

Correlates of Species Richness in Mammals: Body Size, Life History, and Ecology

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ABSTRACT: We present the most extensive examination to date of proposed correlates of species richness. We use rigorous phylogenetic comparative techniques, data for 1,692 mammal species in four clades, and multivariate statistics to test four hypotheses about species richness and compare the evidence for each. Overall, we find strong support for the life-history model of diversification. Species richness is significantly correlated with shorter gestation period in the carnivores and large litter size in marsupials. These traits and short interbirth intervals are also associated with species richness in a pooled analysis of all four clades. Additionally, we find some support for the abundance hypotheses in different clades of mammals: abundance correlates positively with species richness in primates but negatively in microchiropterans. Our analyses provide no evidence that mammalian species richness is associated with body size or degree of sexual dimorphism.

Keywords: nested sister clade comparisons, species richness, phylogeny, speciation, extinction.

The uneven distribution of species among taxa is a pervasive pattern and demands explanation (Dial and Marzluff 1989; Purvis 1996). Phylogenies are often very asymmetric or unbalanced, suggesting that lineages have often

differed in their probabilities of diversifying (Purvis 1996; Mooers and Heard 1997). It has been suggested that certain traits predispose lineages to become diverse (Cracraft 1982). Such hypotheses are routinely tested by comparing the species richness of sister clades that differ in the trait of interest (Barraclough et al. 1998). This approach has successfully identified some key innovations (or key traits; de Queiroz 2002) as likely causes of insect and plant radiations (Mitter et al. 1988; Farrell et al. 1991) and has provided evidence for the role of sexual selection in speciation (Barraclough et al. 1995; Owens et al. 1999; Arnqvist et al. 2000; but see Gage et al. 2002). However, phylogenetic asymmetry is common, and demonstrations of traits having consistent effects on diversification are rare (de Queiroz 2002). Hitherto, tests have mostly focused on single traits hypothesized to affect diversification. This approach may fail to reveal correlations if multiple traits are simultaneously important. Few studies have tested multiple hypotheses about species richness (Owens et al. 1999; Katzourakis et al. 2001; Stuart-Fox and Owens 2003). Here we test both separately and simultaneously four long-standing and current hypotheses that link continuous characters with species richness. We briefly review these hypotheses below.

Body size. The best-studied hypothesis about continuous characters is that species richness is a decreasing function of body size. Small-bodied species may be less prone to extinction or less able to divide niche space more finely (reviewed in Purvis et al. 2003). There have been many tests of the size-diversity hypothesis (Purvis et al. 2003), but support has been restricted to just a few clades (Gittleman and Purvis 1998; Gardezi and da Silva 1999; Orme et al. 2002). However, body size can be correlated, sometimes strongly, with all of the traits listed below (e.g., Peters 1983), thus highlighting the need for a multivariate approach to hypothesis testing.

Life history. Taxa with "fast" life histories (large litters, early maturity, short gestation, and short interbirth intervals; Read and Harvey 1989) may be more adaptable in the face of harsh and changing environments, due to high rates of evolution and population growth (Marzluff and Dial 1991). These species may therefore speciate at a faster

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rate and/or have lower extinction rates, leading to higher species richness in “fast” clades compared with “slow” ones.

Abundance. Several lines of theory link abundance with species richness. Brown (1958) proposed that the foundation of peripheral isolate populations is determined by density-dependent migration. Therefore, clades whose species tend to be locally abundant will produce new species at a faster rate than clades of rare species. In Gavrilets’s (2000) model, abundance interacts with sexual conflict to facilitate speciation; reproductive isolation (and hence the accumulation of species) is faster at high abundance. Hubbell (2001) presented a model in which speciation rate is directly proportional to global population size. Finally, if local abundance is a measure of global population size (Gaston 1994), then abundance provides a natural buffer against extinction and leads to the accumulation of species.

Sexual dimorphism. Several theories have linked sexual dimorphism with low species richness. Williams (1992) argued that, because sexual dimorphism indicates that energy is spent competing rather than reproducing, lineages with high levels of sexual dimorphism ought to fare poorly in clade selection. Parker and Partridge (1998) modeled the effects of intersexual mating conflict on the evolution of reproductive isolation. They showed that speciation is slower in species where males control mating, leading to a prediction of low species richness in lineages where males are much larger than females. Finally, if dimorphism is associated with increased mortality, for example, through intrasexual aggression, then dimorphic lineages may suffer higher rates of extinction (Coyne and Orr 2004). An alternative is that sexual dimorphism is a by-product of sexual selection for male ornaments, which would lead to divergence in female choice and increased species richness (Barracough et al. 1995; Gage et al. 2002).

We test these hypotheses using nested sister clade comparisons on complete species-level phylogenies of four mammalian clades: bats, carnivores, marsupials, and primates. To date, this is the largest data set used to test proposed correlates of species richness.

Methods

Phylogenies and Data Sources

We used complete species-level phylogenies of four orders that together contain 37% of described mammalian species. The orders are Carnivora (271 species; Bininda-Emonds et al. 1999), Chiroptera (bats, 916 extant species; Jones et al. 2002), Marsupialia (272 species; Seal 1997), and Primates (233 species; modified from Purvis 1995 to the taxonomy in Wilson and Reeder 1993). The full data set contains 973 nodes (58% resolution of 1,688 possible

nodes), of which 445 are bifurcating and contain more than two species, thus making them informative for correlations with species richness. Complete phylogenetic resolution would yield about two comparisons for every three nodes, so the coverage of our data set is about 40% ($445/[1,688 \times 0.67]$).

Data were collected from a wide range of literature sources. We used average adult body mass of males and females (in grams) from Jones et al. (2003) for bats, Purvis et al. (2000) for carnivores and primates, and Silva and Downing (1995) for marsupials. We collected the four traits to be representative of life-history variation: gestation period (days), age at sexual maturity (months), interbirth interval (months), and litter size. We used data from Jones et al. (2003) for bats, Purvis et al. (2000) for carnivores and primates, and Hayssen et al. (1993) for marsupials. Species averages were calculated after removing obviously incorrect outliers, using data from wild animals where possible, and preferring means or medians over minima or maxima. Around 0.5% of our species values are based solely on minima or maxima. Numbers of live offspring were used in preference to numbers to embryos, and gestation periods were excluded if delayed implantation was suspected. We used population density and group size as surrogate measures of abundance, taking data from Jones et al. (2003) for bats (colony group size), Purvis et al. (2000) for carnivores and primates, and Johnson (1998) for marsupials. Group size is a measure of local abundance, but it is also relevant to Brown’s (1958) hypothesis because animals that live in large groups can migrate and disperse as groups, such that viable isolated populations may arise from a single colonization event. We calculated species values of mass dimorphism (male mass/female mass) and length dimorphism (male length/female length) using data from Jones et al. (2003) for bats, Smith and Jungers (1997) for primates, Gittleman (1994) for carnivores, and Silva and Downing (1995) for marsupials. All data were log_e transformed. Table 1 shows sample sizes for each variable and phylogeny. The phylogenies and data sets can be found in the zip file in the online edition of the *American Naturalist*.

Analyses

We compared the shape of the four phylogenies with a Markovian null model using two symmetry measures: I' (Agapow and Purvis 2002) and M_{II}^* (Moore et al. 2004). Values of $I' > 0.5$ and $M_{II}^* < 0$ identify phylogenies that are more asymmetric than expected under the null model, suggesting that lineages have differed in net diversification rates.

We used MacroCAIC, version 1.1 (Agapow and Isaac 2002) to calculate phylogenetically independent contrasts

Table 1: Summary information for the four data sets: sample sizes, number of species, and phylogenetic shape scores

Hypothesis and variable	Carnivora	Chiroptera	Marsupials	Primates
Body size:				
Adult body mass	240	653	215	194
Life history:				
Age at sexual maturity	104	67	79	96
Gestation period	134	128	68	120
Interbirth interval	117	0	56	112
Litter size	171	327	118	172
Abundance:				
Population density	70	0	87	107
Group size	109	152	0	187
Sexual dimorphism:				
Mass dimorphism	101	346	113	189
Length dimorphism	89	47	0	0
Number of tips	271	916	272	233
I'	.60**	.65***	.59*	.53
M_{Π}^*	-.61**	-.76***	-.62**	-.54

Note: Sample sizes for each predictor variable are grouped by hypothesis. Phylogenetic tree shape statistics (mean I' and median M_{Π}^*) are calculated by randomization and estimate departures from the null (Markovian) model of constant diversification.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

in the predictor traits, using a Brownian motion model of character change. All clades were analyzed with branch lengths set equal; Carnivora and Primates were also analyzed with branch lengths set proportional to time. While analyses with branch lengths are more robust (Isaac et al. 2003), estimates of node age contain considerable errors (Moore et al. 2004). We measured species richness differences using the relative rate difference (RRD; $\ln[n_i/n_j]$, where n_i and n_j are the number of species in the clade with the larger and smaller value of the predictor trait; Isaac et al. 2003). We repeated the analyses using the proportional dominance index (PDI; $n_i/[n_i + n_j]$) for all equal branch length analyses, as recommended by Isaac et al. (2003). Results for PDI, using equal branch lengths for Carnivora and Primates, are reported only where the different analyses disagreed about whether a relationship is significant.

Within each data set, we looked for a monotonic relationship between each predictor trait (X) and species richness using regression through the origin (Garland et al. 1992). Most hypotheses were tested using multiple variables, so we used a sequential Bonferroni test (Rice 1989) to assess the P values from the regressions within each hypothesis. The complete set of predictor variables was entered into a multiple regression model to reveal the minimum set of additive linear effects on species richness for each order (but not interactions among traits; de Queiroz 2002). These models were simplified in order to generate a minimum adequate model (MAM) by sequentially

removing the predictor with least explanatory power until all variables were significant at $\alpha = 0.05$. Missing data could lead to important variables being omitted, so we countered this in two ways. First, we reintroduced recently discarded variables at any iteration where sample size increased by more than five species (Purvis et al. 2000). Second, we added each discarded parameter back into the MAM in turn to see if it explained significant additional variance. For each data set, we generated a correlation matrix to test for collinearity among contrasts in the predictor variables. Just one pairwise correlation (of 106) was strong enough to cause problems for the multiple regression: carnivore home range versus population density ($r = -0.76$; $\text{abs}(r) < 0.55$ in all other cases). Accordingly, we ran the carnivore model starting with either home range or population density, but not both.

We combined the data for the four clades into a pooled regression analysis (single and multiple), using equal branch lengths throughout, in order that contrasts were measured in the same units for all four clades (Orme et al. 2002). We additionally measured the qualitative strength of associations using a one-sample sign test. The sign test examines the consistency of relationships between traits and species richness, whereas the regression looks at mean effect size (cf. Nee et al. 1992). As a nonparametric statistic, the sign test is more conservative yet also more robust than the regression. We used two-tailed tests throughout to make the results comparable across hypotheses.

We tested the robustness of each relationship in five different ways. First, we conducted the model criticism procedures described by Garland et al. (1992). Second, we tested for constancy of variance in RRD (the dependent variable) by regressing the absolute values of RRD against the total number of species at each node. Third, we used the Shapiro-Wilks test to check that residuals were normally distributed. Fourth, we examined the scatter plot of X against RRD to look for obvious outliers, in which case we determined whether the relationship remained after the outlier was removed. Finally, we regressed the absolute residuals against the predicted values of RRD in order to test the assumption of constant error variance.

Results

Our tests of phylogenetic tree shape found significant variation in among-lineage diversification rates in carnivores, bats, and marsupials (table 1). No evidence for rate variation was found in primates, although significant radiations within this order have been identified using other methods (Purvis et al. 1995; Moore et al. 2004).

Table 2 presents the results of the simple regression analyses within each of the four data sets. No single variable is correlated with species richness in all four data sets, and in no data set are more than two variables significantly correlated with RRD.

Two traits are associated with high species richness in the carnivores: small body size ($r^2 = 0.04$) and short gestation period ($r^2 = 0.09$). However, the body size effect disappears when gestation period is controlled for by mul-

tipale regression (mass $P > .4$); gestation period is the only predictor in the MAM for this order. Qualitatively identical results are found using equal branch lengths.

No variable correlates significantly with species richness in bats, although clades with small group sizes tend to contain more species ($P = .06$). This relationship is significant in the Microchiroptera even after removing one extreme outlier (*Tadarida brasiliensis*; $r^2 = 0.13$, $t = -2.18$, $df = 32$, $P = .037$), although not at the table-wide level after sequential Bonferroni correction.

Two traits are associated with marsupial species richness: large litters ($r^2 = 0.14$) and high population density ($r^2 = 0.12$). The relationship with litter size is robust, but the correlation with population density is not; it is strongly influenced by the comparison between Dasyuridae (61 species) and the monotypic Myrmecobiidae, and it is not significant when we use PDI instead of RRD ($t = 1.77$, $df = 39$, $P = .084$). Furthermore, it is not significant in a multiple regression with litter size; the MAM for marsupials contains litter size as the sole predictor.

Results in the Primates are influenced by the choice of branch lengths. Population density is the only variable that is correlated with species richness and the only variable in the MAM ($r^2 = 0.10$) when branch lengths are set proportional to time. However, the contrasts in population density do not have a constant variance (contrasts vs. their standard deviation: $b = -0.055$, $P = .02$). Using equal branch lengths, the population density correlation is robust but weaker ($P = .06$), with group size the only significant correlate of species richness ($r^2 = 0.04$, $P = .05$). However, group size does not displace population density

Table 2: Correlates of mammalian species richness partitioned by data set and hypothesis

Hypothesis and variable	Carnivora	Chiroptera	Marsupials	Primates
Body size:				
Adult body mass	-2.17*	.52	-.22	-.56
Life history:				
Age at sexual maturity	-.37	-1.15	-.25	-.25
Gestation period	-2.62*	-.47	-.14	-.10
Interbirth interval	-.84	NA	-.06	-.01
Litter size	.51	1.59	3.02*	1.47
Abundance:				
Population density	.29	NA	2.26	2.76*
Group size	.46	-1.90	NA	.82
Sexual dimorphism:				
Mass dimorphism	.86	-1.25	.76	-1.93
Length dimorphism	.57	.02	NA	NA

Note: Data are t scores from regression through the origin of relative rate difference on contrasts in the predictor variable. Contrasts were calculated using branch lengths proportional to time (Carnivores and Primates) or set equal (Chiroptera and Marsupials). NA = not available.

* $P < .05$ after sequential Bonferroni correction for multiple tests within each hypothesis.

from a multiple regression model using equal branch lengths.

Similar patterns are found when the data are pooled. In the single-predictor regressions gestation period, litter size and population density are each correlated with RRD (table 3), although the relationship with gestation period is marginally nonsignificant after applying a Bonferroni correction for multiple tests. The relationships between species richness and gestation period and population density are not significant using PDI instead ($P = .10$ and $.056$, respectively). Furthermore, the relationship between RRD and population density is not significant after removing the high leverage comparison associated with *Erythrocebus patas* ($P > .1$). Gestation period is the only significant predictor of RRD in a multiple regression, even though contrasts in gestation period cannot predict the sign of the species richness difference (one-sample sign test; table 3). The sign test reveals trends that were not apparent in the regression analysis; clades are likely to be more speciose if the species mature at an early age.

Discussion

Our results indicate that mammalian species richness involves multiple factors acting in combinations that differ among lineages. Fast life histories and high abundance are correlated with increased species numbers in the pooled analysis, although our clade-by-clade analyses reveal considerable heterogeneity of pattern, in common with previous studies of mammalian species richness (Gittleman and Purvis 1998; Gardezi and da Silva 1999). However,

the results demonstrate that correlations at low taxonomic level are unlikely to be lost when clades are combined. This suggests that large phylogenies stand a disproportionately large chance of detecting such correlates as do exist. We advocate that multivariate approaches and tests of phylogenetic heterogeneity of pattern should be used whenever possible to give the clearest picture of which factors might have been responsible for such diversity among lineages.

The life-history model of taxonomic diversity (Marzluff and Dial 1991) is the most consistently supported of all the hypotheses tested here. There is separate support for this model in the Carnivora (gestation period), Marsupialia (litter size), and pooled data set (both variables). This is not surprising because gestation and litter size are highly correlated in mammals (Read and Harvey 1989). Gestation period is the best predictor of species richness differences across the four orders. What, then, is the mechanistic link to diversification? Reduced extinction is a strong candidate; life history and anthropogenic extinction risk are correlated in carnivores (Purvis et al. 2000), bats (Jones et al. 2003), and quaternary mammals (Johnson 2002), although not in marsupials (Fisher et al. 2003) or primates (Purvis et al. 2000). However, it is not clear whether life history is an important driver of extinction in the absence of people or whether anthropogenic extinction has been sufficient to cause the observed correlation with species richness. Marzluff and Dial's (1991) model suggests two ways in which fast life histories might reduce extinction: a higher intrinsic rate of population growth allows populations to recolonize former ranges,

Table 3: Correlates of species richness across pooled contrasts from all four mammalian clades

Hypothesis and variable	n_c	n_{pos}	n_{neg}	P^a	r^b	b	t	P^b
Body size:								
Adult body mass	436	196	223	.123	<.001	-.17	-.84	.402
Life history:								
Age at sexual maturity	195	77	112	.013	<.001	-.67	-1.00	.320
Gestation period	230	112	105	.684	.018	-2.41	-2.14	.033
Interbirth interval	173	73	95	.105	<.001	-.77	-1.11	.268
Litter size	325	132	92	.058	<.001	2.33	2.75	.006*
Abundance:								
Population density	152	80	67	.322	.012	.51	2.31	.022*
Group size	206	99	75	.081	.007	-.22	-1.29	.198
Sexual dimorphism:								
Mass dimorphism	302	145	145	1.00	.006	-2.36	-1.37	.173
Length dimorphism	69	38	29	.328	<.001	1.39	.69	.493

Note: The number of contrasts (n_c) is given, as well as the numbers where clade with the larger value of the predictor trait contained more species (n_{pos}) and vice versa (n_{neg}); b and t are parameters of the regression through the origin of relative rate difference on contrasts in the predictor variable.

^a Sign test.

^b Regression through the origin.

* $P < .05$ after sequential Bonferroni correction for multiple tests within each hypothesis.

and faster evolution enables species to track changing environments. While tests of these mechanisms are possible, they would not be conclusive evidence for the extinction pathway because the same traits are also proposed to make speciation more likely (Marzluff and Dial 1991). Therefore, it will be difficult to test unambiguously which mechanism is most likely (Coyne and Orr 2004). This level of theoretical development is symptomatic of macroevolutionary biology and illustrates the need for clear mechanistic models that make unambiguous predictions.

There is some evidence that high population density and species richness are correlated in marsupials and primates. However, neither result is very robust. Furthermore, Isaac and Purvis (2004) found that this relationship was not significant using other taxonomic arrangements of primates. We are therefore cautious about placing undue emphasis on these findings and instead look forward to tests of the putative mechanisms. For instance, Brown's (1958) density-dependent dispersal hypothesis suggests covariation between species' mean abundance, dispersal strategy, and degree of population genetic structure. Gavrilets's (2000) intersexual coevolutionary arms race model predicts a strong relationship between species richness and more direct measure of sexual conflict such as mating frequency. Likewise, the idea that high population density might protect against extinction is dependent on a link between local and global abundance, which is not always found (Gaston 1994). None of these mechanisms can account for the negative correlation between group size and species richness in the Microchiroptera because the relationship is in the opposite direction to that predicted. One explanation is that splitting the population into small groups enables bats to found a large number of populations with uncoupled population dynamics (thus reducing the chances of extinction for the entire species). Alternatively, the relationship may arise because bat species with small colonies tend to have low wing aspect ratios (Jones et al. 2003). Low aspect ratio is likely to drive reproductive isolation (and hence speciation) because these bats are inefficient at flying long distances (Norberg and Rayner 1987) and are unlikely to exchange individuals with neighboring colonies (Entwistle et al. 2000). We found a negative relationship between aspect ratio (data in Jones et al. 2003) and species richness in microchiropterans, but only after removing *Tadarida brasiliensis* (an extreme outlier).

The remaining two hypotheses were not supported by our analyses. Although Gittleman and Purvis (1998) found evidence for the body size hypothesis in the Carnivora, we have shown that the variation in species richness is better explained by the pattern of life-history evolution, specifically gestation period. This result highlights the value of our multivariate approach. Nor did we find a relationship between species richness and sexual size di-

morphism, in common with Gage et al. (2002; but see Stuart-Fox and Owens 2003). The lack of significant correlation could indicate that neither male-dominated sexual conflict nor female preference for secondary sexual characteristics have been important in the diversification of mammals. However, it is equally possible that sexual size dimorphism could arise for reasons other than sexual conflict and sexual selection.

To this point, we have used species numbers without criticism. In the literature, many species definitions are used (Mayden 1997), which can generate lists with different numbers of species (Agapow et al. 2004), thus creating uncertainty for hypotheses testing (Isaac et al. 2004). In order to minimize this problem, we have standardized each of the four data sets to a single taxonomic authority (Wilson and Reeder 1993). However, some groups are extremely well studied, while others are not, leading to differences in the confidence with which any given species concept can be applied (Isaac et al. 2004). The limited evidence in hand suggests that taxonomic uncertainty can lead to different conclusions being drawn from the same data set (Isaac and Purvis 2004). Accordingly, we believe this is a key area of concern for macroevolutionary biologists. However, the conclusion that fast life history and species richness are correlated in mammals seems unlikely to be a taxonomic artifact. Slow species probably tend to be described sooner than fast ones (Collen et al. 2004), so any artifact would lead to a correlation between species richness and slow, not fast, life histories.

Other sources of error could have affected our results. Like all phylogenetic comparative analyses, our results are dependent on the phylogenetic hypothesis used. The four phylogenies in this study are all supertrees, which are extremely efficient tools for generating complete phylogenies from multiple incomplete ones (Bininda-Emonds 2004), although several weaknesses have been identified (Gatesy et al. 2002). Three of the phylogenies are also highly asymmetric (table 1), which could lead to nonindependence among comparisons (Isaac et al. 2003). Available evidence suggests that any increase in Type I errors is slight (Isaac et al. 2003), although the effects of systematic and extreme asymmetry have not been assessed.

None of the relationships in this article has high explanatory power. One reason is that incomplete phylogenetic information (polytomies) has reduced the number of available comparisons. This may explain why few significant correlations were found in the Chiroptera (47% resolved, compared with 70% for the other taxa), in spite of the fact that it is the largest and most unbalanced of the four phylogenies (table 1). The power of our MAMs for the other orders ($r^2 = 0.09\text{--}0.14$) fall within the range of values from other studies with higher phylogenetic resolution ($r^2 = 0.01\text{--}0.25$; Gittleman and Purvis 1998; Gar-

dezi and da Silva 1999; Stuart-Fox and Owens 2003), which suggests that low power might be a general feature of tests for correlates of species richness. A possible explanation is that a general correlate of species richness may be apparent only among lineages of at least a certain age or, as a rough proxy, taxonomic level. Clades younger than this might not have had time to evolve sufficient variance in traits that might influence diversification rates. Strelman and Danley's (2003) model of radiation in stages suggests that species richness is highly influenced by the stage that a lineage has reached. Moreover, if most speciation and extinction events are driven by extrinsic forces (Cracraft 1982) or are contingent on other factors (de Queiroz 2002), then lineage sorting or trait-dependent diversification would only become evident over long periods. Owens et al. (1999) found support for five separate hypotheses relating continuous characters to species richness using pairs of bird families. While we have used more comparisons in this analysis (445) than any previous sister-clade test, only 49 were above the family level. In addition, diversification rates may be set by interactions among traits (de Queiroz 2002); unless the interaction is modeled explicitly, it can manifest itself in a range of ways (different correlates in different clades or low statistical power generally). Interactions, if complex, could undermine any attempt to explain much of the variation in species richness (de Queiroz 2002). We have considered multiple predictors in some of our models but have so far considered only additive effects.

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