

Relative Brain Size, Gut Size, and Evolution in New World Monkeys

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ABSTRACT

The dynamics of brain evolution in New World monkeys are poorly understood. New data on brain weight and body weight from 162 necropsied adult individuals, and a second series on body weight and gut size from 59 individuals, are compared with previously published reports based on smaller samples as well as large databases derived from museum records. We confirm elevated brain sizes for *Cebus* and *Saimiri* and also report that *Cacajao* and *Chiropotes* have relatively large brains. From more limited data we show that gut size and brain mass have a strongly inverse relationship at the low end of the relative brain size scale but a more diffuse interaction at the upper end, where platyrrhines with relatively high encephalization quotients may have either relatively undifferentiated guts or similar within-gut proportions to low-EQ species. Three of the four main platyrrhine clades exhibit a wide range of relative brain sizes, suggesting each may have differentiated while brains were relatively small and a multiplicity of forces acting to maintain or drive encephalization. *Alouatta* is a likely candidate for de-encephalization, although its “starting point” is difficult to establish. Factors that may have compelled parallel evolution of relatively large brains in cebids, atelids and pitheciids may involve large social group sizes as well as complex foraging strategies, with both aspects exaggerated in the hyper-encephalized *Cebus*. With diet playing an important role selecting for digestive strategies among the seed-eating pitheciids, comparable in ways to folivores, *Chiropotes* evolved a relatively larger brain in conjunction with a moderately large and differentiated gut. *Anat Rec*, 294:2207–2221, 2011. © 2011 Wiley Periodicals, Inc.

Key words: New World monkeys; platyrrhines; brain size; gut size; diet; sociality; Expensive Tissue Hypothesis

The relationship between brain size and body size continues to tempt and vex attempts to identify the role of cognition in primate evolution. Are simple measures of absolute brain size more informative than indices anchored to body size, phylogeny, or allometry (Marino, 2006; Deaner et al., 2007). What constitutes a reliable data set (Isler et al., 2008), and who are the arbiters of that reliability (e.g., Smith and Jungers, 1997)? One point of

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agreement would seem to be that an outcome as complex as the ontogeny and phylogeny of the nervous system cannot and should not be reduced to simple correlations of cause and effect (Healy and Rowe, 2007).

New World monkeys (NWM) would seem to offer an enticing natural experiment in how cognition evolves in connection with brain size given the likely method by which they colonized a vast but isolated continental habitat as nascent anthropoid primates some 35–40 million years ago perhaps (e.g., Poux et al., 2006; Rosenberger et al., 2009). Within this radiation, now extant as 16 recognized genera, are examples of generalist and specialist foragers (e.g., Rosenberger, 1992), generalist and specialist locomotors (e.g., Youlatos and Meldrum, 2011), and a wide variety of behavioral repertoires regarding mating strategies and social organization (see reviews in Campbell et al., 2011). This variation is expressed within an exclusively arboreal milieu and by animals that define the lower limit and low range of average body size among extant and extinct anthropoids of the Old World. Therefore, even relatively crude measures or surrogates of size have a diverse biological and ecological landscape upon which to be correlated. But what inferences can be drawn from them?

Cogent theories of how brains evolve in primates have emerged principally from studies of other anthropoids—Old World monkeys, apes and humans—as well as primate-wide studies and comparisons with other mammals. A brief list of causal correlates and/or constraints includes group size and social system (e.g., Harvey et al., 1980; Dunbar, 1988; Barton, 1996; Dunbar and Shultz, 2007), foraging strategies (Clutton-Brock and Harvey, 1980; Milton, 1988; Barton et al., 1995), maternal energetics (e.g., Martin, 1990), metabolism (McNab and Eisenberg, 1989), phyletic size decrease (Rosenberger, 1992), and shifts in diel cycle (Barton et al., 1995). In the history of most schools of thought on relative brain size as adaptation, from the *Scala Naturae* to the Expensive Tissue Hypothesis (ETH; Aiello and Wheeler, 1995), New World monkeys typically appear as auxiliary or adjuvant data in service to inferences about the rest of the anthropoids (i.e., Fish and Lockwood, 2003). Aside from the obvious reasons for emphasizing the relationships of relative brain size in apes and humans, much of the traction (or lack thereof) in NWM analysis is due to the dearth and quality of relevant data. Apart from the ETH, most discussions have also focused explicitly on brain size increase, while acknowledging that select cases such as *Alouatta* are reminders that decreasing relative brain size may have its own advantages.

This study is a case in point of the difficulty in framing hypotheses when data sets cannot be as thorough as desired. Our initial goal was to test a basic hypothesis of relationship between gut size and brain size in New World monkeys, a slightly modified application of the ETH. An optimal data set would include a robust sample size of individual data for gut size, brain size, and body size across the radiation if not across all genera. Actual data sets are far from the ideal, however, and there is only a limited amount of this information in the literature. For example, while one can compile separate and large databases available from museum records concerning individual body weights and endocranial volumes (Isler et al., 2008), the brain weight data that has fed

several decades of scaling studies involving life histories and ecology come essentially from a single source and its supplements (Stephan and Andy, 1964), or its widely cited derivatives (e.g., Harvey et al., 1987). Attesting to the scarce nature of such data, the substance of the original Stephan and Andy project, based on small samples sizes of many taxa, have apparently not been checked against other samples, nor have the much larger series of brain size proxy measures assembled by Isler et al. been “proofed” against brain size *per se*.

MATERIALS AND METHODS

In this report we bring together three unique data sets with bearing on the issues of brain size and gut morphology in platyrrhines, where the critical measurements have been recorded from single individuals. One sample consists of 162 individual brain weights and body weights of adult New World monkeys (Tables 1 and 2; Appendix 1) culled from the necropsy reports of animals housed at the Japan Monkey Center (JMC). The second is a dataset on 59 individuals, measures pertaining to guts and body weight (Table 3; Appendix 2), assembled by co-author Young Owl from captive colonies (zoos and research institutions) in California, USA. A third set, on gut size and body weight, was graciously made available to us by David Chivers, based on 17 individuals representing 6 species collected in the field by Marcio Ayres. Together, these samples include 15 of 16 living NWM genera, lacking only *Brachyteles*, and about 35 species (depending on how these are classified). For each of these samples, we deleted individuals whose weights seemed excessively low by comparison to means or minima of published wild weights (Ford and Davis, 1992; Rosenberger, 1992). Finally, some of our comparisons employ individual endocranial volume and body weight data provided by Isler et al. (2008), for the purpose of corroboration with the JMC data and thus possible augmentation of sample sizes. Gut size data were also synthesized from Chivers and Hladik (1980, 1984) and Ferrari and Lopes (1995).

The JMC brain weight data represent an important addition to the rare primary data on New World monkeys that can be anchored to real individual body weights. The data we present are for adult specimens as transcribed from a computerized listing of individuals ordered by JMC specimen number. The computerized listing was derived from hand-written records ordered by species, copies of which accompanied the computerized list for verification. Because the original records are in hard-copy form there is an inevitable possibility of transcription error between the originals and the data as they appear in Table 1. The likelihood of such an error was mitigated via two proofreads by independent reviewers. Species names are those indicated in the original records.

The data derived from the Isler et al. (2008) supplementary appendix includes all adult NWM specimens for which both body weight and endocranial volume were indicated ($n = 606$ total individuals). The species names reflect those used by the authors, which they note to be in accordance with Groves (2005). Most if not all of the nomenclatural discrepancies between the Isler and JMC lists can likely be reconciled as arbitrary differences in taxonomy rather than the identifications of

TABLE 1. Body and brain weights of New World monkeys in grams (g) from the Japan Monkey Center (JMC) series

Genus	Species		JMC Body wt. (g)	JMC Brain wt. (g)	Wild Body wt.	Stephan Brain wt.	JMC/wild Body wt.	JMC/Stephan Brain wt.
<i>Alouatta</i>	<i>caraya</i> (3)	Mean	5100.0	50.33	5206 (15)	52 (2) *	0.98	0.97
		S.D.	636.4	4.97				
		C.V.	212.1	1.66				
<i>Alouatta</i>	<i>seniculus</i>	Mean	3900.0	54.0	8168 (8)	108 (1)	0.95	1.00
		S.D.	7775.0	108.03				
		C.V.	1043.6	9.72				
<i>Ateles</i>	<i>geoffroyi</i> (4)	Mean	7775.0	108.03	7803 (F)		0.91	
		S.D.	1043.6	9.72				
		C.V.	260.9	2.43				
<i>Ateles</i>	<i>paniscus</i>	Mean	7000.0	97.5	6887	101 (3)	1.06	1.18
		S.D.	7200.0	130.0				
		C.V.	6900.0	119.5				
<i>Lagothrix</i>	<i>lagotricha</i>	Mean	6900.0	119.5	7700.0			
		S.D.	7700.0	100.5				
		C.V.	3800.0	81.5				
<i>Cacajao</i>	<i>rubicundus</i>	Mean	2900.0	68.0	819 (2)		0.86	
		S.D.	800.0	13.9				
		C.V.	880.0	19.0				
<i>Aotus</i>	<i>trivirgatus</i> (8)	Mean	837.5	18.06	860 (16)	17.1 (5)	0.97	1.05
		S.D.	126.6	1.59				
		C.V.	15.8	0.20				
<i>Cebus</i>	<i>albifrons</i>	Mean	2800.0	73.0	2428 (15)	71 (2) *	1.15	1.03
		S.D.	2400.0	60.0				
		C.V.	3150.0	91.0				
<i>Cebus</i>	<i>apella</i>	Mean	3150.0	91.0	2110 (38)		1.32	
		S.D.	638.4	22.93				
		C.V.	125.2	3.66				
<i>Saimiri</i>	<i>sciureus</i> (17)	Mean	638.4	22.93	722(36)	24 (1)	0.88	0.96
		S.D.	125.2	3.66				
		C.V.	7.4	0.22				
<i>Callimico</i>	<i>goeldii</i>	Mean	480.0	13.0	481 (11)	11 (1)	0.98	1.18
		S.D.	485.0	13.00				
		C.V.	30.0	0.91				
<i>Leontopithecus</i>	<i>rosalia</i> (4)	Mean	485.0	13.00	495 (20)		0.98	
		S.D.	30.0	0.91				
		C.V.	7.5	0.23				
<i>Saguinus</i>	<i>fuscicollis</i>	Mean	250.0	6.0	380 (75)		1.03	
		S.D.	390.0	8.4				
		C.V.	391.2	10.93				
<i>Saguinus</i>	<i>geoffroyi</i> (6)	Mean	391.2	10.93	486 (53)		0.80	
		S.D.	108.9	0.77				
		C.V.	18.2	0.13				
<i>Saguinus</i>	<i>labiatus</i>	Mean	450.0	10.1	491		0.76	
		S.D.	300.0	11.8				
		C.V.	315.3	10.0				
<i>Saguinus</i>	<i>leucopus</i> (3)	Mean	315.3	10.0	440 (F)		0.72	
		S.D.	19.3	0.50				
		C.V.	6.4	0.17				
<i>Saguinus</i>	<i>mystax</i> (5)	Mean	435.0	11.5	509 (182)		0.85	
		S.D.	74.2	0.71				
		C.V.	14.8	0.14				
<i>Saguinus</i>	<i>nigricollis</i> (19)	Mean	325.0	8.6	435 (F)		0.85	
		S.D.	61.1	1.21				
		C.V.	3.22	0.06				
<i>Saguinus</i>	<i>oedipus</i> (37)	Mean	342.4	10.2	432 (25)	10 (3)	0.79	1.02
		S.D.	73.80	0.84				
		C.V.	1.94	0.02				
<i>Callithrix</i>	<i>argentata</i> (4)	Mean	292.5	7.6	338 (F)		0.87	
		S.D.	37.7	0.61				
		C.V.	9.44	0.15				
<i>Callithrix</i>	<i>geoffroyi</i> (7)	Mean	361.1	8.6	359 (46)		1.01	
		S.D.	59.0	0.56				
		C.V.	8.43	0.08				
<i>Callithrix</i>	<i>jacchus</i> (8)	Mean	266.3	7.7	294 (51)	7.6 (4)	0.91	1.01
		S.D.	11.3	0.65				
		C.V.	1.42	0.08				
<i>Callithrix</i>	<i>penicillata</i>	Mean	260.0	7.0	116 (71)	4.5 (2)	0.84	1.00
		S.D.	97.1	4.5				
		C.V.	22.2	0.60				
<i>Cebuella</i>	<i>pygmaea</i> (20)	Mean	97.1	4.5	116 (71)	4.5 (2)	0.84	1.00
		S.D.	22.2	0.60				
		C.V.	1.11	0.03				

Summary statistics are provided for samples greater than two individuals. Sample sizes in parentheses. S.D., standard deviation; C.V., coefficient of variation. Individualized data for the entire sample are presented in the Appendix. Comparative published samples for wild body weight are from Rosenberger (1992), or from Ford and Davis (1992) when indicated (F). Brain weights for the same species from Stephan et al. (1981) are also presented, with unidentified species of *Alouatta* and *Cebus* indicated by an asterisk.

TABLE 2. Comparisons of individual body weight, brain weight, and endocranial volume data between Japan Monkey Center records (JMC) and Isler et al., 2008 (ECV), for genera represented adequately in both datasets

Taxa	Sample group	Sample size	Mean body weight	Mean brain weight/ECV	JMC:ECV body weight permutation t-test [P(same mean)]	JMC:ECV brain weight/ECV weight permutation t-test [p(same mean)]
<i>Alouatta</i>	JMC	1 (f) 3 (m)	n/a (f)	n/a (f)	$P = 0.166$ (m)	$P = 0.043$ (m)
	ECV	25 (f) 27 (m)	5133 (S.E. 864.7) 4927 (S.E. 192.2) 6435 (S.E. 293.5)	52.2 (S.E. 2.83) 56.2 (S.E. 0.96) 59.89 (S.E. 1.07)		
<i>Aotus</i>	JMC	5 (f) 3 (m)	769.6 (S.E. 27.59) 906.67 (S.E. 58.12)	17.64 (S.E. 0.850) 18.77 (S.E. 0.393)	$P = 0.660$ (f) $P = 0.362$ (m)	$P = 0.817$ (f) $P = 0.239$ (m)
	ECV	17 (f) 19 (m)	828.5 (S.E. 66.67) 828.0 (S.E. 35.23)	17.44 (S.E. 0.390) 17.98 (S.E. 0.241)		
<i>Ateles</i>	JMC	6 (f) 0 (m)	7550.0 (S.E. 360.32)	109.9 (S.E. 5.339)	$P = 0.193$ (f)	$P = 0.411$ (f)
	ECV	16 (f) 12 (m)	8154.3 (S.E. 243.77) 7907.8 (S.E. 231.21)	114.02 (S.E. 2.212) 106.39 (S.E. 3.381)		
<i>Callithrix</i>	JMC	7 (f) 13 (m)	316.29 (S.E. 17.08) 298.00 (S.E. 17.72)	8.13 (S.E. 0.267) 7.89 (S.E. 0.225)	$P = 0.734$ (f) $P = 0.60$ (m)	$P = 0.303$ (f) $P = 0.178$ (m)
	ECV	6 (f) 7 (m)	325.83 (S.E. 23.89) 357.86 (S.E. 22.78)	8.55 (S.E. 0.355) 8.39 (S.E. 0.246)		
<i>Cebus</i>	JMC	0 (f) 3 (m)	2783.33 (S.E. 216.67)	74.67 (S.E. 8.988)	$P = 0.204$ (m)	$P = 0.947$ (m)
	ECV	81 (f) 128 (m)	2473.57 (S.E. 39.47) 3240.05 (S.E. 53.87)	69.36 (S.E. 0.711) 74.92 (S.E. 0.585)		
<i>Saguinus</i>	JMC	45 (f) 29 (m)	342.8 (S.E. 11.20) 354.35 (S.E. 14.97)	9.898 (S.E. 0.198) 9.848 (S.E. 0.264)	$P = 0.001$ (f) $P = 0.001$ (m)	$P = 0.538$ (f) $P = 0.820$ (m)
	ECV	41 (f) 64 (m)	459.07 (S.E. 11.78) 445.14 (S.E. 10.78)	10.063 (S.E. 0.173) 9.915 (S.E. 0.191)		
<i>Saimiri</i>	JMC	4 (f) 13 (m)	562.50 (S.E. 23.94) 661.69 (S.E. 37.04)	22.750 (S.E. 0.323) 22.985 (S.E. 1.169)	$P = 0.003$ (f) $P = 0.002$ (m)	$P = 0.103$ (f) $P = 0.018$ (m)
	ECV	35 (f) 55 (m)	763.91 (S.E. 22.15) 838.91 (S.E. 23.61)	24.473 (S.E. 0.443) 25.115 (S.E. 0.334)		

the populations from which the data were derived. The species recognized by Groves would have been considered, in all likelihood, to be subspecies of the corresponding genera and species identified by the JMC, which probably followed the systematic arrangements of authorities such as Hershkovitz (1977) and Napier (1976). The same holds for identifications of Ayres/Chivers and Young Owl, as well as the published information provided by Chivers and Hladik (1980, 1984) and Ferrari and Lopes (1995).

Specifics on the arrangement of our data matrices and definition of gut variables are addressed below in context.

RESULTS AND DISCUSSION

The data reported here on body and brain weights from necropsy reports on 162 New World monkeys is the largest series of such measures that have been assembled. For most species samples, the recorded body weights align with published (Ford and Davis, 1992; Rosenberger, 1992) wild weights (Table 1), though individuals (e.g., *Cebus apella*) of sexually dimorphic species may appear to be outliers when compared with the species means. Systematic departures from wild weights are evident among the JMC callitrichines, where a dozen species average about 0.85 lighter than the weights of wild individuals. For the smaller Young Owl data set, the average difference between captive and wild weight values is 2% for the seven samples where means can be

calculated from more than two individuals. Among them, the only serious deviation involves *Leontopithecus rosalia*, where the four specimens average 17% heavier than the wild norms.

For brain weight, our data compare quite favorably with the measurements of platyrrhine brain weights provided by Stephan et al. (1981), which have been used extensively in studies of primate brain size and life histories. For seven of the nine species in common, including three callitrichines from different genera, there is no more than a 2% difference in the average values of the samples. Our weights are 106% of Stephan et al. measures for *Aotus* and 118% of *Callimico*. In both cases, the Stephan et al. sample was an N of 1, as is ours for *Aotus*. Our measures of brain weight are also comparable to the endocranial volume measurements culled from museum skulls, and from the corresponding wild shot body weights given in museum records, but our measures have the distinct advantage of being drawn from the same individuals at a single institution, where methodology would have been standardized. Overall, for platyrrhines, the brain size metrics, whether they are measures of weight or of endocranial volume, are bound by small sample sizes in various species. Their homogeneity and cross-comparability cannot be verified, so the data are not interchangeable. However, the consistency with which these data from disparate sources align means that the plentiful endocranial volumes available through museum collections can serve as a surrogate for brain weight.

TABLE 3. Gut area, coefficient of gut differentiation (CGD) and encephalization quotient (EQ) for individual specimens of available taxa

		Gut Area	CGD	EQ mean	Relative Gut Mass Residual	Relative Brain Mass Residual
<i>Alouatta</i>	<i>belzebul</i> (I)	1494	1.04	1.44	0.85	-0.13
<i>Alouatta</i>	<i>caraya</i> (I)			1.49		
<i>Alouatta</i>	<i>caraya</i> (J)			1.41		
<i>Alouatta</i>	<i>guariba</i> (I)			1.45		
<i>Alouatta</i>	<i>palliate</i> (I)	1504	1.60	1.41	0.71	
<i>Alouatta</i>	<i>seniculus</i> (I)	1483	1.39	1.46	0.84	-0.14
<i>Aotus</i>	<i>lemurinus</i> (I)			1.63		
<i>Aotus</i>	<i>trivirgatus</i> (I)			1.43		
<i>Aotus</i>	<i>trivirgatus</i> (J)	239	0.75	1.67	0.69	-0.12
<i>Ateles</i>	<i>belzebuth</i> (I)			2.34		
<i>Ateles</i>	<i>geoffroyi</i> (I)			2.20		
<i>Ateles</i>	<i>geoffroyi</i> (J)			2.24		
<i>Ateles</i>	<i>paniscus</i> (J)	459	0.59	2.49	0.27	0.03
<i>Cacajao</i>	<i>melanocephalus</i> (I)			3.14		
<i>Cacajao</i>	<i>rubicundus</i> (J)			2.71		
<i>Callicebus</i>	<i>discolor</i> (I)			1.48		
<i>Callicebus</i>	<i>moloch</i> (J)	265	0.82	1.50	0.69	-0.09
<i>Callimico</i>	<i>goeldii</i> (I)			1.52		
<i>Callithrix</i>	<i>argentata</i> (J)			1.42		
<i>Callithrix</i>	<i>geoffroyi</i> (J)			1.41		
<i>Callithrix</i>	<i>jacchus</i> (J)	83	1.01	1.52	0.77	-0.1
<i>Callithrix</i>	<i>penicillata</i> (I)			1.38		
<i>Cebuella</i>	<i>pygmaea</i> (J)			1.77		
<i>Cebus</i>	<i>albifrons</i> (I)			2.77		
<i>Cebus</i>	<i>apella</i> (I)	245	0.20	2.81	0.25	0.16
<i>Cebus</i>	<i>apella</i> (J)			3.08		
<i>Cebus</i>	<i>capucinus</i> (I)	155	0.31	2.81	0.08	0.16
<i>Cebus</i>	<i>nigritus</i> (I)			2.85		
<i>Cebus</i>	<i>olivaceus</i> (I)			2.85		
<i>Chiropotes</i>	<i>satanus</i> (I)	346	0.79	2.28	0.54	0.07
<i>Chiropotes</i>	<i>israelita</i> (I)			2.74		
<i>Lagothrix</i>	<i>lagotricha</i> (I)	965	0.60	2.38	0.55	0.14
<i>Leontopithecus</i>	<i>rosalia</i> (I)			1.70		
<i>Leontopithecus</i>	<i>rosalia</i> (J)	69	0.43	1.72	0.31	-0.06
<i>Pithecia</i>	<i>monachus</i> (I)			1.79		
<i>Pithecia</i>	<i>pithecia</i> (I)	334	0.80	1.76	0.55	-0.03
<i>Saguinus</i>	<i>fuscicollis</i> (I)			1.26		
<i>Saguinus</i>	<i>fuscicollis</i> (J)	199	0.89	1.26	0.95	-0.14
<i>Saguinus</i>	<i>geoffroyi</i> (I)	112	0.70	1.38	0.64	-0.11
<i>Saguinus</i>	<i>geoffroyi</i> (J)			1.73		
<i>Saguinus</i>	<i>labiatus</i> (I)			1.31		
<i>Saguinus</i>	<i>labiatus</i> (J)			1.78		
<i>Saguinus</i>	<i>leucopus</i> (I)			1.37		
<i>Saguinus</i>	<i>leucopus</i> (J)			1.77		
<i>Saguinus</i>	<i>midas</i> (I)			1.48		
<i>Saguinus</i>	<i>mystax</i> (I)			1.35		
<i>Saguinus</i>	<i>nigricollis</i> (J)			1.50		
<i>Saguinus</i>	<i>niger</i> (I)			1.57		
<i>Saguinus</i>	<i>oedipus</i> (I)			1.46		
<i>Saguinus</i>	<i>oedipus</i> (J)	82	0.81	1.75	0.51	-0.08
<i>Saimiri</i>	<i>sciureus</i> (I)			2.42		
<i>Saimiri</i>	<i>sciureus</i> (J)	124	0.32	2.57	0.37	0.12
<i>Saimiri</i>	sp.	115	0.38		0.36	

Sources are indicated in parentheses. (I) or (J) indicates that the EQ data are derived from the Isler et al. (2008) dataset or the Japan Monkey Center dataset, respectively. Gut Area and Coefficient of Gut Differentiation (CGD) are derived from Chivers and Hladik (1980, 1984) and Marcus Young Owl (unpublished data). Encephalization Quotient (EQ) is derived from Jerison (1973). Relative gut mass and relative brain mass residuals employ the formulas used by Aiello (1997). The EQ values calculated in this table all derive from cases of known individual body weights and brain weights, not species means.

To evaluate relative brain size in New World monkeys the brain weight and body weight measurements from the JMC were regressed against each other (Fig. 1). Alignment of taxa around either a reduced major axis or

an ordinary least squares axis is broadly similar to regressions based on cranial morphometrics (Hartwig, 1993) or summary mean data (Hartwig, 1996). The regression splits *Ateles* and *Lagothrix* and, as expected,

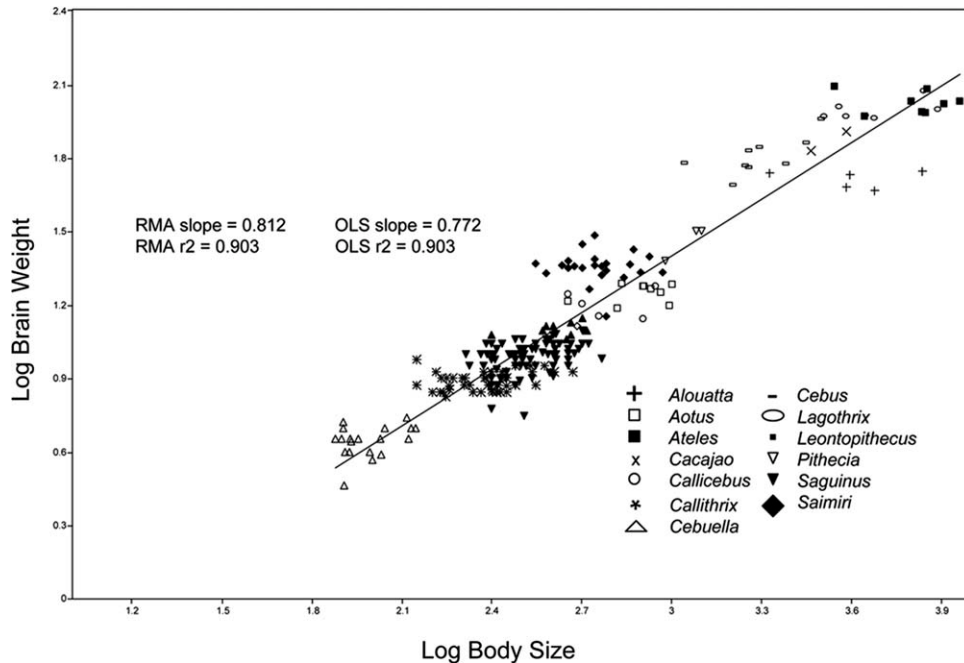


Fig. 1. Brain weight regressed against body weight for individual New World monkey specimens in the JMC dataset. Each symbol represents an individual from Appendix 1. The line represents the reduced major axis.

most *Alouatta* individuals are distributed well below the line. *Cebus* and *Saimiri* fall above the line, as expected. The two specimens of *Cacajao* in the JMC data set distribute slightly above the line of regression as well. The JMC data set did not include *Chiropotes*. Also notable is the position of most *Aotus*, at roughly the same body size as *Saimiri*. They tend to fall on the opposite side of the regression line.

The conservative sample profile of these primary data invites comparison to the larger data sets compiled from museum collections. Isler et al. (2008) offers perhaps the largest aggregation of well-controlled endocranial volume estimates on wild-caught individuals of known body weight. Using endocranial volume as a surrogate for brain weight yields a remarkably similar regression against body size for platyrrhines as a whole (Fig. 2). While this provides mutual confirmation of the integrity of both data sets, even small differences in sample configuration highlight some patterns more clearly. For example, hidden behind the density of the *Cebus* distribution are four specimens of *Cacajao* and 21 specimens of *Chiropotes*, each of which is distinctly above the line of regression. It is worth noting that Martin (1990), who presented one of the most comprehensive analyses of relative brain size (i.e., endocranial volume) in primates, with a separate table showing values calculated for platyrrhines, did not sample either of these two genera or *Pithecia*, their nearest living relative. In these new datasets, *Pithecia* falls near (JMC) or systematically below (Isler) the regression line. With this augmented taxonomic sample, the position of *Aotus* consistently below the regression line is also clarified, as is the similar plots of *Callicebus*, which was represented by only two individuals in the JMC data set.

Combining the two data sets produces a regression nearly identical in reduced major axis and least-squares regression values to the JMC data alone (Fig. 3). However, in each genus for which “adequate” sample sizes are available across species in both the JMC and the Isler et al. (2008) databases, there is heterogeneity between the samples (Table 2). For example, the JMC individuals of *Alouatta*, *Saguinus* and *Saimiri* tend to be lighter in body size and smaller in brain size. This indicates that these samples are not interchangeable, and caution must be applied (see Isler et al., 2008) when assuming the endocranial volumes of museum specimens are equivalent to actual brain weights at the genus level in New World monkeys.

An additional regression was executed without *Cebus*, one of the most highly encephalized primates (e.g., Martin, 1990), in order to clarify the position of *Chiropotes* and *Cacajao*, genera of about the same body size (Fig. 4). Now, both of the latter distribute above the regression lines when all the other taxa are included. And although the sample size for *Cacajao* individuals of known body weight is limited ($N = 6$ in this study), it is notable that there is complete transpositional separation among *Pithecia*, *Chiropotes*, and *Cacajao* when taking a finer grained look at this monophyletic group (Fig. 5). Furthermore, when removing the influence on the intercept and slope of the large sample of highly encephalized *Cebus*, *Pithecia* no longer appears to have a relatively small brain for a platyrrhine of its body size, but relative brain size is still elevated in *Cacajao* and *Chiropotes* by comparison to *Pithecia* and other platyrrhines. The impact on the positions of *Aotus* and *Callicebus* is less trenchant.

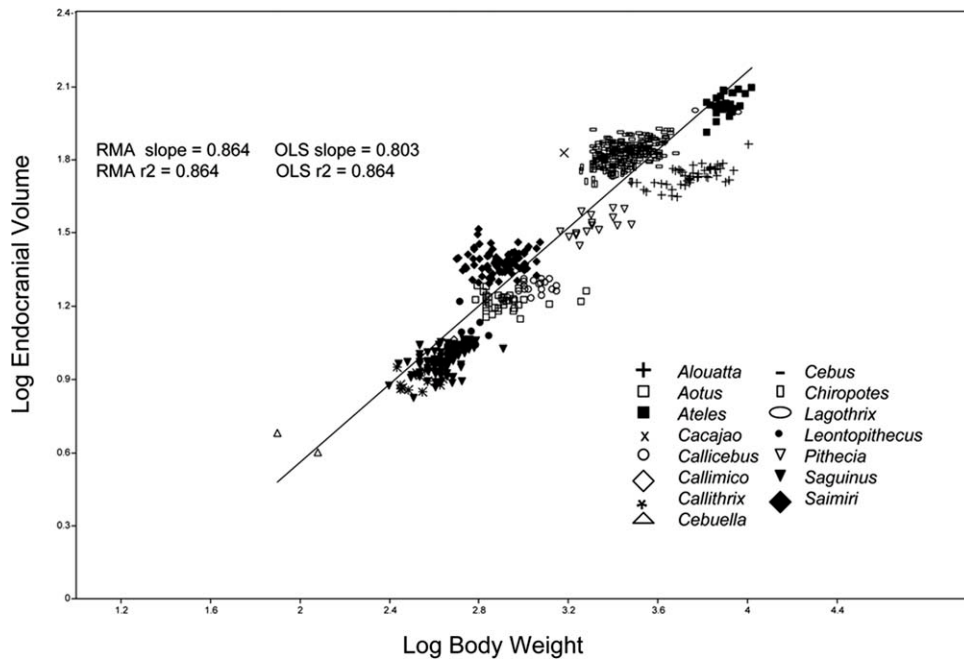


Fig. 2. Endocranial volume regressed against body size for New World monkey adults of known individual body weight as reported in Isler et al. (2008). The reduced major axis line is shown.

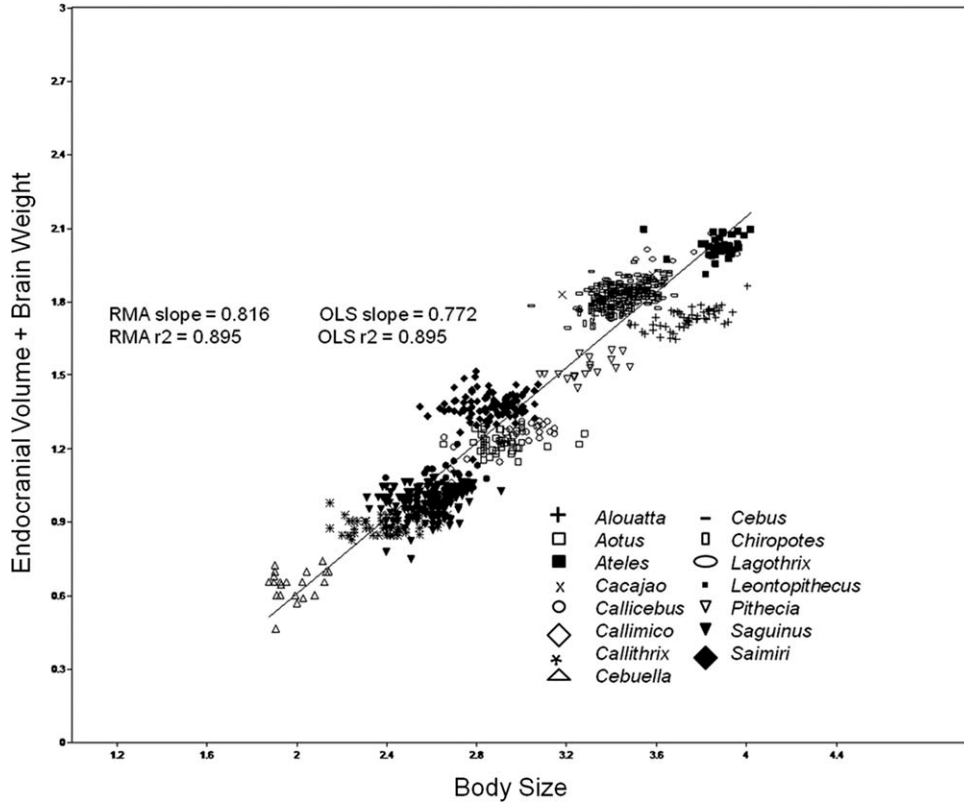


Fig. 3. Regression of brain weight or endocranial volume on body weight by combining the JMC and Isler et al. (2008) data sets. The line shown is the reduced major axis.

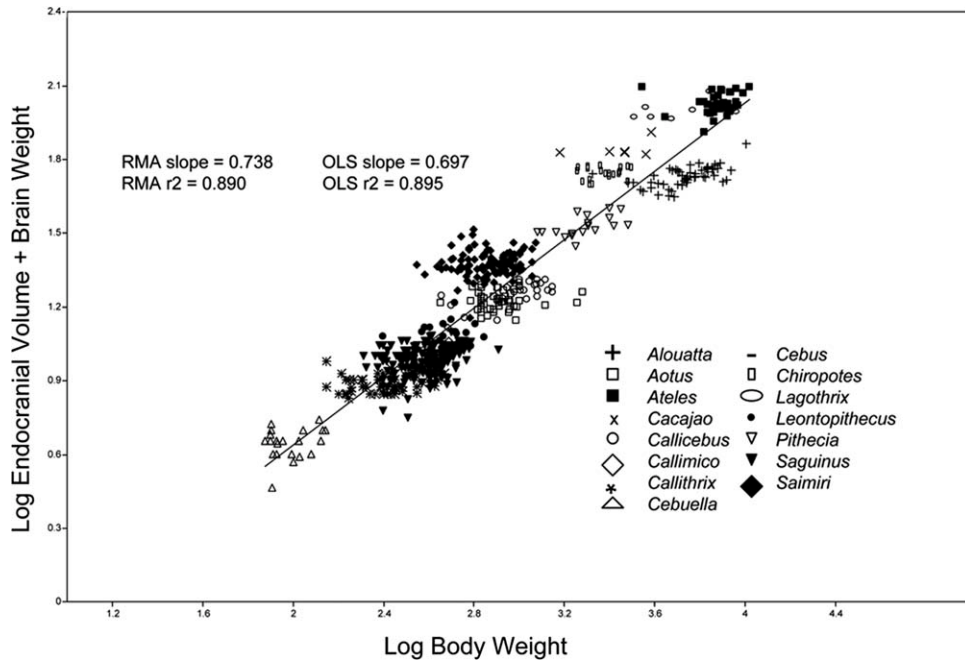


Fig. 4. Regression of brain weight or endocranial volume against body size for the JMC data and the Isler et al. (2008) data, with *Cebus* removed. The reduced major axis line is shown. The slope is less than in the regressions that include *Cebus*, as predicted, and so any inferences of relative brain size are qualified accordingly. Removal of *Cebus* enables the relative distribution of *Chiropotes* and *Cacajao* to be visible.

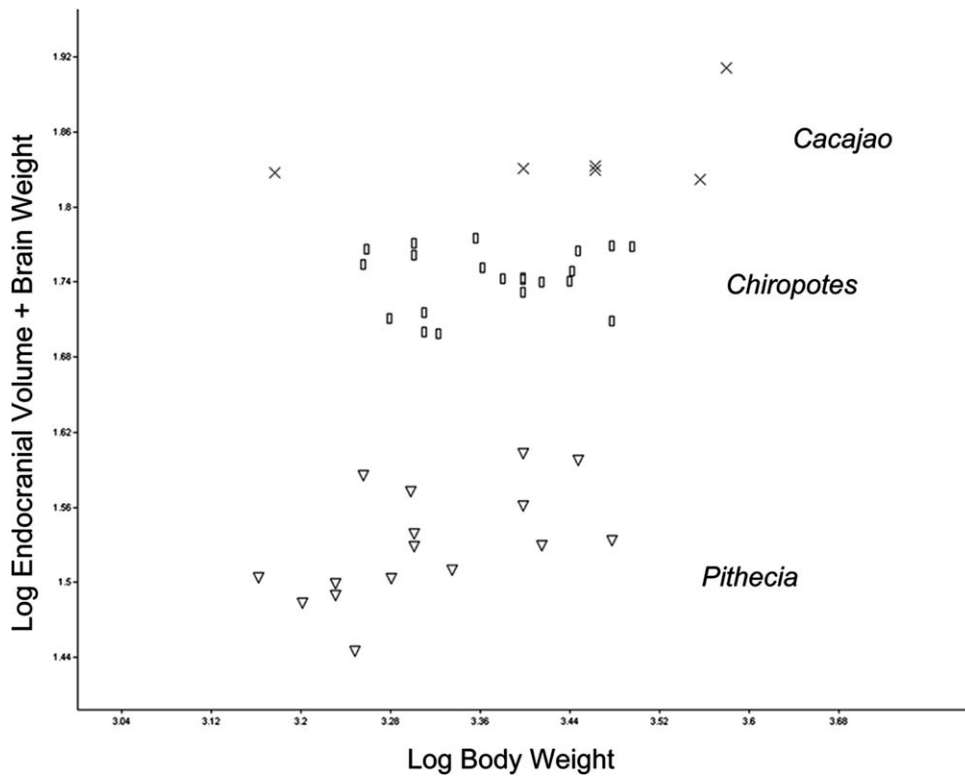


Fig. 5. Isolation of the plotted points in the brain size regression of *Pithecia*, *Chiropotes*, and *Cacajao*, indicating the degree of overlap in body weights and nonoverlap in measures of brain size.

To compliment these analyses, the Encephalization Quotient (EQ) was calculated (Jerison, 1973) for each genus (Table 3). As expected, when viewed in their cladistic context especially, the elevated relative brain sizes of *Saimiri* and *Cebus* (Fig. 6) are evident, as is the de-encephalized status of *Alouatta* (see Martin, 1990). New to this study, however, are the values for *Chiropotes* and *Cacajao*. Relative to other pitheciids (*Pithecia*, *Aotus*, *Callicebus*), the brains of both are quite encephalized. While the value of *Cacajao*, based on a small sample ($N = 6$), needs to be viewed with caution, it is higher than the computed for *Cebus*, which is based on a robust Isler et al. sample. The data for *Chiropotes* is more secure than for *Cacajao*, and it, too, indicates an elevated brain size that approaches the *Cebus* condition. Both are more encephalized than *Saimiri*.

To the extent that these regressions represent a robust display of the conservative nature of brain:body size proportions in New World monkeys, metrics relating to gut size and proportions presents just the opposite picture when compared with relative brain size measures. Table 3 documents the 18 species for which a coefficient of gut differentiation (CDG; = stomach + colon + caecum area/small intestine area) could be combined with known individual body weight. Figure 7 provides bivariate plots of the data. The distribution of values for *Alouatta*, the genus central to the possibility that poor diet quality could inhibit brain growth and maintenance (e.g., Aiello and Wheeler, 1995), complicates any broad generalizations about how gut size relates to relative brain size at the low end of the brain size spectrum in New World monkeys. *Alouatta* falls among a broad range of platyrrhine genera that combine relatively small brains with relatively large and differentiated guts. Included among them are the frugivorous-predaceous callitrichines and mixed feeders such as *Aotus* and *Callicebus*, which combine different proportions of leaves and/or insects to compliment their mostly frugivorous diet (see Cooke, 2011; Rosenberger et al., 2011).

At the other end of the spectrum (Fig. 7), *Cebus* and *Saimiri* appear to have relatively small guts and *Cebus* has the lowest coefficient of gut differentiation. This is consistent with the Chivers and Hladik (1980, 1984) observation of small, nondifferentiated guts being associated with an insectivorous-predatory feeding regimen. It is also consistent with the ETH (Aiello and Wheeler, 1995) in associating elevated EQs with small guts.

Within pitheciids, the brain:gut relationships are less clearly in evidence though the data are intriguing. Among the five genera sampled, *Cacajao* and *Chiropotes* have the highest EQ values, well above *Aotus*, *Callicebus*, and *Pithecia*. But measures of *Chiropotes* gut size and differentiation (Fig. 7b) are comparable overall to *Aotus*, *Callicebus*, and *Pithecia*.

The hypothesis is appealing that for *Alouatta* developing the kind of gut tube necessary to process a nutrient-poor, bulky diet is incompatible with expending energy simultaneously to develop an energetically expensive brain (e.g., Aiello and Wheeler, 1995; see also Rosenberger et al., 2011). The reverse could be argued for *Ateles*, though less demonstrably, that its proportions (Fig. 7b) can be sustained as a result of an ability to maintain a nutritionally balanced diet (Felton et al., 2008). But what the comparative evidence indicates more consequentially is that arguments for the cause

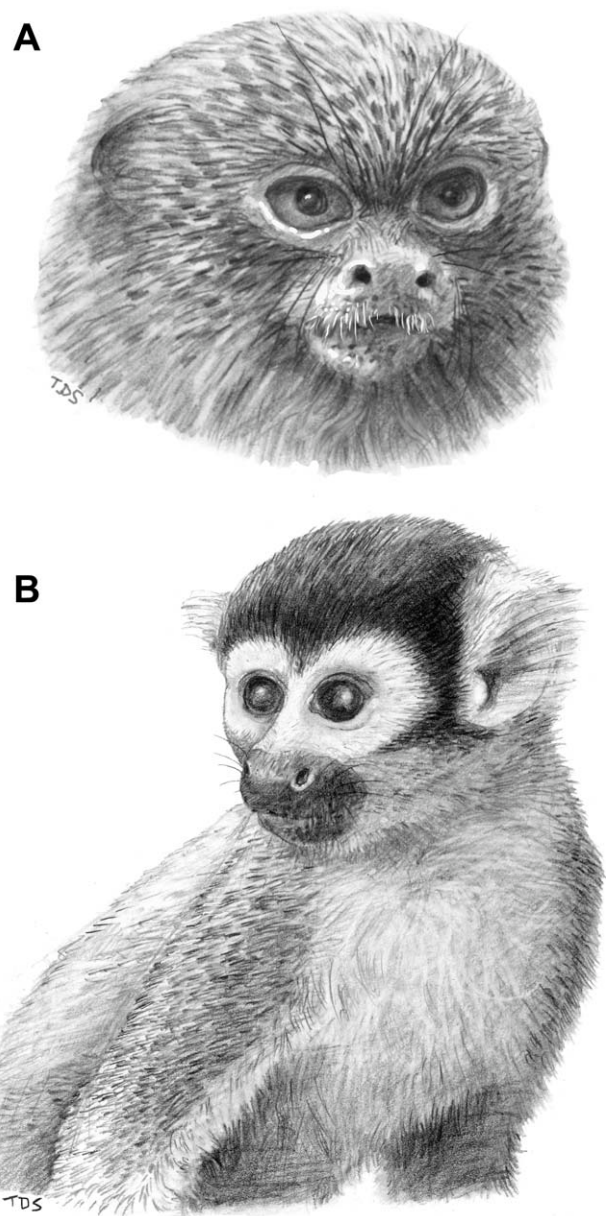


Fig. 6. Portraits of *Cebuella* (a), the smallest platyrrhine and smallest modern anthropoid, and *Saimiri* (b), one of the most encephalized platyrrhines. Original artwork by Tim Smith.

and effect relationship of gut size to brain size need to be made within at most the subfamily level of relatedness among platyrrhines. Also, single-factor explanations are not likely to be robust. While the relatively high brain size and/or encephalization quotient values for *Cacajao*, *Cebus*, and *Saimiri* may have been driven in parallel by the same selective pressures, say group size, and a narrow range of physiological mechanisms can perhaps explain how their conditions are maintained in terms of feeding and energetics, there are likely to be additional reasons for the gap that still separates *Cebus* from *Chiropotes*, for example, and *Saimiri* from *Cebus*.

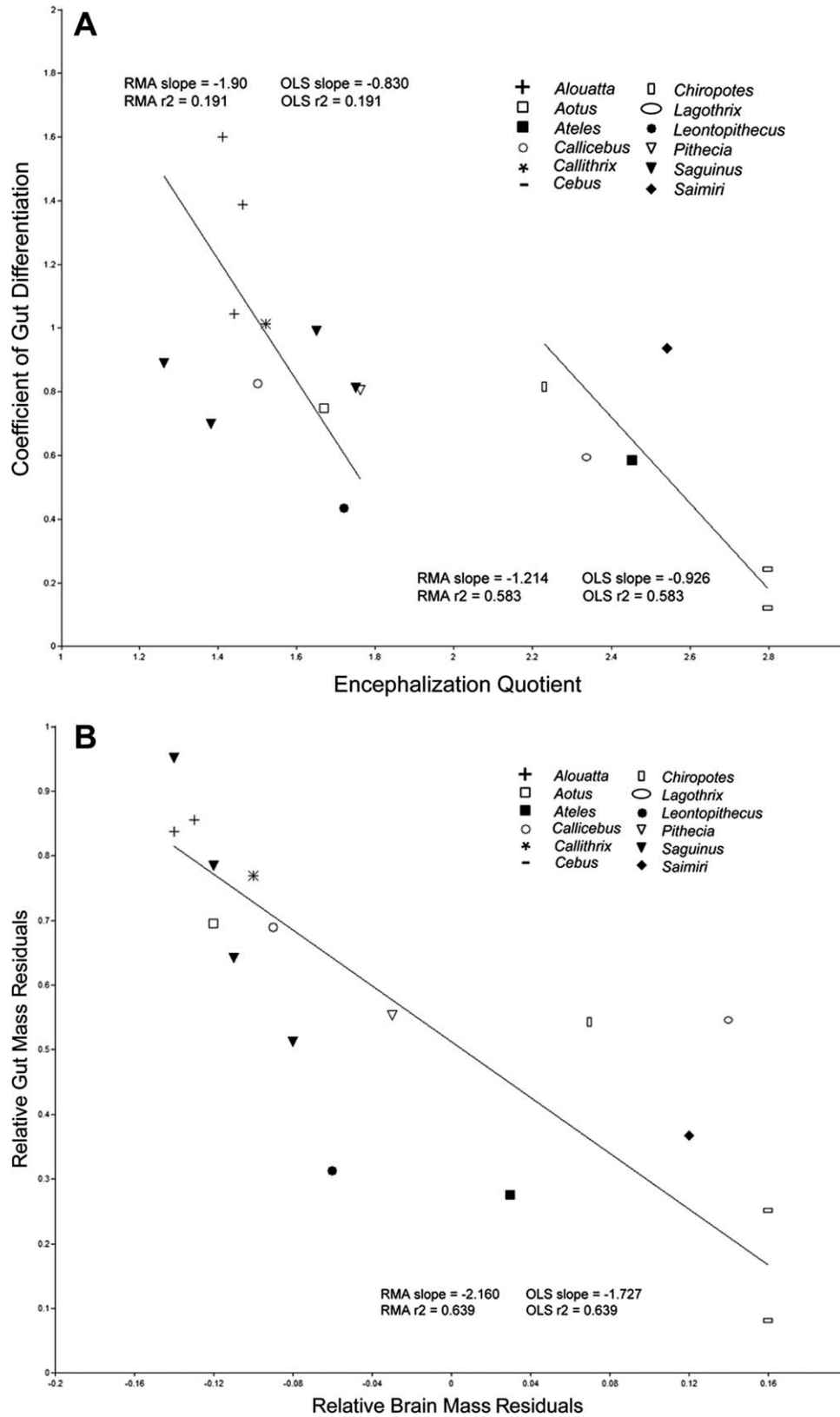


Fig. 7. Two representations of gut size and brain size relationships in New World monkeys. (a) Coefficient of gut differentiation regressed against Encephalization Quotient; (b) Residuals of relative gut mass regressed against residuals of relative brain mass.

CONCLUSIONS

Our data confirm several widely acknowledged outliers among platyrrhines, the relatively small brain size of *Alouatta*, and the relatively large brain sizes of *Cebus* and *Saimiri*. Additionally, we find that *Chiropotes* and *Cacajao* also have relatively large brains. A variety of hypotheses can be invoked to explain these observations. One general point that seems evident is that brain size has increased independently within at least three lineages, in cebines, pitheciins, and atelines. Each of these groups exhibits relatively derived socio-ecological strategies within their own respective clades.

While a trophic, physiological (proximate) adaptation may explain the case of *Alouatta* presently, that is, how a nutritionally poor diet corresponds with a strategy to minimize the metabolic costs of the body's largest energy-hungry organ, this may not provide a fitting evolutionary explanation. Fossil and cladistic evidence suggests the alouattin clade had already evolved a small brain prior to the emergence of dental adaptations exhibiting a full commitment to folivory, (Rosenberger et al., 2011). The Pleistocene Brazilian subfossil *Protopithecus*, a basal member of the alouattin clade, was apparently frugivorous and had a brain that was small relative to atelines, the alouattin sister-group. A closer relative, the Cuban *Paralouatta*, also had a relatively small brain and teeth far less folivorous in design than *Alouatta*.

These observations have several interesting consequences. While revealing that selection for a small brain is not incompatible with frugivory, it also begs the question of what drove the evolution of de-encephalization among alouattins prior to their dietary shift. One possible explanation is that de-encephalization relates to the evolution of the *Alouatta* howling mechanism, a central feature of its adaptive configuration. Brain size in the strict sense, phylogenetically and ontogenetically, must be governed by a network of developmental constraints. The mechanical hafting of the neurocranium on the basiocranium, coupled with the mounting of the pharyngeal arch derivatives (i.e., face) on the ventral side of that same axial plank, mean that extremes of prognathism and endocranial volume cannot coexist. Taxa tend to have big faces or big brains, but not both. In selecting for enlargement of the subbasal space in the throat of prehowlers to accommodate a voluminous hyolaryngeal system, the large facial skeleton was shifted forward and upward, placing it in a more precerebral position, while the caudal position of the foramen magnum was exaggerated. This spatial arrangement may have constrained brain size development, even before the selective imperative to maintain a small brain in connection with a nutritionally limited diet.

A component of the small-brain status of alouattins may be a function of phylogeny also (see Rosenberger et al., 2011). Three major platyrrhine clades, callitrichines being the only exception, present both relatively small-brained and large-brained genera, and the cladistic evidence suggests in several cases that the relatively smaller brains occur in the more basal members. 1) *Alouatta*, and alouattins, have smaller brains than atelines. 2) *Pithecia* has a smaller brain than *Chiropotes* and *Cacajao*, and *Callicebus* and *Aotus* have smaller brains than the latter as well. And, 3) callitrichines – in this case more properly seen as a sister-group of

cebines rather than a more basal member of the cebid radiation – have smaller brains than *Cebus* and *Saimiri*. As noted, this also means that increased encephalization has evolved multiple times in parallel among platyrrhines.

A more general explanation may clarify why *Pithecia*, *Callicebus* and *Aotus* have hypothetically retained primitively small brains. A combination of two factors are worth considering. Relatively small brains are associated in primates with monogamy or relatively small group size (e.g., Harvey et al., 1980; Dunbar, 1998). All three of these genera are typically monogamous (Fernandez-Duque, 2011; Norconk, 2011). In addition, feeding preferences may interplay. Rosenberger et al. (2011) suggest the mixed diets of *Aotus* and *Callicebus*, which involve fairly high proportions of leaves for anthropoids weighing about 1 kg, and leaves plus seeds in *Callicebus*, may subject the animals to the same classes of secondary compounds that folivores face in digesting leaves. Moreover, there is evidence that their guts are more differentiated than those of insectivores, also in analogy with folivores (see Chivers and Hladik, 1980). The avid seed-predator *Pithecia* is probably even more exposed to allelochemicals, which are concentrated in immature fruit and seed coats. Again paralleling folivores, the passage rate of digesta in *Pithecia* is relatively slow (Milton, 1988). Therefore, relatively small brains among these seed-predators are perhaps to be expected if their digestive strategies are comparable to a folivore's, especially at a smaller body size, thus absolutely smaller gut size, than present in colobines (see Davies and Oates, 1994) or platyrrhine semi-folivores (Rosenberger et al., 2011).

The new data for *Cacajao* and *Chiropotes* present something of a paradox. If *Cacajao* follows the same pattern as *Chiropotes*, which is barely distinguishable as a genus in overall morphology, they would share moderately large guts for platyrrhines of their brain size as well as relatively large brains. Based on their demonstrably elevated encephalization quotients, within the pitheciid clade as well as among NWM generally, the ETH model would predict small and well differentiated guts. But as noted, it appears that in primates the latter pattern is associated not only with folivory but also with seed-eating (Rosenberger et al., 2011). It is therefore tempting to explain the relatively high coefficient of gut differentiation values of these genera as a part of their highly modified seed-eating adaptive complex (e.g., Kinzey, 1992; Rosenberger, 1992; Norconk, 2007, 2011; Norconk and Veres, 2011). But this also requires that gut evolution is not yoked to encephalization in the same way it appears to be linked in *Alouatta*. This then may require an additional explanation. In the former case, group size (see Dunbar, 1998) may be an overriding factor. Norconk (2011) reports maximum group sizes for *Cacajao* and *Chiropotes* ranging between 30+ and 40+ individuals, that is, groups much larger than the essentially monogamous units found in their nearest relative *Pithecia*. A second contrast with *Alouatta* relates to the foraging requirements imposed by frugivory and seed-eating. The fruits *Cacajao* and *Chiropotes* feed on are widely distributed in space, as indicated by their large home ranges, which may encompass approximately 130–550 hectares (Norconk, 2011). In contrast, group or community ranges for *Alouatta* average 29 hectares (DiFiore et al., 2011).

The data on relative gut size and differentiation appears to be distributed around a natural break defined by encephalization quotient (Fig. 7b). Looked at in this way, it is of interest that platyrrhines with the largest relative brain sizes show contrasting patterns in gut differentiation. *Cebus* and *Saimiri* are themselves quite different in terms of gut proportions; *Cebus* is definitively quite differentiated, *Saimiri* only moderately so. If the data are robust, this may indicate different factors are involved in determining brain size proportions in the two. Perhaps the *Saimiri* EQ is exaggerated because its small body size is an affectation of dwarfism (see Hartwig, 1995). Notably, the *Alouatta* lineage may also have experienced dwarfism (see Halenar, 2011; Rosenberger et al., 2011), but without having the same effect on encephalization.

The variations exhibited by platyrrhines in relative brain size, relative gut size and within-gut proportions suggest multiple factors are in play and under selection for these variables across clades and dietary guilds. Potential causal factors favored as explanations, such as food (nutritional quality and foraging behavior) and sociality (group size) appear to interact in different ways among outlier taxa. Obviously, body mass is a powerful determinant of brain size for the radiation as a whole. But relative brain size seems to have been highly sensitive to a leafy diet and small group size in the de-encephalized *Alouatta*, while a contrasting frugivorous-predaceous diet and large-group form of sociality may have been selectively responsible for the highly encephalized *Cebus*. Still a third dietary pattern, seed-eating, plus large group size seems to have had a similar effect for *Chirotopes* and *Cacajao*. The latter three genera also may evince a close dietary parallelism as they are selective hard-object feeders. Perhaps this poses a cognitive challenge that we have underestimated.

The widespread occurrence of relatively small-brained platyrrhines, at both large and small body sizes, the commonness with which relatively small brains are found among more basal members of the clades, and the dietary variety exhibited by these animals suggests that the ETH formula oversimplifies the relationship between food quality and encephalization. As proposed (Aiello and Wheeler, 1995), large guts may indeed be a major constraint on the evolution of brain size for metabolic reasons, which also implies that evolving a relatively small gut could serve as a releaser in special cases, potentially with *Cebus*, for example. However, a more general rule possibly applies among platyrrhine no matter the food type. As a way of minimizing metabolic overhead, which is always assumed to be of selective value, brain:gut size and within-gut proportions may be kept in balance over a large range of body sizes, as a primitive condition, unless the relationship is overridden by new selective pressures. The common denominator among the largest brained platyrrhines—predaceous frugivores, seed-eating frugivores and soft-fruit frugivores—does not seem to be a high octane fuel source making big brains possible. But it does seem like large complex social groups makes it advantageous.

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APPENDIX 1. Individual body weight and brain weight data from Japan Monkey Center

Genus	Species	Sex	Body weight (g)	Brain weight (g)		
<i>Alouatta</i>	<i>caraya</i>	f	3800	48.3		
		m	4700	46.7		
<i>Alouatta</i>	<i>seniculus</i>	m	6800	56		
		m	3900	54		
<i>Aotus</i>	<i>trivirgatus</i>	f	660	15.4		
		f	680	19.5		
		f	810	19		
		f	850	18.5		
		f	980	15.8		
		m	800	19		
		m	920	18		
<i>Ateles</i>	<i>geoffroyi</i>	m	1000	19.3		
		f	6800	97.6		
		f	7100	121		
		f	8100	105.5		
<i>Ateles</i>	<i>paniscus</i>	f	9100	108		
		f	7000	97.5		
<i>Cacajao</i>	<i>rubicundus</i>	f	7200	130		
		f	3800	81.5		
<i>Callicebus</i>	<i>moloch</i>	m	2900	68		
		m	800	13.9		
<i>Callimico</i>	<i>goeldii</i>	m	880	19		
		f	480	13		
<i>Callithrix</i>	<i>argentata</i>	f	280	7.4		
		f	300	7.5		
<i>Callithrix</i>	<i>geoffroyi</i>	m	250	7.1		
		m	340	8.5		
		f	300	9		
		f	300	9		
		f	350	7.5		
		f	404	8.5		
		m	335	9		
		m	375	9		
		m	464	8.5		
		m	280	8		
<i>Callithrix</i>	<i>jacchus</i>	m	250	8.5		
		m	252	7		
		m	261	7.5		
		m	267	7		
		m	270	8		
		m	270	8.5		
		m	280	7		
		m	260	7		
		<i>Callithrix</i>	<i>penicillata</i>	m	260	7
				f	65	4.5
<i>Cebuella</i>	<i>pygmaea</i>	f	80	5		
		f	84.5	4.5		
		f	98	4		
		f	100	3.7		
		f	106	4.5		
		f	110	5		
		f	132	4.5		
		f	135	5		
		f	139	5		
		m	75	4.5		
<i>Cebus</i>	<i>albifrons</i>	m	79	4.5		
		m	80	5.3		
		m	80	5.3		
		m	80.5	2.9		
		m	81	4		
		m	84	4		
		m	85	4.4		
<i>Cebus</i>	<i>apella</i>	m	90	4.5		
		m	107	3.9		
		m	130	5.5		
		m	2800	73		
		m	2400	60		
		m	3150	91		

APPENDIX 1. Individual body weight and brain weight data from Japan Monkey Center (continued)

Genus	Species	Sex	Body weight (g)	Brain weight (g)
<i>Lagothrix</i>	<i>lagotricha</i>	m	6900	119.5
		m	7700	100.5
<i>Leontopithecus</i>	<i>rosalia</i>	f	500	14
		f	520	12.5
		m	460	13.5
		m	460	12
<i>Saguinus</i>	<i>fuscicollis</i>	f	250	6
		f	390	8.4
<i>Saguinus</i>	<i>geoffroyi</i>	f	317	11.5
		f	380	11.5
		f	390	11.5
		m	260	10.5
<i>Saguinus</i>	<i>labiatus</i>	m	420	11
		m	580	9.6
		f	450	10.1
<i>Saguinus</i>	<i>leucopus</i>	m	300	11.8
		f	300	10
<i>Saguinus</i>	<i>mystax</i>	m	309	10.5
		m	337	9.5
		f	350	11
		f	400	11
<i>Saguinus</i>	<i>nigricollis</i>	f	500	12.5
		m	400	12
		m	525	11
		f	250	8
		f	250	7.5
		f	255	10
		f	261	7.5
		f	280	8.5
		f	312	9
		f	340	8
		f	350	9
		f	400	9
		f	410	9.5
		m	280	8
		m	290	10
		<i>Saguinus</i>	<i>oedipus</i>	m
m	310			7.8
m	317			9.5
m	320			5.6
m	400			10
m	400			8.1
m	450			10.5
f	250			11
f	250			9.5
f	250			11
f	257			9.5
f	260			10.5
f	267			8
f	270			11
f	285			10
f	300			9
f	312	10		
f	320	10.5		
f	320	10.5		
f	320	10		
f	340	10.5		
f	340	10.5		
f	350	10.5		
f	370	10.2		
f	380	11		
f	410	10		
f	410	12.1		
f	450	9		
f	450	9.5		
f	460	11		

APPENDIX 1. Individual body weight and brain weight data from Japan Monkey Center (continued)

Genus	Species	Sex	Body weight (g)	Brain weight (g)
<i>Saimiri</i>	<i>sciureus</i>	f	470	10.1
		f	500	11
		m	250	10
		m	260	8.7
		m	300	11.5
		m	300	9.5
		m	317	10.5
		m	320	10.5
		m	324	9
		m	351	10.5
		m	380	11.5
		m	384	10
		m	405	10.5
		m	487	10.5
		f	500	22.5
		f	550	23
f	600	23.5		
f	600	22		
m	500	28.1		
m	550	24.5		
m	550	30.5		
m	840	25		
?	530	18.5		
?	580	21.1		
?	583	22.8		
?	603	14.3		
?	688	20.6		
?	721	23.3		
?	743	26.9		
?	785	21.6		
?	929	21.6		

APPENDIX 2. Individual data for specimen body weight, gut area (sum of stomach + colon + caecum), and coefficient of gut differentiation (CGD)

			Body Weight (g)	Gut Area	CGD
Pitheciidae					
<i>Aotus</i>	<i>trivirgatus</i>		970	251.0	0.87
<i>Aotus</i>	<i>trivirgatus</i>		1,008	248.0	0.72
<i>Aotus</i>	<i>trivirgatus</i>		785	120.0	0.70
<i>Aotus</i>	<i>trivirgatus</i>		565	137.0	0.60
<i>Aotus</i>	<i>trivirgatus</i>		797	214.0	0.55
<i>Aotus</i>	<i>trivirgatus</i>		854	360.0	0.89
<i>Callicebus</i>	<i>moloch</i>	f	1,020	277.8	0.97
<i>Callicebus</i>	<i>moloch</i>	m	860	295.0	0.89
<i>Callicebus</i>	<i>moloch</i>	m	1,180	285.0	0.57
<i>Callicebus</i>	<i>moloch</i>	m	1,150	281.0	0.55
<i>Callicebus</i>	<i>caligatus</i>	m	880	187.2	1.13
<i>Pithecia</i>	<i>irrorata</i>		1,580	375.9	1.12
<i>Pithecia</i>	<i>albicans</i>	m	3,000	481.0	0.76
<i>Pithecia</i>	<i>pithecia</i>		1,192	146.0	0.54
<i>Chiropetes</i>	<i>satanus</i>	f	1,700	286.0	0.66
<i>Chiropetes</i>	<i>satanus</i>	m	2,200	245.0	0.83
<i>Chiropetes</i>	<i>satanus</i>	m	2,280	507.0	0.87
Atelinae					
<i>Alouatta</i>	<i>belzebul</i>	f	4,600	683.0	0.83
<i>Alouatta</i>	<i>belzebul</i>	f	5,000	1474.0	1.40
<i>Alouatta</i>	<i>belzebul</i>	f	5,000	1074.0	0.63
<i>Alouatta</i>	<i>belzebul</i>	m	5,600	827.0	1.03
<i>Alouatta</i>	<i>belzebul</i>	m	4,400	913.0	1.32

APPENDIX 2. Individual data for specimen body weight, gut area (sum of stomach colon caecum), and coefficient of gut differentiation (CGD) (continued)

			Body Weight (g)	Gut Area	CGD
<i>Alouatta</i>	<i>seniculus</i>	m	6,150	1996.0	1.31
<i>Alouatta</i>	<i>seniculus</i>	m	4,090	724.0	0.77
<i>Lagothrix</i>	<i>lagothricha</i>		7,900	825.0	0.69
<i>Lagothrix</i>	<i>lagothricha</i>		5,670	1105.0	0.52
<i>Ateles</i>	<i>paniscus</i>		5,902	412.0	0.53
Cebidae					
<i>Saimiri</i>	<i>sciureus</i>	f	850	137.0	0.29
<i>Saimiri</i>	<i>sciureus</i>	m	1,130	110.0	0.34
<i>Saimiri</i>	<i>madeirae</i>		1,010	149.0	0.46
<i>Saimiri</i>	<i>madeirae</i>		880	116.2	0.46
<i>Saimiri</i>	<i>madeirae</i>		970	87.7	0.49
<i>Saimiri</i>	<i>madeirae</i>		820	56.1	0.30
<i>Cebus</i>	<i>apella</i>		2,000	247.0	0.20
<i>Cebus</i>	<i>capucinus</i>		2,800	177.0	0.46
<i>Saguinus</i>	<i>geoffroyi</i>		420	84.0	0.46
<i>Saguinus</i>	<i>midas</i>		426	54.0	0.61
<i>Saguinus</i>	<i>oedipus</i>		430	69.0	0.76
<i>Saguinus</i>	<i>oedipus</i>		379	71.0	0.86
<i>Saguinus</i>	<i>oedipus</i>		435	78.0	0.56
<i>Saguinus</i>	<i>oedipus</i>		455	40.0	0.54
<i>Saguinus</i>	<i>oedipus</i>		357	111.0	0.93
<i>Saguinus</i>	<i>oedipus</i>		454	111.0	1.10
<i>Saguinus</i>	<i>oedipus</i>		365	91.0	0.95
<i>Saguinus</i>	<i>imperator</i>		384	83.0	1.22
<i>Saguinus</i>	<i>imperator</i>		460	79.0	0.72
<i>Saguinus</i>	<i>imperator</i>		328	115.0	0.96
<i>Saguinus</i>	<i>imperator</i>		482	53.0	1.10
<i>Saguinus</i>	<i>imperator</i>		615	79.0	0.69
<i>Saguinus</i>	<i>imperator</i>		490	62.0	0.65
<i>Saguinus</i>	<i>imperator</i>		461	119.0	0.78
<i>Saguinus</i>	<i>imperator</i>		310	134.0	0.91
<i>Saguinus</i>	<i>fuscicolis</i>		410	95.0	0.79
<i>Saguinus</i>	<i>mystax</i>	m	560	199.0	0.99
<i>Leontopithecus</i>	<i>rosalia</i>		530	85.0	0.44
<i>Leontopithecus</i>	<i>rosalia</i>		680	90.0	0.46
<i>Leontopithecus</i>	<i>rosalia</i>		430	45.0	0.41
<i>Leontopithecus</i>	<i>rosalia</i>		680	56.0	0.42
<i>Callithrix</i>	<i>emiliae</i>		327	73.1	1.42
<i>Callithrix</i>	<i>jacchus</i>		210	83.0	1.01

CGD, gut area/small intestine area.