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How do diet and body mass drive reproductive strategies in mammals?

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Larger body size tends to lead to lower reproductive rates in mammals, but we do not understand how diet impacts this relationship. Reproductive strategies vary from *K*-selected (producing few offspring with extensive parental care) to *r*-selected (producing many offspring with little parental care). Here, we investigate how diet and body size impact the reproductive strategies of mammals within a phylogenetic framework using an index for reproductive strategy. For all diet categories we find larger mammals to be more *K*-selected. This relationship is significant for herbivores and omnivores, but not for carnivores, although the relationship for carnivores is comparable to that of herbivores and omnivores. The relationship is non-linear in carnivores and may be a consequence of differences between insect and vertebrate predators. Ultimately, the trend of more *K*-selected strategies with larger body size holds true for herbivores and omnivores, but different trajectories exist for carnivores depending on diet.

ADDITIONAL KEYWORDS: evolution – life history – mammals.

INTRODUCTION

The tempo and mode of reproduction in mammals is the consequence of natural selection acting on ecological pressures and physiological constraints. Two end-member reproductive strategies have been classically identified: *K*-selected, those taxa producing few offspring with extensive parental care, and *r*-selected, those producing many offspring with little parental care (MacArthur & Wilson, 1967; Pianka, 1970). *K*-selected strategies require allocating a considerable amount of energy and resources to the rearing of each individual offspring and are categorized as 'competitors,' as opposed to *r*-selected strategies, which require relatively little energy investment in individual offspring and are generally considered 'colonizers' (MacArthur & Wilson, 1967; Pianka, 1970).

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The independent evolution of body size (Smith *et al.*, 2010, 2016; Slater, 2013) and diet (Price *et al.*, 2012) are understood in mammals and the relationship between these two factors has been well studied in recent years (Price & Hopkins, 2015; Pineda-Munoz, Evans & Alroy, 2016). The relationships between various aspects of reproductive strategy and a large number of life history factors, including body mass and diet, were explored by Eisenberg (1981), but the effects of all these factors on reproductive strategies were not. The relationship between body size and life history traits is well understood (Blueweiss *et al.*, 1978; Western, 1979; Charnov, 1991; Charnov & Berrigan, 1993; Martin & Palumbi, 1993; Isaac *et al.*, 2005; Sibly & Brown, 2007), but quantitative methods have yet to explore the effects of diet on this relationship. These relationships also need to be tested within a phylogenetic framework. The ancestral state for mammalian body size is predicted to be small (Smith *et al.*, 2010) which might yield more *r*-selected

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taxa closer to the base of the tree. The diversification of ecological diversity in Mesozoic mammals could also be correlated with phylogenetic signal in reproductive strategies (Luo, 2007). This gap in knowledge leads us to ask, how does diet impact the relationship between body size and life history in mammals? To answer this question we used phylogenetic comparative methods to investigate the effects of diet on the relationship between body size and reproductive life history in extant mammals.

MATERIALS AND METHODS

We downloaded life history details from 5417 taxa from the PanTHERIA database (Jones *et al.*, 2009). We only used female life history variables in this study. Number of offspring per year is simply litter size multiplied by the number of litters per year. Percentage of year dedicated to parental care adds the gestation age and weaning age and determined what percentage of the year is devoted to those two variables. This variable will be greater than 100% in cases where more than a year is dedicated to these variables. Sexual lifespan is the total lifespan minus the age of sexual maturity. Only 560 mammal species (~10% of species) have all necessary variables. Most families in this study have more than one species present and sample a normal distribution of life history variables. We ran a principal components analysis (PCA) on these three variables to orient the data in a way that minimized the number of variables and maximized the variance. Principal component one was extracted (proportion of variance explained = 64.13% and eigenvalue = 0.6413275) and used as the reproductive strategy index (RSI; External Database S1).

We used a phylogenetically informed analysis of covariance (PANCOVA) to test whether diet, body mass and phylogeny (independent variables) drive the evolution of reproductive strategy (dependent variable). PANCOVA was performed using the caper package version 0.5.2 (Orme *et al.*, 2013) in R version 3.2.3 (R Core Team, 2015). Diet data are available from Price *et al.* (2012) while body mass data are from PanTHERIA (Jones *et al.*, 2009). The diet database was constructed from published accounts reporting data obtained through analysis of stomach, cheek-content, or food stores, behavioural observations, or faecal analysis (Price *et al.*, 2012). A uniform and explicit criterion was applied to these observations to produce a repeatable coding of the carnivore, omnivore and herbivore diet strategies (Price *et al.*, 2012). The result is a high-quality and repeatable diet coding (Price *et al.*, 2012). Phylogenetic signal for RSI was also calculated in caper using Pagel's λ (Pagel, 1997, 1999). We used 101 all-mammal trees based on the topology of Fritz, Bininda-Emonds & Purvis (2009), which had polytomies resolved using a constant rate birth–death process following the methods of Kuhn, Mooers & Thomas (2011). Marine and volant mammals have distinctly different body masses and life history from non-volant terrestrial mammals (Price *et al.*, 2012; Price & Hopkins, 2015) and therefore we removed them from the PANCOVA. R code is presented in External Database S2.

RESULTS

Six life history traits (litter size, number of litters per year, gestation age, weaning age, total lifespan and age at sexual maturity) of mammals, including volant (flying) and marine species, were used to calculate three variables (number of offspring per year, percentage of year dedicated to parental care and sexual lifespan) that were then transformed with a PCA to create the RSI. This index is a numerical proxy for reproductive strategy in which larger values increase along a spectrum from *K*-selection to *r*-selection. We found that reproductive strategies are highly phylogenetically conserved (λ = 0.9451, Supporting Information, Table S1). There is a negative, significant relationship between RSI and body mass independent of diet ($P < 0.001$) as well as for herbivores ($P < 0.0001$) and omnivores ($P = 0.0323$). A non-significant relationship exists between the index of reproductive strategy and body mass for organisms with a carnivorous diet ($P = 0.5217$); however, the slope of the linear relationship for this group is also negative (Fig. 1A, Table S2). Other summary statistics for the PANCOVA are presented in Table S2. When volant and marine mammals are excluded, the overall model is still significant but the results for carnivore are significant (Table S3).

Reproductive strategy in mammals is partially driven by the three factors investigated in this study: phylogenetic relatedness, diet and body mass. It is clear that higher values of RSI (indicating *r*-strategies) are the ancestral state for many mammal lineages, with lower values (*K*-selection) evolving several times throughout the tree (Fig. 2). This evolutionary trajectory fits with the known history of mammals, evolving from small-bodied omnivores in the Mesozoic (Smith *et al.*, 2010), which would be expected to be *r*-selected under this analysis. Although only about 10% of mammal species are included in this study, those species belong to about 77% of orders and about 59% of families. *K*-selection originated twice in marsupials, twice in bats and three times in rodents. All other orders appear to have evolved *K*-selection only

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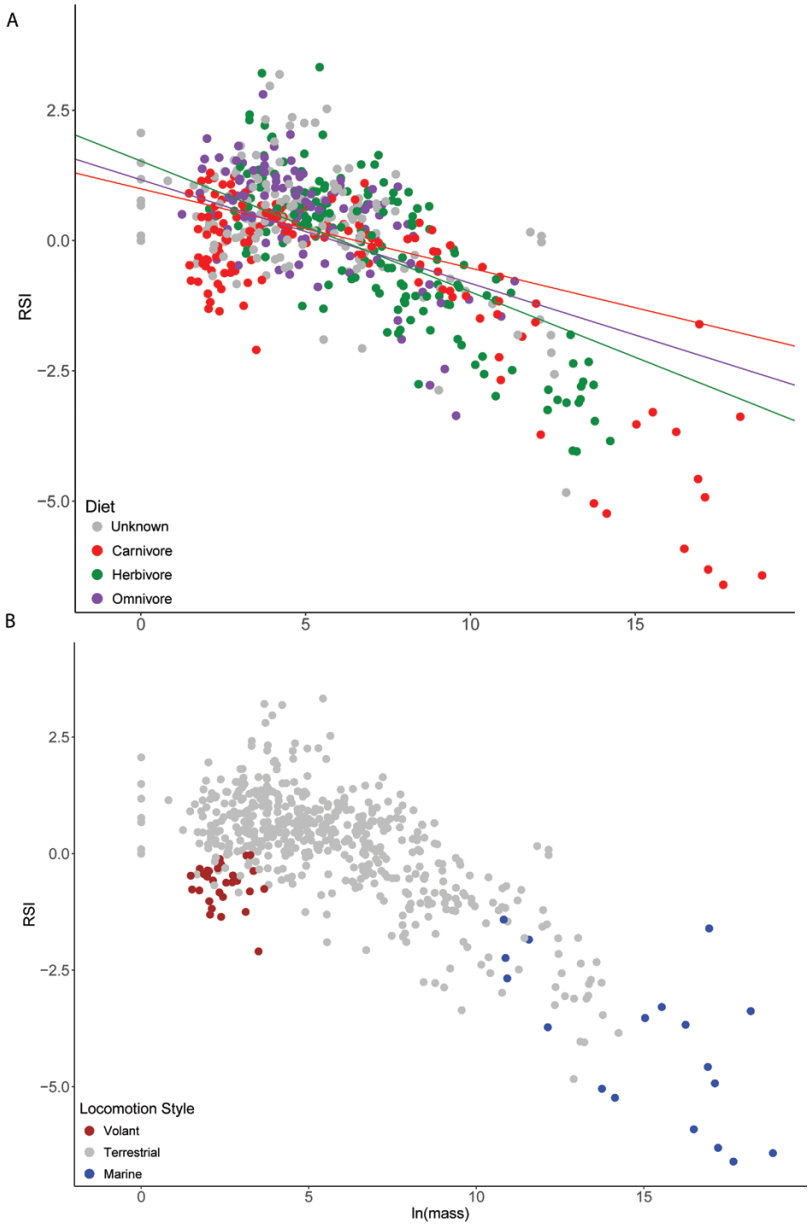

Figure 1. Plot of RSI vs. body mass. Each point represents a single species. A, all data used for the final PANCOVA. The entire model was significant ($P < 0.0001$) as were the herbivore ($P < 0.0001$) and omnivore ($P = 0.0323$) diets. However, the carnivore diet was not significant ($P = 0.5217$). The slope and intercept values for each line are presented in Table S2. B, where the volant and marine mammals used in this study plot in relation to the other mammals. Volant mammals tend to be more *K*-selected than expected for their body mass and the carnivorous marine mammals are on a similar trend with herbivores.

once. Interestingly, the crown-group perissodactyls (e.g. horses, rhinos and tapirs) in this study are entirely *K*-selected (Fig. 2), although it is likely that extinct perissodactyls exhibited the ancestral trait of *r*-selection. Early perissodactyls exhibited small body size (Gould & MacFadden, 2004), and we see a strong correlation between small body size and *r*-selection in our results.

DISCUSSION

Diet has a strong relationship with reproductive strategy in mammals. The importance of diet to reproductive strategy varies among species. Metabolic rate is known to constrain the production of offspring with respect to body size (Brown & Sibly, 2006). Increasing body size leads to a decreased rate in

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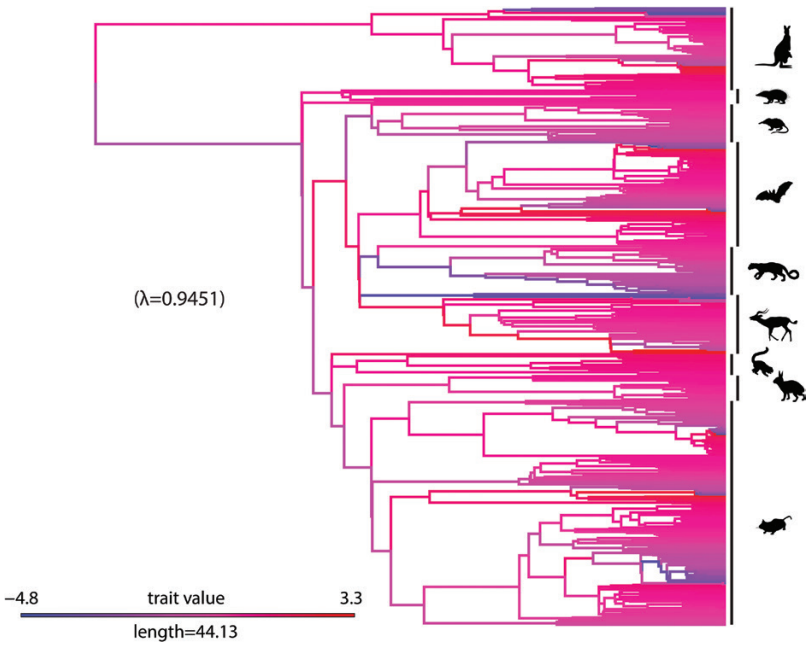

Figure 2. Phylogeny with RSI mapped on the tree using the plotBranchbyTrait function in the phytools R package version 0.6-20 (Revell, 2012) with polytomies resolved (Kuhn *et al.*, 2011). Tree topology follows Fritz *et al.* (2009). Hot colours represent more *r*-selected taxa. Symbols on the right represent major mammalian clades and their position on the phylogeny. From top to bottom they are: Marsupialia, Afrosoricida, Eulipotyphla, Chiroptera, Carnivora, ungulates (Artiodactyla + Perissodactyla), Primates, Lagomorpha and Rodentia.

predation and thus mortality such as when prey species move into a larger size class (Brown & Sibly, 2006). Additionally, an increase in fecundity may occur that results from species being able to exploit new food sources that were previously inaccessible, thus unlocking new sources of energy that could be utilized for other physiological characteristics (Brown & Sibly, 2006). The distribution of resources between carnivores that feed on vertebrate and invertebrate prey is drastically different, as well as the amount of energy available from the food sources, with a diet of invertebrates possessing less energy per unit mass than vertebrates, possibly from the presence of indigestible chitin (Carbone *et al.*, 1999), or in the amount of energy expended in pursuing prey, given that the invertebrates are quantized in much smaller units, and hence take more work to obtain per mass of food (Carbone *et al.*, 1999). Additionally, invertebrates can be either hard- or soft-bodied, which leads to morphological and physiological differences in taxa that specialize on one or the other (Freeman, 1979, 1981; Strait, 1993; Samuels, 2009). There are probably two distinctly different ecological trends between the vertebrate and invertebrate carnivore subdivisions of mammalian ecologies. There may also be a difference in life history and its relationship with mass and diet between social vs. solitary carnivores. Social carnivores could be more *K*-selected because of the energetic and resource distribution among members of the social group (McNab, 1980; Riedman, 1982). Social carnivores are also able to feed on larger prey species than might be expected given their body mass (MacDonald, 1983). However, there are also instances where social carnivores hunt a greater number of individuals of smaller prey species (MacDonald, 1983). In further analysis, a significant result may be yielded by subdividing the carnivore diet category into vertebrate and invertebrate feeders. This was not possible with this study as the diet data used lacked the resolution to investigate this question, so additional data collection will be necessary. When this classification was used in this study, sample size for these categories was too small to draw valuable conclusions from the results (External Database S1).

Our results confirm the hypothesis that mammals with larger body size are more likely to be *K*-selected. The limits on mammalian body size and size of the offspring at birth are directly tied to energetics such that metabolic rate dictates body size (Brown & Sibly, 2006). Mammalian species that produce many offspring (i.e. *r*-selected taxa) dedicate a great deal of their energy to gestation and rearing, which can be invoked to describe the tendency towards smaller body size in these species (Flatt, 2011). Dedication of resources to producing offspring would also mean less time and resources available to increase body size.

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Interestingly, marine and volant mammals tend to be more *K*-selected than expected for their body size (Fig. 1B). Marine mammals in this study, which all happen to be carnivores, plot on the same trend as herbivores, and the reduced effects of gravity on body size in water and more dense distribution of food sources in the marine realm (Price & Hopkins, 2015) probably contribute to the similarity. Most marine mammals in this study are cetaceans and include some of the largest body masses of extant mammals. Whales are essentially falling back onto the bulk eating strategies of their artiodactyl ancestors but are feeding on animal proteins rather than plant material. Thus, it is not surprising that the marine mammals have a similar relationship between these two characters to terrestrial herbivores of similar body size, supporting the major role of diet in reproductive strategies.

Flying mammals (i.e. bats) are on a completely different trajectory from terrestrial mammalian carnivores (Fig. 1B). Body size in volant mammals is controlled much less by physiological constraints and much more by the physical demands of locomotion than in terrestrial and marine mammals. Parental care in bats is high in some species because young bats are unable to fly until they have reached 90% of the adult wing span, and pups commonly fall from roosts and need to be recovered by their parents (Kunz, 1987; Barclay, 1995; Kunz & Hood, 2000). It is common in larger bat species to transport offspring while foraging, but this behaviour is less common in smaller species (Kunz & Hood, 2000). Bats also tend to have relatively small litter sizes for small mammals (Eisenberg, 1981). The additional parental investment for flying is the best explanation for why volant mammals are more *K*-selected than expected.

In conclusion, diet does have an impact on the relationship between body size and reproductive strategy. The effect is far more nuanced in carnivores than in herbivores and omnivores, probably in response to the varying distribution of resources between carnivores which feed on vertebrates and invertebrates. This new method of quantifying reproductive strategy is a powerful tool for exploring the relationships between life history traits and various aspects of ecology.

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REFERENCES

Barclay RMR. 1995. Does energy or calcium availability constrain reproduction by bats? *Symposia of the Zoological Society of London* **67:** 245–258.

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S. 1978. Relationships between body size and some life history parameters. *Oecologia* **37:** 257–272.

Brown JH, Sibly RM. 2006. Life-history evolution under a production constraint. *Proceedings of the National Academy of Sciences of the United States of America* **103:** 17595–17599.

Carbone C, Mace GM, Roberts SC, Macdonald DW. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* **402:** 286–288.

Charnov EL. 1991. Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences of the United States of America* **88:** 1134–1137.

Charnov EL, Berrigan D. 1993. Why do female primates have such long lifespans and so few babies? or life in the slow lane. *Evolutionary Anthropology: Issues, News, and Reviews* **1:** 191–194.

Eisenberg JF. 1981. *The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior*. Chicago: University of Chicago Press.

Flatt T. 2011. Survival costs of reproduction in *Drosophila*. *Experimental Gerontology* **46:** 369–375.

Freeman PW. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. *Journal of Mammalogy* **60:** 467–479.

Freeman PW. 1981. Correspondence of food habits and morphology in insectivorous bats. *Journal of Mammalogy* **62:** 166–173.

Fritz SA, Bininda-Emonds OR, Purvis A. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters* **12:** 538–549.

Gould GC, MacFadden BJ. 2004. Gigantism, dwarfism, and Cope's rule: 'nothing in evolution makes sense without a phylogeny'. *Bulletin of the American Museum of Natural History* **285:** 219–237.

Isaac NJ, Jones KE, Gittleman JL, Purvis A. 2005. Correlates of species richness in mammals: body size, life history, and ecology. *The American Naturalist* **165:** 600–607.

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman GL, Mace GM, Purvis A. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90:** 2648.

Kuhn TS, Mooers AØ, Thomas GH. 2011. A simple polytomy resolver for dated phylogenies. *Methods in Ecology and Evolution* **2:** 427–436.

Kunz TH. 1987. Post-natal growth and energetics of suckling bats. In: Fenton MB, Racey P, Rayner RM V, eds. *Recent advances in the study of bats*. Cambridge: Cambridge University Press, 395–420.

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Kunz TH, Hood WR. 2000. Parental care and postnatal growth in the Chiroptera. In: Crichton EG, Krutzsch PH, eds. *Reproductive biology of bats*. London: Academic Press, 415–468.

Luo ZX. 2007. Transformation and diversification in early mammal evolution. *Nature* **450:** 1011–1019.

MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. Princeton: Princeton University Press.

MacDonald DW. 1983. The ecology of carnivore social behaviour. *Nature* **301:** 379–384.

Martin AP, Palumbi SR. 1993. Body size, metabolic rate, generation time, and the molecular clock. *Proceedings of the National Academy of Sciences of the United States of America* **90:** 4087–4091.

McNab BK. 1980. Food habits, energetics, and the population biology of mammals. *The American Naturalist* **116:** 106–124.

Orme D, Freckleton, R, Thomas, G, Petzoldt, T, Fritz, S, Isaac, N, Pearse, W. 2013. Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2. Available at: https://CRAN.R-project.org/package=caper.

Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* **26:** 331–348.

Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401:** 877–884.

Pianka ER. 1970. On r- and K-selection. *The American Naturalist* **104:** 592–597.

Pineda-Munoz S, Evans AR, Alroy J. 2016. The relationship between diet and body mass in terrestrial mammals. *Paleobiology* **42:** 659–669.

Price SA, Hopkins SSB. 2015. The macroevolutionary relationship between diet and body mass across mammals. *Biological Journal of the Linnean Society* **115:** 173–184.

Price SA, Hopkins SSB, Smith KK, Roth VL. 2012. Tempo of trophic evolution and its impact on mammalian diversification. *Proceedings of the National Academy of Sciences of the United States of America* **109:** 7008–12.

R Core Team. 2015. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3:** 217–223.

Riedman ML. 1982. The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology* **57:** 405–435.

Samuels JX. 2009. Cranial morphology and dietary habits of rodents. *Zoological Journal of the Linnean Society* **156:** 864–888.

Sibly RM, Brown JH. 2007. Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences* **104:** 17707–17712.

Slater GJ. 2013. Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous–Palaeogene boundary (L Harman, Ed.). *Methods in Ecology and Evolution* **4:** 734–744.

Smith FA, Boyer AG, Brown JH, Costa DP, Dayan T, Ernest SK, Evans AR, Fortelius M, Gittleman JL, Hamilton MJ, Harding LE, Lintulaakso K, Lyons SK, McCain C, Okie JG, Saarinen JJ, Sibly RM, Stephens PR, Theodor J, Uhen MD. 2010. The evolution of maximum body size of terrestrial mammals. *Science* **330:** 1216–1219.

Smith FA, Payne JL, Heim NA, Balk MA, Finnegan S, Kowalewski M, Lyons SK, McClain CR, McShea DW, Novack-Gottshall PM, Spaeth Anich P, Wang SC. 2016. Body size evolution across the Geozoic. *Annual Review of Earth and Planetary Sciences* **44:** 523–553.

Strait SG. 1993. Differences in occlusal morphology and molar size in frugivores and faunivores. *Journal of Human Evolution* **25:** 471–484.

Western D. 1979. Size, life history and ecology in mammals. *African Journal of Ecology* **17:** 185–204.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

External Database S1. Reproductive Strategy Index (RSI), diet, and body mass data for each taxon.
External Database S2. R code used for this analysis.
Table S1. Phylogenetic signal for reproductive strategy index (RSI). All reported values are means from 101 analyses. CI = confidence interval, ML = maximum likelihood, λ = Pagel's lambda.
Table S2. Summary statistics from phylogenetically informed analysis of covariance (PANCOVA) for all taxa in this analysis. All reported values are means from 101 analyses.
Table S3. Summary statistics from phylogenetically informed analysis of covariance (PANCOVA) excluding volant and marine mammals. All reported values are means from 101 analyses.

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