



Expensive brains: “brainy” rodents have higher metabolic rate

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Brains are the centers of the nervous system of animals, controlling the organ systems of the body and coordinating responses to changes in the ecological and social environment. The evolution of traits that correlate with cognitive ability, such as relative brain size is thus of broad interest. Brain mass relative to body mass (BM) varies among mammals, and diverse factors have been proposed to explain this variation. A recent study provided evidence that energetics play an important role in brain evolution (Isler and van Schaik, 2006). Using composite phylogenies and data drawn from multiple sources, these authors showed that basal metabolic rate (BMR) correlates with brain mass across mammals. However, no such relationship was found within rodents. Here we re-examined the relationship between BMR and brain mass within Rodentia using a novel species-level phylogeny. Our results are sensitive to parameter evaluation; in particular how species mass is estimated. We detect no pattern when applying an approach used by previous studies, where each species BM is represented by two different numbers, one being the individual that happened to be used for BMR estimates of that species. However, this approach may compromise the analysis. When using a single value of BM for each species, whether representing a single individual, or available species mean, our findings provide evidence that brain mass (independent of BM) and BMR are correlated. These findings are thus consistent with the hypothesis that large brains evolve when the payoff for increased brain mass is greater than the energetic cost they incur.

Keywords: Rodentia, Bayesian inference, correlated evolution

INTRODUCTION

Brain mass (BrM) varies across mammals. While BrM scales with body mass (BM), several other factors seem to influence BrM, such as sociability, environmental and dietary specializations, as well as energetic costs of brain tissue (Mace et al., 1981). Large brains contain more neurons and neural connections, and thus have greater potential for information processing. Large brains also tend to be more modular, which allows a great amount of connections between neurons (Krubitzer and Kaas, 2005). Hence, increased brain mass and potential for neural connections may have facilitated large brained mammals to colonize complex habitats, develop sensory systems and evolved complex societies (e.g., Budeau and Verts, 1986).

While there are many potential benefits of large brains, brain tissue is costly. For example, the mass-specific metabolic rate of the human brain is nine times higher than that of the body as a whole (Martin, 1981). The metabolic costs by having a large brain

must be paid for by a direct mother metabolic constraint or by a trade-off mechanism between brain mass and energy consumption by other functions (e.g., Gibbons, 1998; Pitnick et al., 2006). Other energy allocations such as relative costs of flight and reproductive strategy in birds may also be reduced to shunt energy to an enlarged brain (Isler and van Schaik, 2006). Recent examples also show that BrM may become decoupled from BM over short time spans. For example, Gonzalez-Voyer et al. (2009) found that Tanganyikan cichlid BM exhibited recent bursts of rapid evolution, a process that is consistent with divergence linked to ecological specialization, while BrM showed no bursts of divergence but evolved in gradual manner, consistent with energetic constraints to rapid BM change.

Originally, Aiello and Wheeler (1995) proposed that a primate is able to meet the high metabolic cost of a large brain without incurring a compensatory increase in relative basal metabolic rate (BMR) by decreasing the amount of other metabolically expensive tissues (i.e., heart, lung, kidney, liver, and gastrointestinal tract). A similar hypothesis was recently proposed for fish (Kaufman et al., 2003). Recently, Isler and van Schaik (2009) using a large compilation of brain size, BM, and life history data, found evidence that an energetically costly increase in brain size has to be met by either increasing the total energy budget of a species or by

Abbreviations: AIC, Akaike information criterion; BL, branch lengths in phylogenies; BM, body mass; BMR, basal metabolic rate; BrM, brain mass; CORR, measure of correlated evolution between characters in a Bayesian framework; GTR, general time reversible models of nucleotide substitution; IC, phylogenetic independent contrasts; PDAP, phenotypic diversity analysis programs.

compensating changes of energy allocation to other maintenance functions, such as digestion or growth and offspring production, or a combination of these. Martin, 1981, 1996), for example, found that the energetic investment of the mammalian mother during the development of the fetus and during the postnatal life up to the time of weaning resulted in a weak link between BMR and brain mass. Similarly, Jones and MacLarnon (2004) showed that for certain clades of bats, maternal investment plays an important role in the adult brain mass. While a number of studies have thus focused on these mechanisms of development, little is known about the evolutionary relationship between BMR and BrM. Very few studies have tested the generality of the “costly brain” hypotheses across multiple species with different evolutionary histories, and using phylogenetic approaches.

Basal metabolic rate is a fundamental parameter in comparative studies and lineages-specific exponents characterize its allometric scaling (White et al., 2009). Recently, Isler and van Schaik (2006) controlling both for BM and phylogenetic relationships found evidence that BMR correlated with BrM in large groups of mammals. However, BrM explained a small % of the variation in metabolic rate at the species and family level (2.6 and 10.4%, respectively). At higher taxonomic levels, independent contrast (IC) revealed a significant correlation only for primates.

It is possible that the use of composite phylogenies lacking resolution and accurate estimates of branch lengths (BL) may have obscured the underlying patterns (e.g., Malia et al., 2003). Other potential confounding variables are the different possible ways of controlling for species BM. Here we generated a novel phylogeny of wild rodents using Bayesian analysis of cytochrome b sequence data. We included species where high-quality BMR, BrM, and BM data are available. We then used this analysis to test the hypothesis that BMR and BrM are correlated within rodents, after taking into consideration both BM and phylogeny.

MATERIALS AND METHODS

Cytochrome b for 132 rodent species and six rabbits as outgroups (Wilson and Reeder, 2005) were downloaded from GenBank, and one sequence donated (Table A1 in Appendix). Cytochrome b was chosen as that marker has proven to be of high utility for species level phylogenetics (May-Collado and Agnarsson, 2006; Agnarsson et al., 2010, 2011)

Sequences were aligned using ClustalX 1.83 (Thompson et al., 1997) via Mesquite (Maddison and Maddison, 2008). The preferred model for the Bayesian analyses was selected with Modeltest (Posada and Crandall, 2001) using the AIC criterion (Posada and Buckley, 2004). The best-fitting model was GTR + γ + I (Yang, 1994). Bayesian analyses were carried out using MrBayes V3.12 (Huelsenbeck and Ronquist, 2001) with the settings as specified in Agnarsson and May-Collado (2008). The Markov chain Monte Carlo search was ran with 10,000,000 generations sampling the Markov chain every 1,000 generations, and the sample points of the first 7,000,000 generations were removed (“burnin”), after which the chain had reached stationarity.

Data on the \log of BrM and BM (g), and BMR ($\text{cm}^3\text{O}_2/\text{h}$) were used in this study (Table A1 in Appendix). For studies comparing traits among species, such as regression analyses, it is necessary to account for phylogenetic relationships among the compared

species (Felsenstein, 1985). Ignoring phylogenetic relationships can lead to pseudoreplication as species are not independent data points, rather independent evolutionary changes in the traits being compared are the data points, or the IC (see Felsenstein, 1985; May-Collado et al., 2007) among species and lineages. To describe the evolutionary relationship between BMR and BrM we performed various phylogenetic analyses. (i) The PDAP module in Mesquite (Midford et al., 2008) was used to estimate IC (Felsenstein, 1985). We used BL as estimated by MrBayes testing them for statistic appropriateness using PDAP. To correct for BM we regressed BMR and BrM against BM and subsequently regressed the residuals from these regressions (Garland et al., 1993). If the residuals are correlated then that is consistent with a relationship among these variables (BMR and BrM), that is independent of the BM of, and phylogenetic relationship among, species (e.g., May-Collado et al., 2007). Regression of residuals was performed using SPSS 2007 (SPSS Inc.). We also regressed BMR and BrM directly. (ii) To evaluate the correlated evolution among BMR, BrM, and BM, we assess the phylogenetic effect on the trends in character relationships between taxa (i.e., the observed pattern) using the best model of evolution that was found for each character. To do this we evaluated the significance of the relationships between the pair of characters using a measure of correlated evolution (CORR) in a Bayesian framework implemented in BayesTrait 1.0 (Pagel and Meade, 2007), assessing the probability of positively correlated (CORR > 0) and negatively correlated evolution (CORR < 0). As the null hypothesis we used a model in which the covariance between characters was set to zero (i.e., complete character independence, CORR = 0), and the alternative hypothesis was, then, the observed covariance between characters (Pagel, 1999a, 1999b). If the null hypothesis was rejected (i.e., a significant historical relationship between characters exists), then we concluded that the phylogenetic relationship and the models of evolution of the characters influence the observed patterns, and we corroborate the hypothesis of correlated evolution between BMR, BrM, and BM.

These methods account for phylogenetic uncertainty by running analyses across multiple trees. We used a Bayesian approach based on maximum likelihood with 10 test per tree and estimating Pagel (1999 a,b) escalated phylogenetic parameters (Table A2 in Appendix). The sign test was used for statistical comparisons (Zar, 1996) with STATISTICA 6.0 (StatSoft, 2001).

RESULTS

The novel phylogeny finds support for the monophyly of each currently recognized taxonomical bat family with the exception that Heteromyidae contains Geomyidae, and one species of Muridae, *Sigmodon hispidus*, groups with Cricetidae (Figure A1 in Appendix). The phylogeny overall agrees well with recent rodent phylogenies at higher levels (e.g., Jansa and Weksler, 2004; Montgelard et al., 2008) and thus represents an reasonable hypothesis for to study the evolution of characters (e.g., Pagel and Harvey, 1988)

Independent contrast revealed associations between BM and BMR ($p < 0.0001$; $r^2 = 0.77$), and with BrM ($p < 0.0001$; $r^2 = 0.85$), and between BMR and BrM ($p < 0.0001$; $r^2 = 0.71$). When using a single value to represent species mass we also found significant correlation between BMR and BrM, after

accounting for BM. When using a single individual weight to represent the species, BMR explained 9.7% of the variation in BrM ($p = 0.0003$; $r^2 = 0.097$; **Figure 1A**). Two extreme outliers affected the regression and removing these outliers resulted in much stronger regression ($p < 0.0001$; $r^2 = 0.20$; **Figure 1B**). The outliers represent 3 species of small rodents (Cricetidae, Arvicolinae), that inhabit circumpolar Northern Hemisphere biome (Nowak, 1999). These Lemmings seem to have higher metabolic rate than typical rodents with similar BrM, which may be related to living in extreme climates requiring higher metabolism. This demonstrates that the climate and habitat as well as other potentially confounding factors (BM, food habits, substrate, a restriction to islands or highlands, use of torpor, and type of reproduction) make it difficult to demonstrate a significant correlation between BMR and BrM, even when it exists (e.g., McNab, 2008).

When using species mean BM, BMR explained approximately 3% of variation in BrM ($p < 0.05$, $r^2 = 0.029$). This correlation, however, disappears when using two BM values for each species,

one, the estimated species mean, to calculate residuals of BrM, and the second, of the individuals used for the BMR experiments, to calculate residuals of BMR ($p > 0.05$).

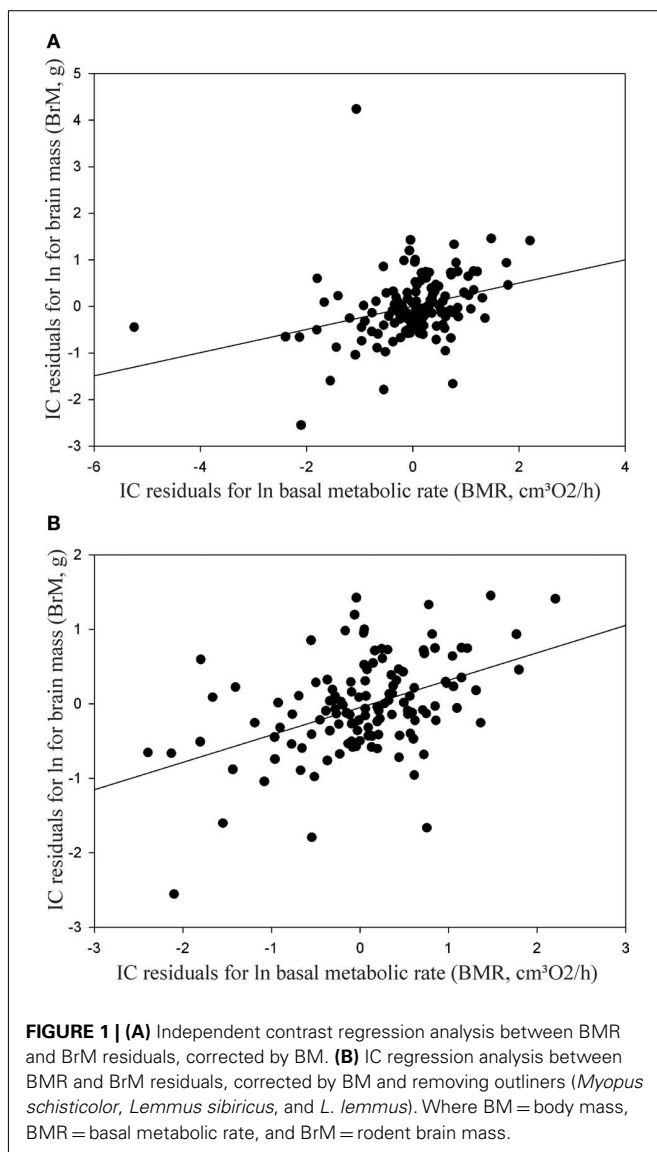
CORR indicated significant correlations between all variables ($p < 0.0001$; $\text{CORR} \geq 1$), with the highest correlation recorded between BM and BrM ($p < 0.0001$; $\text{CORR} = 2.86$; $r^2 = 0.95$; **Figure 2**), followed by BM and BMR ($p < 0.0001$; $\text{CORR} = 2.24$; $r^2 = 0.92$; **Figure 2**), and finally BMR and BrM ($p < 0.0001$; $\text{CORR} = 1.86$; $r^2 = 0.91$; **Figure 2**).

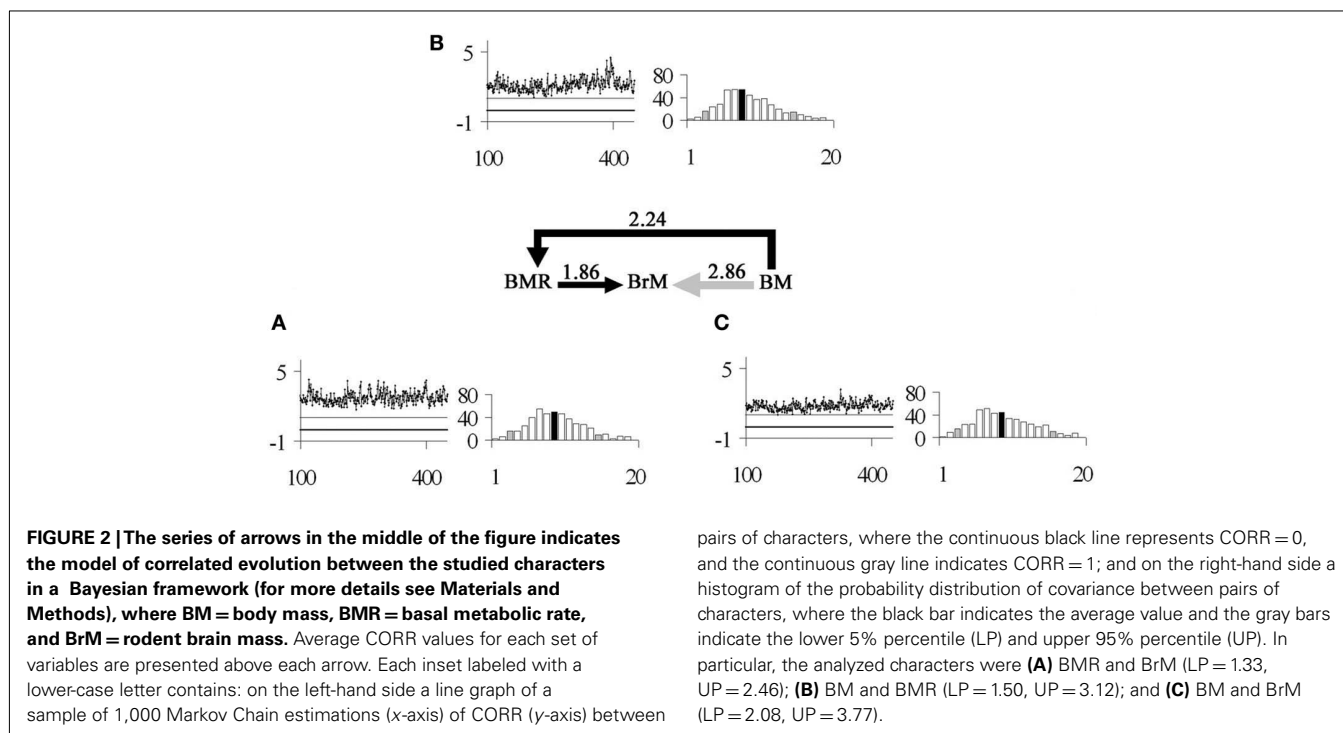
DISCUSSION

Brains are the centers of the nervous system of vertebrates, controlling the organ systems of the body and coordinating responses to changes in the ecological and social environment (Shultz, 2010). Although brain mass per se does not capture the complexity of brain function, there is general evidence that relative brain size roughly correlates with cognitive ability (e.g., Barton and Harvey, 2000). Hence the evolution of brain size is of broad interest, including what factors may favor and constrain the evolution of relatively large, modular and complex brains (Sol, 2009).

Basal metabolic rate is influenced by a variety of factors (BM White and Seymour, 2003; climate Lovegrove, 2000; demography Kurta and Ferkin, 1991). Furthermore, an increase in BrM results in increased costs for maintenance and information processing (Niven and Laughlin, 2008). For example, Karbowski (2007) found that in volume-specific cerebral glucose metabolic rate of different brain structures closely scales with brain volume. These results confirm that information processing in the brain requires large amounts of metabolic energy.

Here, we demonstrate a possible correlation between BMR and BrM within Rodentia. Independent of BM large brained rodents exhibit correspondingly higher BMR. These results contrast previous studies (McNab and Eisenberg, 1989). For instance, Isler and van Schaik (2006) found support for this relationship across all mammals combined, and within primates (IC $p = 0.025$, $r^2 = 0.20$), but not within other orders, such as rodents. Adjustments appear to be clade-specific, the slopes of best-fit lines for BrM against BM tend to be higher in analyses of more inclusive taxa (e.g., orders and suborders) and lower in analyses of less inclusive taxa (families, subfamilies, and genera; e.g., Finarelli and Flynn, 2009). We hypothesize that the discrepancy between our findings and previous studies is potentially caused by two factors. First, the use of a composite versus primary-data based phylogenies, and second, differences in accounting for BM. Composite phylogenies often reflect taxonomy, not necessarily phylogeny, and typically lack accurate BL estimates, two aspects that reduce the efficiency of comparative tests. Accounting for BM is a complicated problem, but we argue that using more than a single value for a species, as have prior studies, may introduce confounding variables. Thus using an estimate of species BM, such as average species BM to generate BrM residuals, and the BM of the individual that happened to be used to evaluate BMR to generate BMR residuals, can likely adds noise that may obscure real patterns. If, for example, the evaluation of BMR happened to have been done on an atypically small or large animal, this would strongly affect the BM-BMR residual, and could readily obscure subtle patterns





across two or more variables that are both highly correlated with BM. Instead using a single value, whether mean BM of a species, or the weight of a single individual seems at least to be a reasonable alternative. Furthermore, species mean BM is a measure independent of the available measures for BMR and BrM (typically single individuals), and as such provides a relatively neutral control unlikely to result in systematic error.

Here, we used a novel primary-data-based phylogeny with BL estimates and single estimates of species BM (species average or single individuals). Considering the compendium of factors that may contribute to BMR, the up to 20% of variation explained by BrM in rodents is high. Clearly, though, further research is necessary to understand the interplay between these variables, and ideally accurate estimates of species means based on multiple individuals would be available for each of these variables (e.g., Smith and Jungers, 1997).

Our study is also consistent with two evolutionary paths “favoring” an increase in BrM across rodent species. First, a “direct” path in which an increase in BMR correlates with an increase in BrM (Figure 2A). Alternatively, an “indirect” and additive path in which the effect of BM on BMR allows BrM to increase (Figures 2A,B). Comparatively, the direct scaling effect of BMR on BrM is the least

important relationship (Figure 2A), but the importance of direct scaling increases when considering the indirect path. Dunbar and Shultz (2007) supported the indirect path scenario in primates, where BMR had a limiting effect on BrM, while BM had an effect on BrM through BMR.

CONCLUDING REMARKS

Here, we corroborate the hypothesis of Isler and van Schaik (2006) that an increase in brain mass is accompanied by an increase in basal metabolic rate, and suggests that this pattern may be general across mammals. Our findings corroborate the hypothesis that large brains evolve when the payoff for increased brain mass is greater than the energetic cost they incur (Niven and Laughlin, 2008).

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APPENDIX

Electronic Supplementary Material to the Manuscript “Expensive brains: ‘brainy’ rodents have higher metabolic rate” by Raul Sobrero, Laura J. May-Collado, Ingi Agnarsson, and Cristian E. Hernandez.

Table A1 | List of species and GenBank accesses of rodent and rabbit for the cytochrome b mitochondrial gene. Data on the *log* of brain mass (BrM, g), body mass (BM, g), and basal metabolic rate (BMR, cm³O₂/h) for rodent species based on McNab and Eisenberg (1989); White and Seymour (2003); and Isler and van Schaik (2006).

Species	BrM	BMR	BMR*	BM	GenBank Accession#
ORDER RODENTIA					
Family Aplodontiidae					
<i>Aplodontia rufa</i>	1.95	6.03	McNab (1979b)	6.69	AJ389528
FAMILY AGOUTIDAE					
<i>Agouti (Cuniculus) paca</i>	3.40	7.92	Arends and McNab (2001)	9.00	AY206551
FAMILY SCIURIDAE					
<i>Ammospermophilus leucurus</i>	0.85	4.54	Lovegrove (2000), Chappell and Bartholomew (1981a,b)	4.66	AY685488
<i>Cynomys ludovicianus</i>	1.79	6.05	Reinking et al. (1977)	6.68	AF157890
<i>Glaucomys volans</i>	0.59	4.51	Lovegrove (2003)	4.29	AJ389531
<i>Marmota monax</i>	2.37	6.50	Benedict (1938)	8.34	AF157953
<i>Marmota flaviventris</i>	2.33	7.34	Reinking et al. (1977)	8.52	AF143927
<i>Paraxerus cepapi</i>	0.51	4.98	Viljoen (1985)	5.26	U59179
<i>Sciurus aberti</i>	1.92	6.07	Golightly and Ohmart (1978)	6.44	U10163
<i>Sciurus carolinensis</i>	1.97	5.91	Bolls and Perfect (1972)	6.35	U46167
<i>Spermophilus beldingi</i>	1.19	5.07	Lovegrove (2003)	5.57	AF157951
<i>Spermophilus richardsonii</i>	1.21	5.08	Lovegrove (2003)	5.87	S73150
<i>Spermophilus tridecemlineatus</i>	0.86	4.64	Lovegrove (2003)	4.93	AF157877
<i>Spermophilus beecheyi</i>	1.63	5.76	Baudinette (1972)	6.38	AF157918
<i>Spermophilus tereticaudus</i>	0.60	4.54	Hudson et al. (1972)	5.05	AF157940
<i>Spermophilus lateralis</i>	1.18	5.46	Lovegrove (2003)	5.51	AF157950
<i>Spermophilus parryii</i>	1.46	6.25	Geiser (1988)	6.18	AY428024
<i>Spermophilus undulatus</i>	1.58	6.50	Casey et al. (1979)	6.59	AF157912
<i>Spermophilus townsendi</i>	0.72	4.86	Lovegrove (2003)	5.29	AF157949
<i>Tamiasciurus hudsonicus</i>	1.34	5.54	Pauls (1981)	5.24	AF147643
<i>Tamias striatus</i>	0.77	4.50	Wang and Hudson (1971)	4.55	AF147670
<i>Tamias amoenus</i>	0.33	4.57	Kenagy and Vleck (1982), Jones and Wang (1976)	3.93	AF147630
<i>Tamias minimus</i>	0.47	4.29	Jones and Wang (1976), Willems and Armitage (1975)	3.81	AF147649
<i>Tamias palmeri</i>	0.68	4.73	Yousef et al. (1974)	4.11	AF147655
<i>Xerus inauris</i>	1.34	5.74	Lovegrove (2003)	6.44	AY452689
FAMILY GEOMYIDAE					
<i>Geomys bursarius</i>	0.71	4.93	Bradley and Yousef (1975)	5.31	AY393941
<i>Thomomys talpoides</i>	0.33	4.86	Lovegrove (2003)	4.79	AF215809
FAMILY HETEROMYIDAE					
<i>Chaetodipus hispidus</i>	-0.39	3.87	Lovegrove (2003)	3.66	AF172832
<i>Dipodomys microps</i>	0.19	4.10	Lovegrove (2003)	4.09	AY926385
<i>Dipodomys agilis</i>	0.29	4.16	Lovegrove (2003)	4.12	U65303
<i>Dipodomys deserti</i>	0.55	4.54	Lovegrove (2003)	4.87	AY926381
<i>Dipodomys heermanni</i>	0.31	4.29	Hinds and Rice-Warner (1992)	4.09	AY926369
<i>Dipodomys merriami</i>	0.05	3.79	Lovegrove (2003)	3.63	AF 173502
<i>Dipodomys ordii</i>	0.32	4.16	Lovegrove (2003)	3.99	AY926365
<i>Heteromys anomalus</i>	0.02	4.61	Arends and McNab (2001)	4.25	DQ168468
<i>Heteromys desmarestianus</i>	0.08	4.60	Hinds and MacMillen (1985)	4.28	DQ168467
<i>Liomys salvini</i>	-0.26	3.88	Lovegrove (2003)	3.80	DQ168546
<i>Microdipodops megacephalus</i>	0.51	3.43	Lovegrove (2003)	2.65	AY926362

(Continued)

Table A1 | Continued

Species	BrM	BMR	BMR*	BM	GenBank Accession#
<i>Perognathus flavus</i>	-1.20	2.85	Hinds and MacMillen (1985)	2.17	DQ168551
<i>Perognathus longimembris</i>	-1.80	2.53	Lovegrove (2003)	2.12	U65302
FAMILY DIPODIDAE					
<i>Jaculus jaculus</i>	0.19	4.52	Hooper and Hilali (1972)	4.01	AJ416890
<i>Napaeozapus insignis</i>	-0.73	3.68	Brower and Cade (1966)	3.14	AJ389535
<i>Zapus hudsonicus</i>	-0.84	3.81	Lovegrove (2003)	2.88	DQ664918
FAMILY CRICETIDAE					
<i>Arvicola terrestris</i>	0.49	4.73	Lovegrove (2003)	5.13	AF119269
<i>Cricetus cricetus</i>	0.90	5.45	Lovegrove (2000), Hart (1971)	5.85	AY275109
<i>Clethrionomys (Myodes) rutilus</i>	-0.58	4.34	Rosenmann et al. (1975)	2.87	AF119274
<i>Clethrionomys (Myodes) gapperi</i>	-0.58	4.09	Lovegrove (2003)	2.83	AF272633
<i>Clethrionomys (Myodes) glareolus</i>	-0.65	4.15	Hart (1971)	2.88	AY309419
<i>Clethrionomys (Myodes) rufocanus</i>	-0.49	4.08	McNab (1992)	3.65	AY309418
<i>Dicrostonyx groenlandicus</i>	-0.33	4.59	McNab (1992)	4.23	AJ131444
<i>Isthmomys pirrensis</i>	0.54	4.80	Hill (1975)	4.58	EF989945
<i>Lemmus sibiricus</i>	0.20	5.06	Lovegrove (2003)	4.17	AJO12671
<i>Lemmus lemmus</i>	-0.15	5.26	Hissa (1970)	4.23	AY219145
<i>Megadontomys thomasi</i>	0.23	4.82	Lovegrove (2000), Hart (1971)	4.49	EF989949
<i>Mesocricetus auratus</i>	0.07	4.99	Hart (1971)	4.72	AF119265
<i>Microtus agrestis</i>	-0.56	4.15	McDevitt and Speakman (1996)	3.10	DQ662102
<i>Microtus arvalis</i>	-0.60	4.13	Lovegrove (2000), Ishii et al. (1996)	3.41	AM991098
<i>Microtus guentheri</i>	-0.37	4.38	Haim and Izhaki (1993)	3.94	AY513807
<i>Microtus mexicanus</i>	-0.62	3.85	McNab (1992)	3.56	AF163897
<i>Microtus townsendii</i>	-0.13	4.50	Kenagy and Vleck (1982)	3.82	AF163906
<i>Microtus pinetorum</i>	-0.58	4.07	McNab (1992)	3.21	AF163904
<i>Microtus ochrogaster</i>	-0.34	4.50	Lovegrove (2003)	3.82	AF163901
<i>Microtus longicaudus</i>	-0.36	4.30	Lovegrove (2003)	3.86	AF187160
<i>Microtus pennsylvanicus</i>	-0.26	4.40	Lovegrove (2003)	3.62	AF119279
<i>Microtus montanus</i>	-0.37	4.40	Lovegrove (2003)	3.68	AF119280
<i>Microtus californicus</i>	-0.25	4.22	McNab (1992)	3.77	AF163891
<i>Myopus schisticolor</i>	-0.58	4.54	Saarela and Hissa (1993)	3.51	EU165268
<i>Neotoma albigula</i>	0.77	4.90	McNab (1986)	5.41	AF108704
<i>Neotoma fuscipes</i>	0.98	4.99	McNab (1970)	5.26	AF376475
<i>Neotoma cinerea</i>	0.97	5.13	McNab (1986)	5.80	AF186799
<i>Ochrotomys nuttalli</i>	-0.37	3.30	Layne and Dolan (1975)	3.07	AY195798
<i>Ondatra zibethicus</i>	1.55	6.47	McNab (1992)	7.22	AF119277
<i>Oligoryzomys longicaudatus</i>	-0.40	3.93	Bozinovic and Rosenmann (1988)	3.28	AY452198
<i>Onychomys torridus</i>	-0.53	3.39	Whitford and Conley (1971)	3.04	EF989967
<i>Peromyscus boylii</i>	-0.34	3.99	Mazen and Rudd (1980)	3.31	AY322506
<i>Peromyscus gossypinus</i>	-0.39	3.61	Glenn (1970), Tannenbaum and Pivorun (1988)	3.18	DQ973102
<i>Peromyscus leucopus</i>	-0.46	3.52	Lovegrove (2003)	2.97	EF989980
<i>Peromyscus polionotus</i>	-0.87	3.07	Glenn (1970)	2.76	EF989995
<i>Peromyscus maniculatus</i>	-0.50	3.60	Lovegrove (2003)	2.93	AF119261
<i>Peromyscus californicus</i>	-0.09	4.06	Lovegrove (2003)	3.70	AF155393
<i>Peromyscus eremicus</i>	-0.62	3.48	Lovegrove (2003)	2.99	AY322503
<i>Peromyscus crinitus</i>	-0.63	3.44	Lovegrove (2003)	2.61	AY376413
<i>Peromyscus truei</i>	-0.29	3.83	Lovegrove (2003)	3.36	AF108703
<i>Peromyscus megalops</i>	0.11	4.51	McNab (1988)	4.09	DQ861377
<i>Phyllotis darwini</i>	-0.66	4.27	Bozinovic and Rosenmann (1988)	3.91	AY956728
<i>Podomys floridanus</i>	-0.06	3.95	Glenn (1970)	3.70	EF989977
<i>Reithrodontomys megalotis</i>	-0.92	3.11	Tomasi (1985), Pearson (1960)	2.37	EF990008
<i>Sigmodon hispidus</i>	0.13	5.44	Bowers (1971), Scheck (1982)	4.89	AF108702

(Continued)

Table A1 | Continued

Species	BrM	BMR	BMR*	BM	GenBank Accession#
<i>Scotinomys teguina</i>	-0.87	3.44	Hill and Hooper (1971)	2.42	EF990029
<i>Scotinomys xerampelinus</i>	-0.65	3.46	Hill and Hooper (1971)	2.72	AF108706
FAMILY SPALACIDAE					
<i>Nannospalax (Spalax) ehrenbergi</i>	0.63	4.70	Lovegrove (2003)	5.28	AJ416891
<i>Tachyoryctes splendens</i>	0.69	5.02	McNab (1979b)	5.46	AF160602
FAMILY MURIDAE					
<i>Acomys cahirinus</i>	-0.43	3.83	Shkolnik and Borut (1969)	3.74	Z96053
<i>Aethomys (Micaelamys) namaquensis</i>	-0.66	3.87	Lovegrove (2003)	3.83	EU3 49731
<i>Apodemus flavicollis</i>	-0.36	5.03	Lovegrove (2003)	3.48	AF159392
<i>Apodemus sylvaticus</i>	-0.53	4.04	Lovegrove (2003)	3.17	AF159395
<i>Conilurus penicillatus</i>	0.65	5.09	Hinds and Rice-Warner (1992)	5.01	AM910935
<i>Desmodillus auricularis</i>	-0.05	4.47	Downs and Perrin (1994)	3.83	AJ851272
<i>Gerbillurus pæba</i>	-0.17	3.55	Downs and Perrin (1990)	3.18	AJ430557
<i>Gerbillus nanus</i>	-0.51	3.19	Lovegrove (2003)	2.64	AJ851270
<i>Hydromys chrysogaster</i>	1.47	6.27	Dawson and Fanning (1981)	6.55	AM408339
<i>Mastomys natalensis</i>	-0.26	3.49	Haim and Fourie (1980)	4.06	AY751296
<i>Meriones unguiculatus</i>	0.12	4.34	Weiner and Gorecki (1981)	4.05	AF119264
<i>Micromys minutus</i>	-1.24	3.05	Lovegrove (2000), Hart (1971)	1.86	AB201996
<i>Mus minutoides</i>	-1.31	3.10	Lovegrove (2003)	1.61	AY057816
<i>Notomys alexis</i>	-0.04	3.81	MacMillen and Lee (1970)	3.61	AY176318
<i>Otomys irroratus</i>	0.32	4.44	Haim (1987)	4.95	AH012645
<i>Paratomys brantsii</i>	-0.48	4.43	Du Plessis et al. (1989)	4.57	AF141224
<i>Pseudomys hermannsburgensis</i>	-0.71	3.15	MacMillen et al. (1972)	2.42	AY176321
<i>Rattus sordidus</i>	0.53	4.67	Collins and Bradshaw (1973)	5.03	EF186477
<i>Rattus fuscipes</i>	0.49	4.44	Collins (1973)	4.91	EF186439
<i>Rattus rattus</i>	0.33	5.12	McNab (1988)	5.01	AB033702
<i>Rhabdomys pumilio</i>	-0.37	3.47	Haim (1987)	3.72	AF533116
<i>Stochomys longicaudatus</i>	0.24	4.58	Lovegrove (2000)	4.17	EU292149
<i>Tatera indica</i>	0.61	4.33	Goyal et al. (1981)	4.94	AJ430563
<i>Tatera (Gerbilliscus) afra</i>	0.44	5.20	Duxbury and Perrin (1992)	4.17	AJ430560
<i>Thallomys paedulus</i>	-0.20	4.47	Lovegrove et al. (1991)	4.39	DQ381926
FAMILY NESOMYIDAE					
<i>Cricetomys gambianus</i>	1.88	6.93	Lovegrove (2003)	7.05	AF160614
<i>Saccostomus campestris</i>	-0.20	3.94	Haim et al. (1991)	3.92	EF529796
FAMILY BATHYERGIDAE					
<i>Cryptomys hottentotus</i>	-0.66	4.17	Lovegrove (2003)	4.84	AY425891
<i>Heliophobius argenteocinereus</i>	0.36	4.31	McNab (1979a)	5.08	U87527
<i>Heterocephalus glaber</i>	-0.65	3.25	Lovegrove (2003)	4.11	AF155870
FAMILY CHICHILLIDAE					
<i>Chinchilla lanigera</i>	1.66	5.64	Lovegrove (2003)	6.26	AF283981
<i>Lagostomus maximus</i>	2.80	7.55	Arends and McNab (2001)	8.45	AF245485
FAMILY CAVIIDAE					
<i>Cavia porcellus</i>	1.55	5.85	Arends and McNab (2001)	6.01	NC_000884.1
FAMILY HYDROCHAERIDAE					
<i>Hydrochaeris (Hydrochoerus) hydrochaeris</i>	4.32	8.79	Arends and McNab (2001)	10.81	Unpublished**
FAMILY DASYPROCTIDAE					
<i>Dasyprocta leporina</i>	3.13	7.35	Arends and McNab (2001)	8.01	AF437783
FAMILY OCTODONTIDAE					
<i>Spalacopus cyanus</i>	0.46	4.53	Lovegrove (2003)	4.53	AF007061
<i>Octodon degus</i>	0.73	5.15	Lovegrove (2003)	5.35	AF422914
FAMILY HYSTRICIDAE					
<i>Hystrix africaeaustralis</i>	3.11	7.77	Haim et al. (1990)	9.78	X70674

(Continued)

Table A1 | Continued

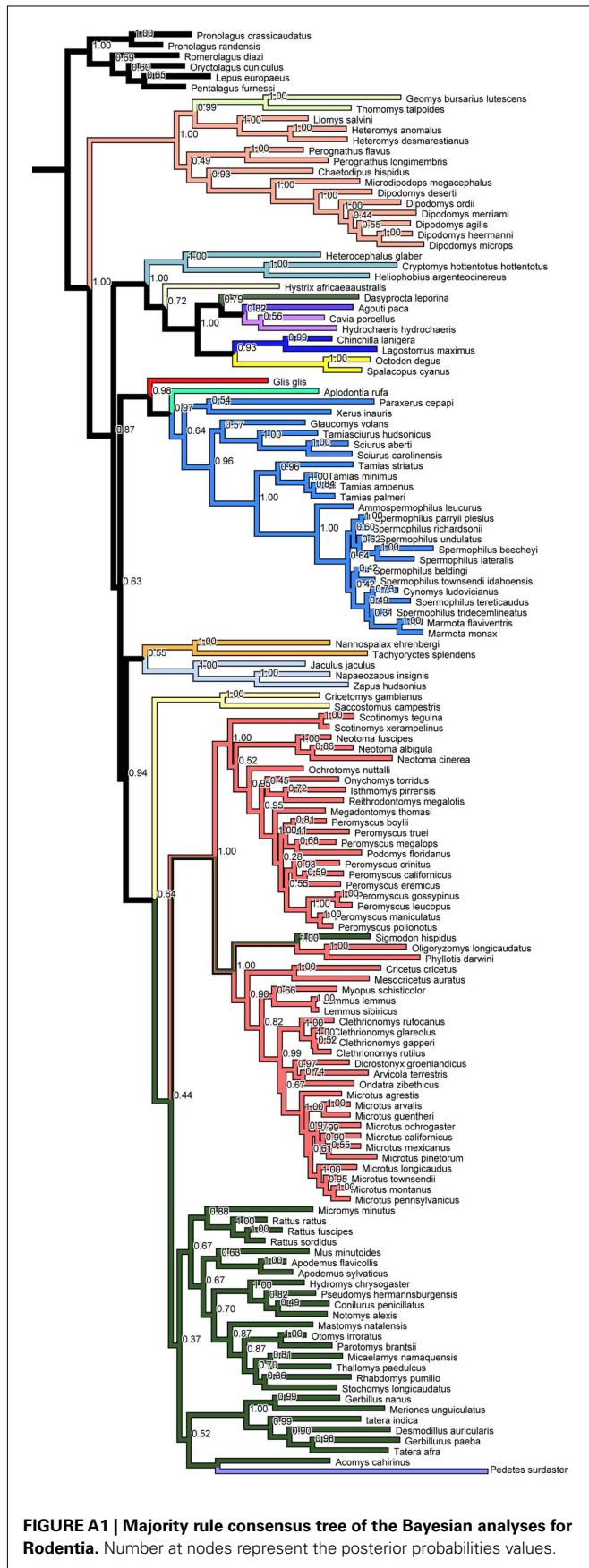
Species	BrM	BMR	BMR*	BM	GenBank Accession#
FAMILY GLIRIDAE					
<i>Myoxus (Glis) glis</i>	0.57	5.06	Geiser (1988)	4.86	NC_001892.1
FAMILY PEDETIDAE					
<i>Pedetes capensis</i>	2.41	6.68	Lovegrove (2000)	8.06	U59176
Out groups					
Order Lagomorpha					
FAMILY OCHOTONIDAE					
<i>Ochotona alpina</i>					DQ335487
<i>Ochotona turuchanensis</i>					DQ335507
<i>Ochotona princeps</i>					NC_005358.1
FAMILY LEPORIDAE					
<i>Lepus europaeus</i>					NC_004028.1
<i>Oryctolagus cuniculus</i>					EU285255
<i>Pentalagus furnessi</i>					AY292720
<i>Pronolagus crassicaudatus</i>					AY292738
<i>Pronolagus randensis</i>					AY292737
<i>Romerolagus diazi</i>					AY292734

*Original sources for BMR data.

**Sequence (714 bp) donated by Sharon A. Jansa (University of Minnesota, US) and Guillermo D'Elia (Universidad de Concepcion, Chile).

Table A2 | Results of Bayesian estimations of lambda (λ) and kappa (κ) phylogenetic parameters of Pagel (2002) under a Continuous Random Walk model. In this approach: (1) λ , reveals whether the phylogeny fits to the patterns of covariance among species for a given trait. If a trait is not evolving among species this parameter will take the value 0, indicating that a phylogenetic correction is not necessary. If traits are evolving as expected given the tree topology, λ , takes the value of 1.0. Values of $\lambda = 1.0$ are consistent with the constant-variance model (sometimes called Brownian motion) and is therefore a correct representation of the data; (2) κ scales the relationship between individual branch lengths and trait evolution (Pagel, 1994, 2002). The value of this parameter is the power to which individual branch lengths should be raised in order to maximize the fit of the model of evolution to the data. If κ is 1, trait evolution is directly proportional to branch length and, then, the gradual mode of trait evolution is better supported. Values of κ greater than 1 signify proportionally more evolution in longer branches. Values of κ less than 1 signify proportionally more evolution in shorter branches. In the extreme case of $\kappa = 0$, trait evolution is independent of branch length, which is consistent with a punctuational mode of evolution.

Variable	BrM		BMR		BM	
	Mean	SD	Mean	SD	Mean	SD
	0.962	0.027	0.865	0.067	0.991	0.007
	1.652	0.328	1.644	0.368	1.218	0.039



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