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Body size and species-richness in carnivores and primates

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We use complete species-level phylogenies of extant Carnivora and Primates to perform the first thorough phylogenetic tests, in mammals, of the hypothesis that small body size is associated with species-richness. Our overall results, based on comparisons between sister clades, indicate a weak tendency for lineages with smaller bodies to contain more species. The tendency is much stronger within caniform carnivores (canids, procyonids, pinnipeds, ursids and mustelids), perhaps relating to the dietary flexibility and hence lower extinction rates in small, meat-eating species. We find significant heterogeneity in the size–diversity relationship within and among carnivore families. There is no significant association between body mass and species-richness in primates or feliform carnivores. Although body size is implicated as a correlate of species-richness in mammals, much of the variation in diversity cannot be attributed to size differences.

Keywords: macroevolution, primates, carnivores, body size, species-richness, independent comparisons

1. INTRODUCTION

Species are often distributed very unequally among lineages (Dial & Marzluff 1989). Explaining this pattern is a major goal in evolutionary biology. Historically, a statistic derived from a taxonomy (e.g. number of species per genus) has been compared across taxa having different biological attributes (e.g. Dial & Marzluff 1988; Marzluff & Dial 1991; Martin 1992). This approach, however, is flawed for two reasons. The units of comparison (e.g. genera) may not be equivalent among taxa (Simpson 1953), and related clades may inherit features from a common ancestor rather than evolve them independently (Harvey & Pagel 1991; Mooers *et al.* 1994). Comparisons of sister taxa avoid both pitfalls (Cracraft 1984), but require well-resolved phylogenies. Consequently, there have been surprisingly few demonstrations to date of evolutionary correlates of species-richness, and none in mammals (Purvis 1996).

The hypothesis with perhaps the longest pedigree is that small body size is associated with high species diversity (see Brown 1995). Many mechanisms have been proposed for such an effect. Habitats may contain more niches for small organisms than for large ones (Hutchinson & MacArthur 1959), or diversity differences may be caused by some other variable correlated with body size such as metabolic rate (Glazier 1987), reproductive rate (Marzluff & Dial 1991), or brain size (Jerison 1973). Taxonomic analyses (e.g. Dial & Marzluff 1988; Martin 1992) have shown an association between small size and high diversity but were flawed for the reasons given above. Here, we present the first phylogenetic tests of the size–diversity hypothesis in mammals. We base our tests on complete species-level phylogenies of Carnivora (Bininda-Emonds *et al.* 1998) and Primates (Purvis 1995). These orders are good testing grounds for the hypothesis: carnivores span more than four orders of magnitude in body mass—more than any other mammalian order (Gittleman 1985)—and primates span more than three; furthermore, both orders show significant differences in species-richness among lineages of the same age (Purvis *et al.* 1995; Bininda-Emonds *et al.* 1998).

2. MATERIALS AND METHODS

(a) *Data*

We collected body mass data from the literature for 240 carnivore and 175 primate species. The main sources were Gittleman (1985), Silva & Downing (1995), Harvey *et al.* (1987), Damuth (1993), Fleagle (1988), Kappeler (1991), and Ford & Davis (1992). Where possible, we used the average of within-sex means. Otherwise, we used the mean of values where the sex was unspecified. We corroborated our data wherever possible in three ways. First, when sources differed greatly, we followed the majority opinion where possible, or preferred values based on larger samples. Second, we regressed our data against head and body lengths and inspected outliers particularly carefully. Last, we checked our values against ranges from encyclopaedic sources (Macdonald 1984; Nowak 1991). We paid particular attention to species-poor lineages with species-rich sister taxa, because our analyses are most sensitive to the data for these taxa. We took natural logarithms of all data prior to analysis. The full data set, with references, is available on request. Figure 1 shows histograms of the body mass distribution for (*a*) carnivores and (*b*) primates.

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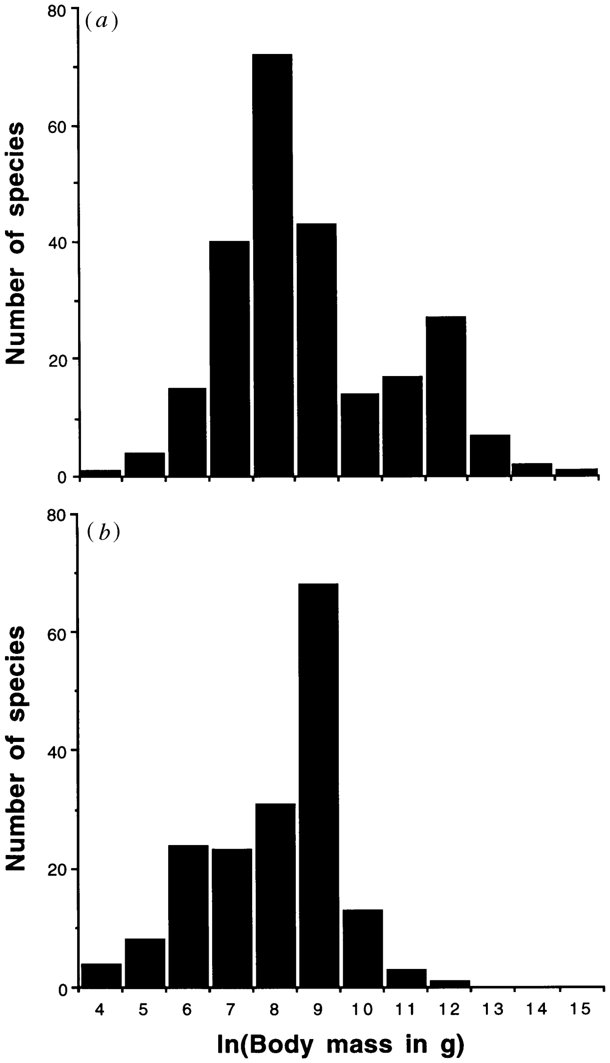

Figure 1. Body size distributions of species in (*a*) carnivores and (*b*) primates.

(b) *Methods*

Phylogenetic information came from Purvis (1995) for primates, and Bininda-Emonds *et al.* (1998) for carnivores. Some of our tests require estimates of body mass for each clade in each phylogeny. We used algorithms from Pagel (1992; implemented by Purvis & Rambaut (1995)) to estimate these values in two ways, first using branch lengths proportional to time, then setting all branches to be equal in length. Essentially, a random walk model of character change is assumed (Felsenstein 1985); the first set of analyses corresponds to gradual change, and the second to a more punctuational model. Once body masses had been calculated for each clade, differences between sister clades were used as the body mass contrasts. Polytomies in phylogenies generally represent ignorance of the true branching structure, so do not provide useful comparisons. Comparisons between sister species are also uninformative, because there can be no difference in species-richness. Remaining comparisons were analysed in three ways, as follows.

(i) Under the null hypothesis of no association, the larger-bodied clade will contain more species than the smaller-bodied clade in about half of the comparisons. A sign test was used to assess the significance of departures from this null prediction.

(ii) The magnitudes of the species-richness differences can be accommodated in various ways (e.g. Nee *et al.* 1996). We have calculated the species-richness contrasts at each node as: ln(no. of species in large-bodied clade/no. of species in small-bodied clade).

The contrasts were roughly normally distributed with a variance independent of the total number of descendant species. We used *t*-tests to test whether the mean of these contrasts differed from zero.

(iii) Regression uses magnitudes of both variables. We used least-squares regression through the origin (Garland *et al.* 1992) to test whether differences in body mass predicted the species-richness contrasts. Inspection of bivariate plots did not indicate marked heterogeneity of variance. In some regressions, one body mass contrast was much larger than the rest, so exerted extreme influence on the line: in such cases we also regressed the species-richness contrasts on the ranks of the body mass contrasts, and have reported both results.

Two-sample *t*-tests and multiple regressions through the origin (with X variables being the body mass contrasts and product of the body mass contrasts and a dichotomous grouping variable: Garland *et al.* 1992), were used to test whether the relationship differed between selected sister clades. To test whether the association between species-richness and body mass varied with body mass itself (as expected if there were an intermediate optimal body size), we regressed the diversity contrasts on the mean body mass of the clades being compared. Similarly, we used regression through the origin of clade size contrasts on clade age to assess whether recent clades showed a different pattern from older lineages.

In the above tests, we have used hierarchically nested comparisons. Nested comparisons are commonly preferred in comparative tests of correlated character evolution, because they maximize sample size and use all of the data (Harvey & Pagel 1991). Previous phylogenetic tests of correlation with species-richness, however, have often used non-nested comparisons for two reasons: they do not require a complete phylogeny; and, nested comparisons lose strict independence if the model adopted for character evolution is inappropriate (Harvey & Purvis 1991).

Because of the possibility of non-independence, we have also analysed a set of non-nested comparisons. We have made as many non-nested comparisons as possible between sister taxa differing in species-richness. In most comparisons, the two lineages did not overlap in body mass, making it easy to decide which was larger-bodied. When faced with overlap, we proceeded as follows. We made a more inclusive comparison (involving one or more outgroup lineages), if doing so removed the overlap without impinging upon any other comparison (for instance, *Macaca cyclopis* is intermediate in body mass between *M. fuscata* and *M. mulatta*, which constitute its sister clade, but all three are larger than *M. fascicularis*, the nearest outgroup). Otherwise, we compared mean body masses for the two lineages. Non-nested comparisons were analysed in the same ways as the nested ones above.

We have used one-tailed tests when assessing the size–diversity relationship, because theory predicts a negative correlation not a positive one. Other tests are two-tailed.

3. RESULTS

Altogether, 209 nested sister-taxon comparisons were available for testing the size–diversity hypothesis, 117 of them within Carnivora. With either choice of branch length, the smaller-bodied clade contained more species in just over half of the comparisons, but the pattern was not significant as judged by sign tests (overall: 105 or 106 versus 89 or 88, $p=0.14$; Carnivora: 62 versus 49 with six zeroes, $p=0.12$; Primates: 43 or 44 versus 40 or 39 with nine zeroes, $p=0.4$). The trend is stronger but still not significant in the non-nested comparisons (34 versus 22: sign test, $p=0.07$).

When magnitudes of the comparisons are considered, there is considerable evidence of a negative association between size and diversity. The *t*-tests on the nested clade size contrasts show the association to be significant for the data set as a whole, and stronger in Carnivora than in Primates (table 1). In these as in most of the following tests, equal branch lengths yield less significant results than branch lengths proportional to time. The non-nested comparisons give similar but less significant results (overall: $t_{55}=-1.43$, $p=0.08$; Carnivora: $t_{31}=-1.32$, $p=0.1$; Primates: $t_{23}=-0.70$, $p=0.25$).

Regression (table 1) shows a significant negative relationship between clade size and body mass within Carnivora, but not within Primates or overall (though the trends are negative). Inspection of bivariate plots (figures 2 and 3) show that each order yields one comparison between two clades differing greatly in body mass, which exerts a great deal of influence on the regression line. In primates, the comparison is between tarsiers (four species, median body mass 119 g) and anthropoids (160 species, median mass 6200 g). In carnivores, it is between pinnipeds (34 species, median mass 190 kg) and a clade comprising mustelids, procyonids, and the red panda (84 species, median mass 2 kg). If body mass comparisons are ranked, the overall regression has a negative slope (branch lengths proportional to time: $t_{208}=-2.79$, $p=0.01$; equal branch lengths: $t_{208}=-1.73$, $p=0.04$). A similar result is found within Carnivora (branch lengths proportional to time: $t_{116}=-2.31$, $p=0.01$; equal branch lengths: $t_{116}=-1.66$, $p=0.05$). Although the primate slope is negative, it is not near to significance ($p=0.2$, for either choice of branch length). Regressions of non-nested comparisons again show similar patterns without reaching significance (overall: $t_{55}=-1.16$, $p=0.13$; Carnivora: $t_{31}=-1.07$, $p=0.15$; Primates: $t_{23}=-0.54$, $p=0.30$).

Table 1 suggests that the tendency for small-bodied lineages to be rich in species is strongest within the carnivore clade uniting mustelids, procyonids, the red panda, and pinnipeds. The non-nested comparisons, too, point to this conclusion: the 14 comparisons possible within this clade show a strong negative association (sign test: 12 versus 2, $p=0.007$; *t*-test: $t_{13}=-3.25$, $p=0.003$; regression: $t_{13}=-2.12$, $p=0.03$). In nested comparisons from primates, the association has a negative sign in most major clades and is significant within lorisoids, catarrhines, and their component clade the hominoids (table 1). The non-nested comparisons do not approach significance within the order.

Table 2 indicates that the size–diversity relationship is not constant across Carnivora. There is some evidence that phocines, fox-like canids (e.g. *Vulpes*) and felines show a more strongly negative correlation than do their respective close relatives, the monachines, dog-like canids (e.g. *Canis*) and pantherines. Lutrines and mephitines show a less negative association than other mustelines, mustelids show a more negative association than do procyonids, and the correlation is more negative within caniforms than within feliforms. These results must be interpreted cautiously, however: only one test gives $p<0.01$, and there are many tests. We found much less heterogeneity of pattern in primates, the only example being that lemurids show a negative association more strongly than the clade comprising indriids, *Lepilemur* and *Daubentonia*. Table 2 suggests a borderline significant difference between regressions for carnivores and primates. However, the discrepancy is almost entirely due to the influential comparison between tarsiers and anthropoids: if body mass comparisons are ranked, there is no evidence of heterogeneity between orders.

There was no evidence that the association between body mass and clade size depended upon body mass ($t_{208}=0.20$, $p=0.8$) or clade age ($t_{208}=-0.82$, $p=0.4$).

4. DISCUSSION

In assessing the size–diversity relationship, we have used a range of tests differing slightly in their assumptions, and have sometimes obtained qualitatively different results. There is at present no consensus on which methods are most valuable for testing hypotheses of correlates of species-richness (Slowinski & Guyer 1993; Nee *et al.* 1996), especially when the hypotheses relate to continuous variables (Purvis 1996). Regression uses information about the magnitude of both Y and X, so is expected to be more powerful than the *t*-test or sign test; branch length information can also add more precision to comparative tests. We therefore emphasize the regressions in section (*a*) of table 1, excepting those analyses, highlighted above, in which single points were highly influential: in those cases, we favour regression using ranked body size comparisons.

Small-bodied carnivore and primate lineages do indeed tend to be species-rich, but the strength of this tendency is never great and varies among clades. Carnivores, especially caniforms, show the relationship more strongly than primates, and there is significant heterogeneity of pattern both within and among carnivore families.

The association is strongest in the clade containing mustelids, procyonids, *Ailurus* and the pinnipeds. These taxa constitute a diverse group. Their body masses range from an average of 0.5 kg in *Mustela* to over 80 kg in *Phoca*, and they have very different biogeographical patterns (Hunt 1996); for example, mustelids arose in Holarctica, whereas the pinnipeds underwent a major Neogene radiation in the Nearctic, and the procyonids radiated successively in the New World. Radiations have occurred from the mid-Oligocene (*Ailurus*) through the early Miocene (*Phoca*) up to the more recent Pliocene (*Mustela*). The history of carnivore evolution shows considerable iteration, with cycles of predator extinction and ecological replacement; the classic case is sabre-toothed predators evolving independently at least four times (Van Valkenburgh 1991). During periods showing marked fluctuations of carnivores (particularly, in the Miocene and the Plio-Pleistocene), many smaller taxa flourished or at least remained stable while larger carnivores (especially canids, ursids and felids) experienced higher extinction rates (Webb 1984; Gingerich 1984). In both fossil and extant lineages dental characteristics suggest that, in larger species, 'hypercarnivory' or the tendency to strictly eat only vertebrate flesh, may reflect an ecological

Table 1. *The relationship between species-richness and body size, assessed by t-test and by least-squares regression through the origin*

(N_{s}, number of species in the clade, not all of which were in the data set; N_{c}, number of comparisons analysed; range, range of body sizes in the clade, expressed as ln(biggest/smallest); b, slope of regression; s.e., standard error of regression slope. Probabilities, p, are one-tailed. See text for explanation.)

				(*a*) branch lengths proportional to time						(*b*) branch lengths equal					
				t-test		regression				*t*-test		regression			
clade	N_{s}	N_{c}	range	t	p	b	s.e.	t	p	t	p	b	s.e.	t	p
combined analysis	474	209	10.61	−2.21	0.01	−0.16	0.104	−1.55	0.06	−1.91	0.03	−0.11	0.103	−1.06	0.2
all Carnivora	271	171	10.34	−1.92	0.03	−0.30	0.128	−2.33	0.01	−1.35	0.1	−0.23	0.128	−1.76	0.04
Mustelidae	65	22	5.93	−3.13	0.003	−0.68	0.258	−2.63	0.008	−2.12	0.02	−0.58	0.260	−2.22	0.02
Procyonidae	18	4	2.08	0.55	>0.5	0.84	0.644	1.31	>0.5	0.55	>0.5	0.80	0.648	1.24	>0.5
Otariidae	14	5	2.64	−0.73	0.3	−1.01	0.800	−1.27	0.1	−0.73	0.3	−0.80	0.811	−0.99	0.2
Phocidae	19	10	3.72	−2.77	0.01	−0.78	0.358	−2.17	0.03	−0.40	0.4	−0.55	0.417	−1.33	0.1
Ursidae	8	3	2.24	0.16	>0.5	0.68	1.760	0.39	>0.5	0.16	>0.5	0.45	1.796	0.25	>0.5
Canidae	34	11	3.48	0.16	>0.5	0.30	0.749	0.40	>0.5	0.16	>0.5	0.52	0.860	0.60	>0.5
Felidae	36	24	4.74	0.06	>0.5	0.01	0.282	0.02	>0.5	−0.71	0.2	−0.17	0.318	−0.53	0.3
Herpestidae	37	6	2.77	0.90	>0.5	0.07	0.646	0.10	>0.5	0.90	>0.5	0.22	0.621	0.35	>0.5
Viverridae	34	20	3.06	0.00	0.5	−0.15	0.397	−0.38	0.4	−0.08	0.5	−0.26	0.382	−0.68	0.3
Mustelidae+Procyonidae	83	27	5.93	−2.16	0.02	−0.47	0.256	−1.85	0.04	−1.44	0.08	−0.37	0.253	−1.47	0.08
Pinnipedia	34	17	3.91	−2.74	0.008	−0.97	0.274	−3.55	0.002	−1.25	0.1	−0.82	0.310	−2.63	0.009
Herpestidae+Viverridae	71	27	3.86	0.49	>0.5	−0.07	0.310	−0.21	0.4	0.42	>0.5	−0.07	0.297	−0.24	0.4
Mustelidae+Procyonidae+ *Ailurus*+Pinnipedia	118	46	10.34	−3.65	0.0004	−0.54	0.176	−3.08	0.002	−2.30	0.01	−0.44	0.178	−2.45	0.009
Caniformia	160	62	10.34	−2.91	0.003	−0.47	0.170	−2.75	0.004	−1.90	0.03	−0.34	0.171	−1.99	0.03
Feliformia	111	54	6.41	0.22	>0.5	−0.08	0.198	−0.42	0.3	0.05	>0.5	−0.07	0.197	−0.37	0.4
all Primates	203	92	7.75	−1.14	0.1	0.13	0.176	0.74	>0.5	−1.36	0.09	0.14	0.175	0.78	>0.5
Lemuroidea	24	12	5.12	0.41	>0.5	0.29	0.328	0.89	>0.5	−0.32	0.4	0.26	0.347	0.75	>0.5
Lorisoidea	15	4	2.92	−2.45	0.05	−0.81	0.299	−2.71	0.04	−2.45	0.05	−0.78	0.28	−2.78	0.03
Platyrrhini	66	26	4.44	−0.21	0.2	−0.19	0.347	−0.54	0.3	−0.40	0.3	−0.21	0.348	−0.59	0.3
Cercopithecinae	52	26	2.79	−0.80	0.2	−0.03	0.670	−0.05	0.5	−0.97	0.2	−0.11	0.602	−0.18	0.4
Colobinae	28	10	1.50	−0.94	0.2	−0.58	0.940	−0.61	0.3	−0.25	0.4	0.01	0.951	0.02	>0.5
Hominoidea	14	7	3.14	−1.97	0.05	−0.47	0.510	−0.92	0.2	−1.97	0.05	−0.38	0.52	−0.74	0.2
Cercopithecidae	80	37	2.79	−1.22	0.1	−0.18	0.540	−0.34	0.4	−1.05	0.2	−0.10	0.494	−0.21	0.4
Catarrhini	94	45	4.63	−1.89	0.03	−0.40	0.379	−1.06	0.15	−1.73	0.05	−0.30	0.364	−0.82	0.2
Strepsirhini	39	17	5.12	−0.11	0.5	0.10	0.274	0.37	>0.5	−0.80	0.2	0.05	0.283	0.18	>0.5
Haplorhini	164	74	7.01	−1.31	0.1	0.11	0.219	0.51	>0.5	−1.27	0.1	0.16	0.214	0.73	>0.5

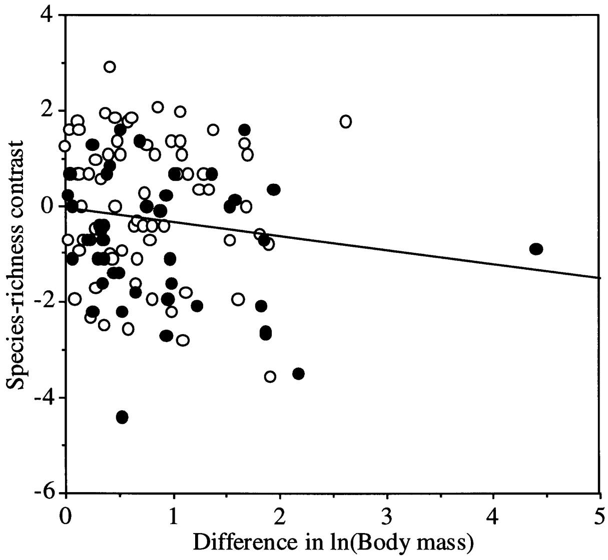

Figure 2. Species-richness and body size in carnivores. Closed circles represent comparisons within the clade (mustelids+procyonids+*Ailurus*+pinnipeds); other comparisons are indicated by open circles. The line is the least-squares regression line through the origin. The comparison on the extreme right is between *Ailurus* and the mustelid/procyonid clade. See also text and table 1.

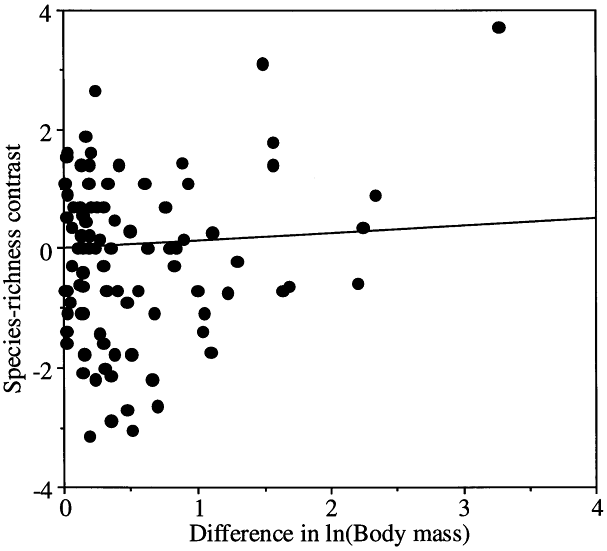

Figure 3. Species-richness and body size in primates. The line is the least-squares regression line through the origin. The comparison on the extreme right is between tarsiers and anthropoids. See also text and table 1.

specialization leading to more rapid species turnover (Van Valkenburgh 1991). A smaller species that is a strict carnivore can rely on other foods during periods of low food availability easier than a large species (Gittleman 1985). Perhaps the species-richness of small-bodied carnivore lineages has been underpinned by their more general dentitions and flexible feeding habits, permitting adaptation to environmental shifts.

Why do primates not show a significant size–diversity relationship? It may be that the relationship does not exist, or that it is too weak for our tests to discern with present data. Figure 1(*b*) indicates that the modal body mass for primates is higher than the mean. This pattern does not preclude a general negative relationship between body size and diversity, however, the high mode is mainly due to the large body sizes found in the species-rich family Cercopithecidae. The size–diversity association is negative within most major primate groups, including the Cercopithecidae, but is seldom significant and never highly so (table 1). Our tests are likely to be less powerful within the Primates than within the Carnivora: the body mass differences between sister taxa tend to be greater in carnivores than in primates (pooled t-test: $t_{207}=2.84$, $p=0.005$, two-tailed). This perhaps reflects the tendency for carnivore species to be more distantly related to one another than is typical of primate species: 19 carnivore species, but only three primates, last shared a common ancestor with another living species more than 15 million years ago (Purvis 1995; Bininda-Emonds *et al.* 1998). Another possible reason for primate clades to be more similar in size relates to diet: if primates are more phylogenetically conservative than carnivores in the general nature of their diet then, given the implications of diet for body size (Fleagle 1988), body size, too, may be more conservative. Any mechanism relating size or a correlated trait to species-richness will have greater force when lineages vary markedly in that trait. The diversity contrasts also tend to be more extreme in carnivores, but not significantly so (pooled t-test: $t_{207}=1.10$, $p=0.3$, two-tailed).

The association between diversity and body mass is likely to reflect differential extinction more than differential speciation. Both orders in this study have suffered recent large-scale, partly size-selective, extinctions. On Madagascar, surviving primates in several clades are smaller-bodied than their extinct relatives (Walker 1967). Many large carnivores went extinct in the Pleistocene, at least partly because of the extinction of their megaherbivore prey (Owen-Smith 1988). Interestingly, Bennett & Owens (1997) showed that, in birds, a high risk of extinction was associated both with large body mass and being a member of a species-poor lineage, suggesting that size-selective extinctions may have been going on in that clade too. An earlier study (Nee *et al.* 1992) found no relationship between species-richness and body mass in birds, but their results are not directly comparable with ours: no species-level phylogeny was available, so all their sister-taxon comparisons were between much higher taxa.

Little is known about the robustness of comparative tests such as ours when phylogenies are incorrect (Donoghue & Ackerly 1996). The sometimes very divergent results between our two choices of branch length indicate that they, as well as topology, can matter. The estimates of phylogeny we have used were constructed using information from literally hundreds of sources, but the strength of support for the composite topology varies systematically within each order (Purvis 1995; Bininda-Emonds *et al.* 1998): in general, less is known about more recent divergences, and support is stronger in better-studied groups. Could this patchiness be responsible for the heterogeneity of association in our results? We find no evidence that it is: the regression slopes in table 1 are not significantly correlated, among higher taxa within each order, with the mean support score (Carnivora: $n=9$, $r_s=0$, n.s.; Primates: $n=5$, $r_s=-0.4$, n.s.). (The phylogenies assessed support differently, precluding comparison between orders.)

Table 2. *Comparing the size–diversity relationship between clades, using t-tests and multiple regression (MR)*
(N = number of comparisons in each clade, where $t > 0$, the first-named clade shows a more positive relationship between body mass and species-richness than does the second-named clade. Probabilities, p, are two-tailed. See text for explanation.)

					(*a*) branch lengths proportional to time				(*b*) branch lengths equal			
					t-test		MR		*t*-test		MR	
	clade	N	clade	N	t	p	t	p	t	p	t	p
	Lutrinae+Mephitinae	8	other Mustelidae	14	1.86	0.08	2.42	0.03	1.05	0.3	2.02	0.06
	Phoca–Erignathus	5	*Hydrurga–Monachus*	4	−2.75	0.03	−3.13	0.02	0.01	1.0	−1.59	0.2
	Canis–Nyctereutes	4	*Vulpes–Otocyon*	6	2.67	0.03	1.76	0.12	2.67	0.03	1.77	0.1
	Panthera–Leopardus	13	*Felis–Leptailurus*	5	1.75	0.1	3.35	0.004	1.22	0.2	2.51	0.02
	Genetta–Civettictis	10	*Paradoxurus–Cynogale*	7	−1.50	0.2	−0.73	0.5	−1.14	0.3	−0.46	0.7
A	Mustelidae	22	Procyonidae	4	−1.79	0.09	−2.10	0.05	−1.37	0.2	−1.87	0.07
B	Otariidae+*Odobenus*	6	Phocidae	10	−0.02	1.0	−0.81	0.4	−0.95	0.4	−0.92	0.4
C	Herpestidae	6	Viverridae	20	0.92	0.4	0.32	0.8	0.96	0.4	0.73	0.5
D	Mustelidae/ Procyonidae/*Ailurus*	28	Pinnipedia	17	0.22	0.8	0.94	0.4	−0.25	0.8	−0.85	0.4
E	D	46	Ursidae	3	−1.10	0.3	−0.93	0.4	−0.77	0.5	−0.65	0.5
F	E	50	Canidae	11	−1.65	0.1	−1.21	0.2	−1.14	0.3	−1.15	0.3
G	C	27	Felidae/Hyaenidae	26	0.38	0.7	0.00	1.0	0.46	0.7	−0.08	0.9
H	Caniformia (F)	62	Feliformia (G)	54	−2.14	0.03	−1.47	0.2	−1.36	0.2	−1.02	0.3
I	Lemuridae	5	Indroidea/*Lepilemur*/ *Daubentonia*	3	−4.11	0.006	−3.19	0.02	−1.44	0.2	−2.64	0.04
J	I	9	Cheirogaleidae	2	−0.03	1.0	0.99	0.3	−0.37	0.7	0.74	0.5
K	J	12	Lorisoidea	4	1.26	0.2	1.57	0.1	0.86	0.4	1.51	0.2
L	Callitrichidae	10	*Cebus*/*Saimiri*	3	0.02	1.0	0.28	0.8	0.02	1.0	0.14	0.9
M	L	14	*Aotus*/*Callicebus*	4	−0.60	0.6	−1.12	0.3	−0.22	0.8	−0.99	0.3
N	M	19	pitheciines+atelines	6	0.69	0.5	0.14	0.9	0.59	0.6	0.13	0.9
O	*Macaca*	9	Papionini	5	−1.20	0.3	−0.57	0.6	−0.12	0.9	−0.51	0.6
P	O	15	Cercopithecini	10	−1.40	0.2	−0.04	1.0	1.26	0.2	0.00	1.0
Q	*Colobus*/*Procolobus*	4	other colobines	5	0.72	0.5	1.06	0.3	0.08	0.9	0.67	0.5
R	*Hylobates*	3	Pongidae	3	−1.71	0.2	−1.84	0.1	−1.71	0.2	−1.70	0.2
S	Cercopithecinae (P)	26	Colobinae (Q)	10	0.24	0.8	0.43	0.7	−0.34	0.7	−0.10	0.9
T	Cercopithecidae (S)	37	Hominoidea (R)	7	0.79	0.4	0.35	0.7	0.85	0.4	0.36	0.7
U	Catarrhini (T)	45	Platyrrhini (N)	26	−1.11	0.3	−0.38	0.7	−0.89	0.4	−0.17	0.9
V	Strepsirhini (K)	17	Haplorhini (U)	74	0.50	0.6	−0.03	1.0	−0.04	1.0	−0.27	0.8
	Carnivora	117	Primates	92	−0.49	0.6	−1.94	0.05	0.05	1.0	−1.64	0.1

When species-richness is of interest, another source of error becomes important: 'splitting' versus 'lumping' can make a big difference to estimates of species numbers. Some groups in our study (e.g. *Procyon, Bassaricyon*) are likely to include more species than are biologically valid, whereas others (e.g. Galagidae) may contain far fewer.

Although small size is correlated with species-richness, the association is weak and inconsistent. Most variation in species-richness between sister-taxa is independent of body mass differences. Although body size is of central importance in life history and ecology for mammals, perhaps its role is not on a macroevolutionary scale (Jablonski 1997). Jablonski (1996) has shown that, in Late Cretaceous molluscs, body size was not associated with other facets of macroevolution, persistence and taxon survivorship. Jablonski (1996) argues that inconsistency of pattern may reflect biological reality rather than methodological flaws. Indeed, theoretical predictions for macroevolutionary change are often based on uniform (intuitive) predictions about size, fecundity and abundance patterns in terrestrial vertebrates; a lack of pattern may be the true biological signal, with significant trends being interpreted as 'context dependent'. Body size may matter within guilds, or within regions, for instance, but not among them. Effects of body size in mammals as well as other taxa may well not be uniform (McKinney 1990): only further work will show whether the pattern we have found is pervasive. Tests of the size–diversity relationship within species-rich small-bodied clades such as myomorph rodents would help clarify the situation, as would tests at higher phylogenetic levels than those presented here, but suitable phylogenies are not yet available. Other studies suggest that life history (Marzluff & Dial 1991), social structures (Wilson 1975), or various 'key innovations' (Hunter & Jernvall 1995) may underpin patterns in species-richness. Comparative analyses of other traits such as life histories, behaviour and ecology may reveal further correlates of species-richness in carnivores, primates and other groups.

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