree (Bininda-Emonds et al. 2007; Fritz et al. 2009). This analysis revealed a strong phylogenetic signal. This may be because shared evolutionary histories impose limits to how quickly traits can evolve, resulting in non-independence among closely related species (e.g., Felsenstein 1985). However, this is not the case for all traits. For example, some behavioral traits show a weak phylogenetic signal compared to other traits (Blomberg et al 2003). In order to address the issue of non-independence in understanding the scaling of brain size further, we first evaluated additional allometries using only the median species by genera (n = 694), family (n = 136), and order (n = 28) using the same OLS regression analysis of log–log plots as above. We use this as an alternative approach to ensure evolutionary independence and interpreting the scaling parameters from traditional PGLS. This prevents speciose lineages with similar lifestyles, brain, and body size (e.g., Myomorpha rodents) from driving the regression analysis. At higher taxonomic levels, our approach ensures that each point represents a species that has evolved independent lifestyles and ecologies often on the order of hundreds of thousands to millions of years. Secondly, we conducted taxon-level allometries following Pagel and Harvey (1988) within orders for those with > 10 species with brain size data. This shows how different taxonomic and lifestyle groups compare to each other in allometric parameter estimates (Sibly and Brown 2007). We separate cetaceans and artiodactyls because of distinct functional lifestyles despite lack of monophyly in the latter. Finally, we plotted violin plots of brain size residuals from the allometry (observed–expected) for each species in the data to visually show the variation in relative brain size among major taxonomic and lifestyle groups. All analyses were conducted in R using the following packages: *ggplot2*, *phytools*, *caper*, *dplyr*, and *nlme*.

RESULTS

The allometry of brain size to body size across mammal species in our datasets is $(Brain) = -1.26\,(Body)^{0.75}$ (Fig. 1). The confidence intervals of the slope (0.742, 0.758) exclude linear scaling (slope = 1) and two-thirds scaling. Phylogenetic analysis showed a strong signal: Pagel's λ = 0.935 (Pagel 1999) with allometric parameters as intercept = –0.83 and slope = 0.57. Allometries at coarser taxonomic scales using median species at the order, family, and genus levels approximate 3/4 scaling (Fig. 2). Residual deviations about this allometry vary by taxonomic and lifestyle groups (Fig. 3). Allometric slopes by orders are generally shallower (Table 1) and range from 0.24 in the Australidelphia marsupials in the order Peramelemorphia (bandicoots and bilbies) to 0.81 in Chiroptera (bats), with a median value of 0.64. There is also variation in the elevation (intercepts) of the slopes by taxonomic groups. Primates and bats have steeper allometries compared to other orders; primates are significantly above the line for all mammals (Table 1). Lagomorpha and Soricomorpha also have similar slopes to the overall allometry but with lower intercepts.

Published data on brain size are lacking for the majority of extant mammals (> 70% of species; Appendix I), with the best representation (> 65% of species) in the following orders: Primates, Carnivora, Perissodactyla, and the Australidelphian marsupials (orders Dasyuromorphia, Diprotodontia, Peramelemorphia). Several orders are underrepresented in the brain size data, including Soricomorpha, Rodentia, Lagomorpha, Didelphimorphia, and Scandentia, all having less than 20% of their respective species represented in the brain size data. R-squared values for the allometries by taxonomic order were not related to sampling (i.e., percentage of species with brain size by order): $R^2 = 0.09$, $P < 0.001$.

DISCUSSION

Brain size allometry and its deviations.—Across taxa, the three-fourths scaling reveals economies of scale where brain size increases sublinear to body size. There is a strong phylogenetic signal in the residual deviations in Fig. 1 and PGLS analysis reveals a shallower slope than the allometry across all species. This is evident in the variation among different lifestyles among taxonomic groups, possibly reflecting developmental, physiological, and ecological constraints on morphology and anatomical design. For example, other taxa in addition to Primates also show large brain size, including Carnivora, tree-shrews of the order Scandentia, and the odontocete cetaceans. In contrast, manatees, Australidelphia marsupials, and perissodactyls have relatively small brains. Rodents and artiodactyls have medium-sized brains, although these orders show the greatest variation in brain size. Cetaceans have the largest variation in residual values of any order, with baleen whales having relatively small brains and toothed whales having large brains (Boddy et al. 2012; Fox et al. 2017; Fig. 3).

Our analysis across all species showed a strong phylogenetic signal. We therefore conducted additional scaling analyses at higher taxonomic levels using only median values from each order, family, and genus. In these analyses, each datum or species represented a distinct evolutionary lineage, typically separated by hundreds of thousands to millions of years of independent evolution. This was an alternative approach to interpreting the allometric scaling coefficients from the PGLS. Instead of weighting species by their shared ancestry with other species in the dataset, this approach stays true to the original brain size data. Moreover, using median values at higher taxonomic levels increases the evolutionary independence of data points by removing the potential for highly speciose lineages to drive the allometry. We acknowledge that even at these higher taxonomic levels, there is some degree of non-independence of data points because some lineages are more closely related evolutionarily than others. Yet, our taxonomic-level

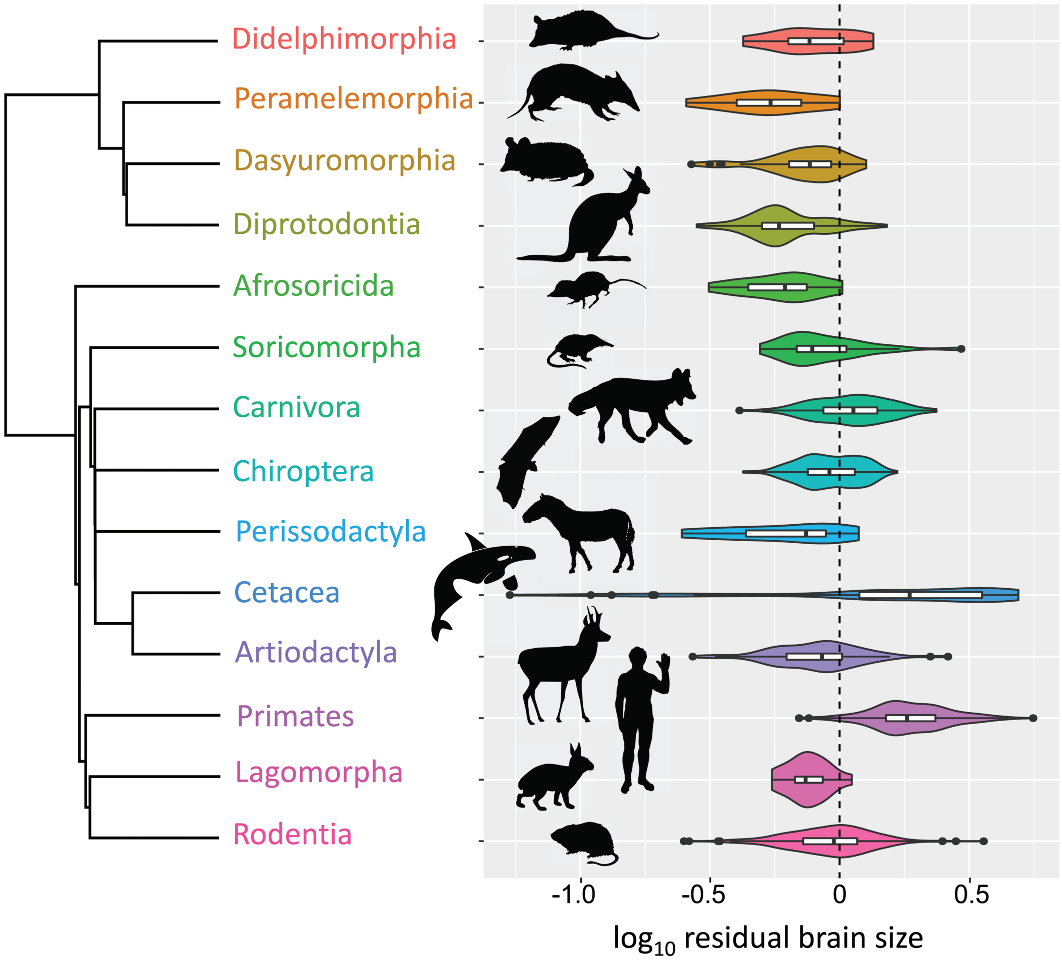

Fig. 3.—The phylogenetic distribution and violin plots of residual brain sizes by taxonomic order. Plots show mirror curves of kernel density estimation of the data. Inserted box and whisker plots show range (whiskers), interquartile ranges (white boxes), and median values (horizontal black lines) of the data. Circles in plot tails indicate outliers. Vertical dashed line at 0 corresponds with dashed lines in Fig. 1. Taxonomy based on Wilson and Reeder (2005) and mammal supertree from Bininda-Emonds et al. (2007) and Fritz et al. (2009).

Table 1.—Allometries for log10 brain size versus log10 body size across mammals and orders with > 10 species for which we have brain size data. *CI* = confidence interval.

Order	R^2	*n* = species	Slope (95% *CI*)	Intercept (95% *CI*)
Afrosoricida	0.85	13	0.54 (0.38, 0.699)	−1.07 (−1.4, −0.743)
Artiodactyla	0.89	95	0.56 (0.518, 0.599)	−0.44 (−0.637, −0.246)
Carnivora	0.96	199	0.65 (0.632, 0.669)	−0.83 (−0.908, −0.762)
Cetacea	0.74	43	0.29 (0.238, 0.35)	1.51 (1.19, 1.83)
Chiroptera	0.93	309	0.81 (0.786, 0.835)	−1.37 (−1.41, −1.34)
Dasyuromorphia	0.95	50	0.64 (0.597, 0.687)	−1.21 (−1.3, −1.12)
Didelphimorphia	0.93	16	0.56 (0.472, 0.652)	−0.94 (−1.15, −0.792)
Diprotodontia	0.95	112	0.63 (0.604, 0.658)	−1.08 (−1.17, 0.99)
Lagomorpha	0.96	15	0.75 (0.742, 0.759)	−1.26 (−1.29, −1.24)
Peramelemorphia	0.43	14	0.24 (0.056, 0.423)	−0.06 (−0.594, 0.466)
Perissodactyla	0.44	11	0.35 (0.0286, 0.67)	0.74 (−1.06, 2.54)
Primates	0.92	248	0.79 (0.764, 0.825)	−1.14 (−1.24, −1.03)
Rodentia	0.92	351	0.64 (0.622, 0.663)	−1.06 (−1.11, −1.02)
Soricomorpha	0.88	28	0.75 (0.634, 0.864)	−1.32 (−1.47, −1.16)
All mammals	0.96	1,552	0.75 (0.742, 0.758)	−1.26 (−1.28, −1.24)

allometries showed robust and consistent ~3/4 scaling at all levels, suggesting strong and ubiquitous convergence to a general allometric scaling rule. Presumably, this is due to fundamental underlying constraints on brain size evolution across evolutionary scales and body sizes.

Our findings differ from some previous studies that report 2/3 scaling (e.g., Dubois 1898; Jerison 1973; Sol et al. 2008) but are consistent with others reporting ~3/4 scaling (Isler and van Schaik 2009; Boddy et al. 2012; Stankowich and Romero 2017). A recent large comparative analysis reports ~0.5 scaling using phylogenetic analysis

(Tsuboi et al. 2018), which is similar to our 0.57 scaling using PGLS. This is likely because slopes within taxonomic orders are typically shallower than median values among orders (Table 1) as noted earlier (Pagel and Harvey 1988). Notable exceptions, however, are bats and primates, which show steeper slopes (Table 1). Lagomorphs and soricomorphs also have slopes ~3/4 and intercepts below the allometry for all mammals. Previous authors (e.g., Lande 1979; Pagel and Harvey 1988; Smaers et al. 2012; Tsuboi et al. 2018) have discussed the myriad selection pressures that can act on both brain size as well as body size, providing different scenarios of correlated trait evolution. With the emergence of new datasets and statistical approaches, opportunities abound to understanding the role of selection on both brain and body size in producing relative brain size across phylogenetic scales (Smaers et al. 2012; Tsuboi et al. 2018).

Filling the gaps in brain size data.—We have incomplete brain size data with roughly 70% of mammal diversity missing and clear taxonomic bias in brain size data in the literature (Appendix I). This dataset is biased, with best representation (> 65% of species) from Australidelphia marsupials (Dasyuromorphia, Diprotodontia, Peramelemorphia), primates (66% of species), carnivorans (70% of species), and perissodactyls (65%). Brain size is typically quantified from the endocranial volume of skulls by plugging holes and filling the cavity with seeds, buckshot, or glass beads and then decanting them into a graduated cylinder to measure volume (Gittleman 1986; Iwaniuk and Nelson 2002). Brain size is occasionally measured as wet mass and comparisons between techniques using wet mass and endocranial volume from skulls have been validated (Iwaniuk and Nelson 2002; Logan and Clutton-Brock 2013). However, Ridgeway et al. (2017) report that an erroneous value of blue whale (*Balaenoptera musculus*) brain size spread through the literature because specimens stored in alcohol shrank over time. We have corrected this value in our dataset. Yet, this points to the need for more studies to compare different methodologies to measure brain size, including comparisons of endocranial volume from beads and computed tomography scans to wet mass of brains before and after storage in alcohol. Museum collections can play an important role in resolving these issues and reducing the bias in brain size data in the literature.

Why 3/4 scaling?—Empirical scaling patterns in mammals have been central to recent advancements towards "universal scaling laws" that seek to integrate form and function across levels of biological processes based on fundamental constraints on physiology, morphology, behavior, life history, and populations (Sibly et al. 2012). Understanding the evolutionary significance of brain size scaling has much potential to unite the common currencies of energy and information to understand the dual processes governing complex biological systems. The scaling of brain size with body size to the three-fourths power mirrors the scaling of metabolic rate with body size that is central to the metabolic theory of ecology (Brown et al. 2004, 2018; Sibly et al. 2012). However, the link between brain size and metabolic scaling is not so clear. Several studies have tested the correlation between residual deviations in brain size and metabolic rate when controlling for body size. These results generally support a positive relationship between relative brain size and metabolic rate (Martin 1981; Armstrong 1983); however, the correlation is weak (e.g., Isler and van Schaik 2006) and variable at different taxonomic scales and sensitive to phylogenetic analyses (Sobrero et al. 2011). Understanding how brain size fits into a complete energetic framework that captures all of the tradeoffs associated with competing energy demands, including other expensive tissues (Aiello and Wheeler 1995; Navarrete et al. 2011), life history traits (e.g., Isler and van Schaik 2012), and parental care strategies (e.g., Gittleman 1994) that contribute to survival and reproduction is still needed.

The allometry of brain size is unique among organs, which typically scale with steeper slopes close to linear or isometric with body size (Peters 1986). Organs such as the stomach, heart, lungs, and liver are highly vascularized and feature fractal-like resource distribution networks that produce ~3/4 scaling (West et al. 1997; Banavar et al. 2010). While the size of these organs scale linearly with body size, their metabolic rates scale to the ~3/4 power, consistent with metabolic scaling theory. In contrast, the mammalian brain scales sublinearly with body size. It is possible that this is a result of increased modularity and folding that allows for the observed economies of scale in energy use with increasing size. However, other vertebrate taxa with smooth brains that lack modular folding show sublinear scaling different from 3/4 (Fristoe et al. 2017; Tsuboi et al. 2018). There is evidence from functional magnetic resonance imaging scans from a few mammals that the basal metabolic rate of the brain scales steeper and close to linear (~5/6) with brain size (Karbowski 2007). Energy use scales linearly with the number of neurons, which is highly correlated with brain size (Herculano-Houzel 2011). A possible unique characteristic of the brain is that brain metabolism scales linearly with brain size while the brain scales sublinearly to body size. This would result in the scaling of total energy allocation to the brain approximating 3/4, as with other organs showing isometry with body size. Understanding the scaling of size and metabolic costs of the brain and other organs across body sizes and evolutionary lineages is much needed to further understand the significance of sublinear scaling of brain size in mammals.

ACKNOWLEDGMENTS

M. J. Hamilton, J. H. Brown, P. R. Stephens, A. D. Davidson, T. S. Fristoe, J. M. Grady, F. A. Smith, and A. H. Hurlbert provided helpful discussions. We thank J. Gittleman, S. Reader, and K. Isler for providing versions of published datasets that we cross-checked in compiling our dataset. We acknowledge funding from an American Society of Mammalogists Shadle Fellowship, The McNair Scholars Program, and a UNC Carolina Postdoctoral Fellowship for Faculty Diversity awarded to JRB.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Brain size data for 1,552 mammal species.

Supplementary Data SD2.—Brain size references.

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Submitted 16 October 2018. Accepted 14 February 2019.

Associate Editor was Loren Hayes.

APPENDIX I

Percent of orders with brain size data. Taxonomy based on Wilson and Reeder (2005).

Order	# of species	Species with brain data	% of order with brain data
Rodentia	2,277	351	15.42
Chiroptera	1,116	309	27.69
Soricomorpha	428	28	6.54
Primates	376	248	65.96
Carnivora	286	199	69.58
Artiodactyla	240	95	39.58
Diprotodontia	143	112	78.32
Lagomorpha	92	15	16.30
Didelphimorphia	87	16	18.39
Cetacea	84	43	51.19
Dasyuromorphia	71	50	70.42
Afrosoricida	51	13	25.49
Erinaceomorpha	24	7	29.17
Peramelemorphia	21	14	66.67
Cingulata	21	7	33.33
Scandentia	20	4	20.00
Perissodactyla	17	11	64.71
Macroscelidea	15	5	33.33
Pilosa	10	7	70.00
Pholidota	8	3	37.50
Paucituberculata	6	2	33.33
Monotremata	5	3	60.00
Sirenia	5	2	40.00
Hyracoidea	4	3	75.00
Proboscidea	3	2	66.67
Notoryctemorphia	2	1	50.00
Dermoptera	2	0	0.00
Microbiotheria	1	1	100.00
Tubulidentata	1	1	100.00
TOTAL	5,416	1,552	28.67