

The life history legacy of evolutionary body size change in carnivores

A. J. WEBSTER,*†§ J. L. GITTLEMAN‡ & A. PURVIS*

*Department of Biological Sciences, Imperial College, Silwood Park, Ascot, Berkshire, UK

†School of Animal and Microbial Sciences, University of Reading, Whiteknights, Reading, UK

‡Department of Biology, Gilmer Hall, University of Virginia, Charlottesville, Virginia, USA

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Abstract

We estimate the body sizes of direct ancestors of extant carnivores, and examine selected aspects of life history as a function not only of species' current size, but also of recent changes in size. Carnivore species that have undergone marked recent evolutionary size change show life history characteristics typically associated with species closer to the ancestral body size. Thus, phyletic giants tend to mature earlier and have larger litters of smaller offspring at shorter intervals than do species of the same body size that are not phyletic giants. Phyletic dwarfs, by contrast, have slower life histories than nondwarf species of the same body size. We discuss two possible mechanisms for the legacy of recent size change: lag (in which life history variables cannot evolve as quickly as body size, leading to species having the 'wrong' life history for their body size) and body size optimization (in which life history and hence body size evolve in response to changes in energy availability); at present, we cannot distinguish between these alternatives. Our finding that recent body size changes help explain residual variation around life history allometries shows that a more dynamic view of character change enables comparative studies to make more precise predictions about species traits in the context of their evolutionary background.

Introduction

Body size has long been known to correlate strongly with many aspects of life history and ecology across mammalian species. Comparative studies have repeatedly shown that differences in body size are related to a multitude of traits such as gestation length, reproductive rate, neonatal weight, home range size, basal metabolic rate and population density. Recent work further indicates that the scalings of many of these relationships are invariant, consistently generating quarter power exponents that can explain everything from the duration of embryonic growth to the structure of ecological communities (West *et al.*, 1997; Enquist *et al.*, 1998).

These important comparative results have emerged from a historical comparisons among present-day species: phylogeny is considered by comparing extant species with each other, rather than comparing descendants with ancestors [i.e. the comparisons are 'cross-sectional' rather than 'longitudinal': (Pagel, 1997)]. This has been a pragmatic response to the difficulty of reading evidence about ancestors from the fossil record (Smith, 1994). However, longitudinal comparisons have the potential to give a more detailed and dynamic view of character change (Harvey & Pagel, 1991; Harvey & Purvis, 1991; Pagel, 1997). Such analysis can potentially detect evolutionary trends (Jablonski, 1997; Alroy, 1998, 2000; Oakley & Cunningham, 2000), determine the order in which traits have evolved (Tullberg & Hunter, 1996; Bleiweiss, 1997) and identify the leading trait in correlated evolutionary change (Hibbett & Donoghue, 2001). Here, we explore whether the biological attributes of species may reflect not only their present-day body size, but also the body size of their ancestors and hence the direction and amount of recent size change. In an earlier

Correspondence: A. Purvis, Department of Biological Sciences, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, UK.

Tel.: 0207 594 2327; fax: 0207 594 2339;

e-mail: a.purvis@imperial.ac.uk

§Present address: School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK.

comparative study of mammalian life history, Purvis & Harvey (1996) found that species in the smallest quartile of a taxonomic family – presumed to be mostly smaller than their ancestors – produced smaller litters of larger neonates after a longer gestation period than expected for their body size, indicating a legacy of recent size change. These findings were only preliminary because body size transitions were not identified rigorously.

Ideally, body size transitions would be measured directly by comparing extant species with fossils of their ancestors but, with the exception of a few small studies (e.g. Oakley & Cunningham, 2000; Polly, 2001; Webster & Purvis, 2002a,b), the incompleteness of the fossil record and the difficulties of placing fossils in a phylogeny of living species have precluded such an approach. However, the development of statistical methods for estimating ancestral values of continuous variables using explicit models of character evolution (e.g., Martins & Hansen, 1997; Schluter *et al.*, 1997; Pagel, 1999) permits inference of the direction, magnitude and rate of recent body size change in a lineage from information about extant descendants. If these inferred changes correlate with other attributes of species' biology, independently of their present body size, then the dynamics of character change need to be considered explicitly when trying to explain current characteristics of species. Such a finding could open up a new front for the comparative study of trait evolution.

In this paper, we present the first phylogenetic tests of whether the inferred recent history of size change in a species is correlated with life history traits, using a set of data for five variables in the mammalian order Carnivora. Carnivores are an ideal testing ground for phylogenetic comparisons of concomitant change in size and life histories because a complete species-level phylogeny is available (Bininda-Emonds *et al.*, 1999), body size variation is greater than any other mammalian order (Gittleman, 1985) and life history variables scale allometrically with body size: larger species mature later, and have smaller litters of larger neonates at longer intervals and following longer gestation periods (Gittleman, 1986, 1994).

Materials and methods

Data

Data for body mass, litter size, neonatal mass, gestation length, inter-birth interval, age at sexual maturity and island living are primarily from Gittleman (1986, 1993), supplemented with information from more recent publications; details of the complete database are available from the first author. Where possible, body mass was an average of male and female body mass, and all continuous variables were logarithmically transformed prior to analysis. Phylogenetic information is from a complete super-tree of all extant species (Bininda-Emonds *et al.*, 1999).

Methods

Estimating ancestral characters from data on descendants raises the problem of statistical nonindependence when the ancestors and descendants are then compared (Harvey & Purvis, 1991). We have ameliorated this problem by using a two-stage analysis, described in detail below. First, we used body size data for extant species to estimate ancestral sizes and used these to compute an index of size change for each species. Secondly, the size change index (SCI) was then tested for correlation with other variables using cross-sectional phylogenetic comparisons. Finally, to ensure any correlation found between size change and life history is not simply attributable to the difference between mainland and island living, we examined the variation of size change with island living after body size effects were taken into account.

Ancestral reconstruction

We estimated ancestral body mass from extant species data and phylogenetic information by maximum likelihood (ML) under a Brownian motion model of evolution (Schluter *et al.*, 1997). This method yields the most likely ancestral trait values under the specified model and apparently performs as accurately as any other when the estimates of the phylogeny and the data are considered reliable (Webster & Purvis, 2002b). For further justification of the method used for this analysis, see the Discussion. Ancml (Schluter *et al.*, 1997), the programme used to calculate ancestral character states, does not permit the inclusion of missing data or soft polytomies. Species lacking body size data were removed from the phylogeny. Soft polytomies were eliminated by excluding from each one those species for which least life history information was available. The resulting phylogeny is shown in Fig. 1; remaining polytomies indicate series of bifurcations having the same estimated date. Brownian motion, the evolutionary model implemented by Ancml, assumes rate constancy across the phylogeny. Earlier work (Webster, 2001) showed that the rate of body mass evolution, calculated using independent contrasts (Garland, 1992), differs significantly among, but not within, the seven clades highlighted in Fig. 1, we therefore used Ancml on each of the seven clades in turn rather than perform a global analysis.

Measures of size change

First we quantified the difference in body size between each extant species and the most recent ancestor shared with its closest living relative using the SCI. SCI describes the relative change in size between ancestor and descendant (equation 1), Fig. 2 gives an example of how this is calculated. Positive values indicate an increase in size (phyletic gigantism), negative values a decrease (phyletic dwarfism).

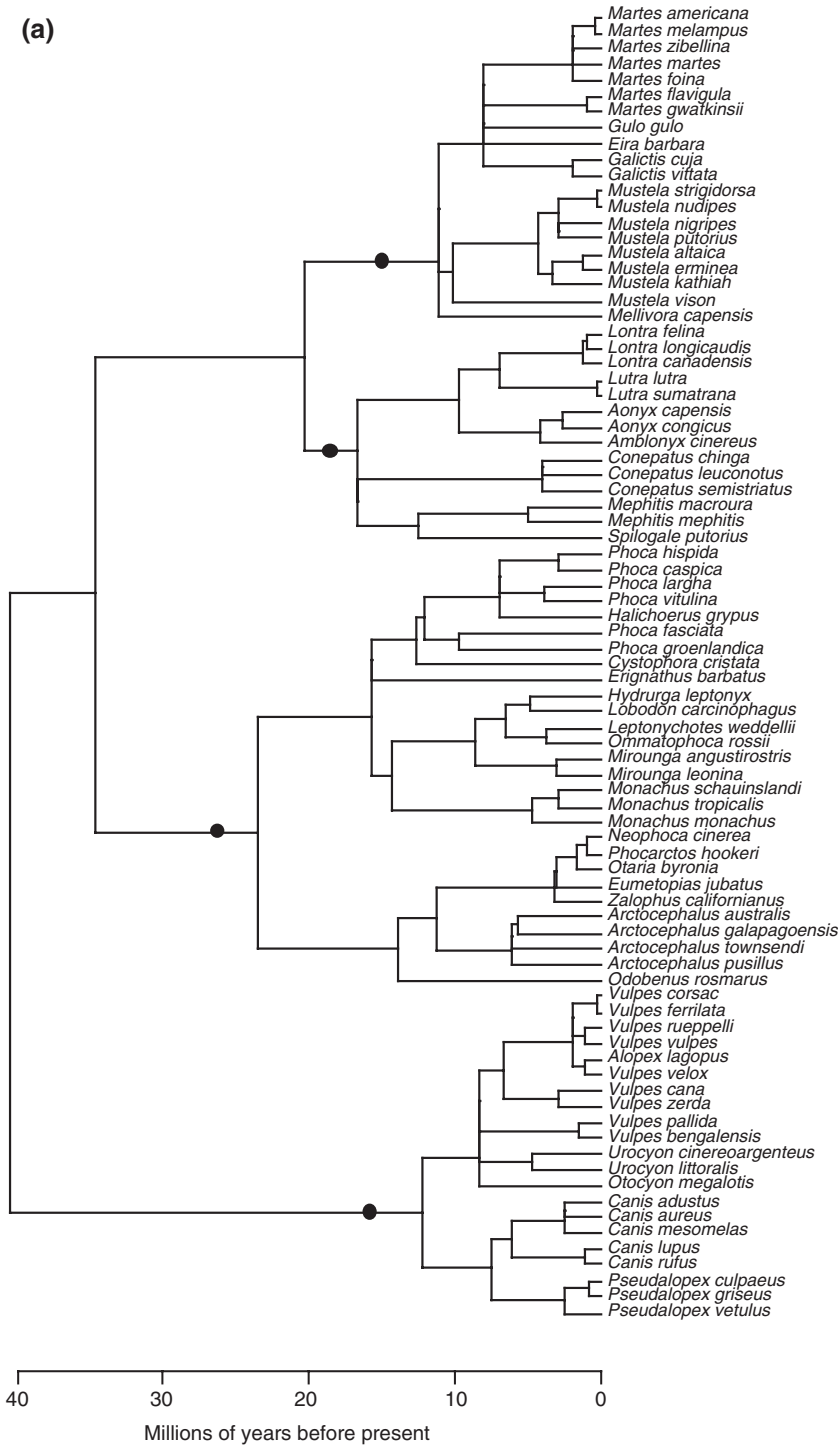


Fig. 1 (a) Caniform phylogeny and (b) feliform phylogeny which, when combined, make up the carnivore phylogeny used in this study. Dots indicate where the phylogeny was split into seven clades for analysis (see text).

$$SCI = \ln \left[\frac{\text{descendant body size}}{\text{ancestral body size}} \right] \quad (1)$$

The SCI focuses on the magnitude of recent size change. An alternative is to focus on the rate, allowing the impact of the speed of body size change to be

assessed. The rate of the change can be incorporated by dividing SCI by the square root of the branch length (following the model of Brownian motion), so giving a linear rate of size change (rate of size change index, RSCI) (equation 2). Again, Fig. 2 shows how RSCI is calculated.

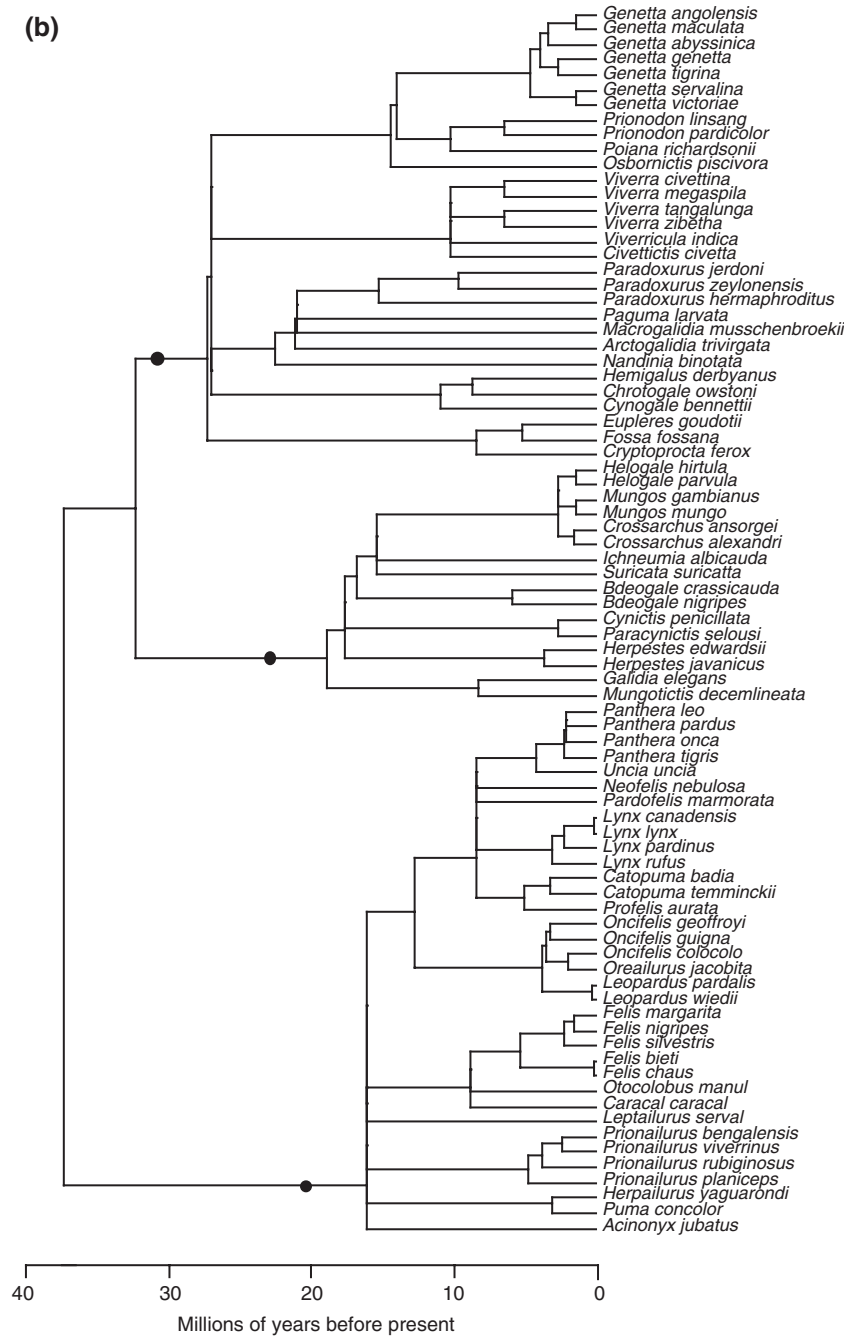


Fig. 1 Continued.

$$RSCI = \frac{SCI}{\sqrt{\text{Time between ancestor and descendant}}} \quad (2)$$

Life history correlates of the size change indices

We calculated standardized independent contrasts (Felsenstein, 1985; Purvis & Rambaut, 1995) before using least-squares multiple regression through the origin (Garland *et al.*, 1992) to look for correlates of size change.

We first regressed each of the five selected life history traits against body mass and either SCI or RSCI, the null hypothesis being that neither index adds explanatory power when body size is already in the model. In analyses using SCI, a positive correlation indicates that increases in the body size-independent value of the life history trait are associated with recent body size increases (gigantism). Conversely, a negative correlation indicates that the size-independent value of the life history trait increases when

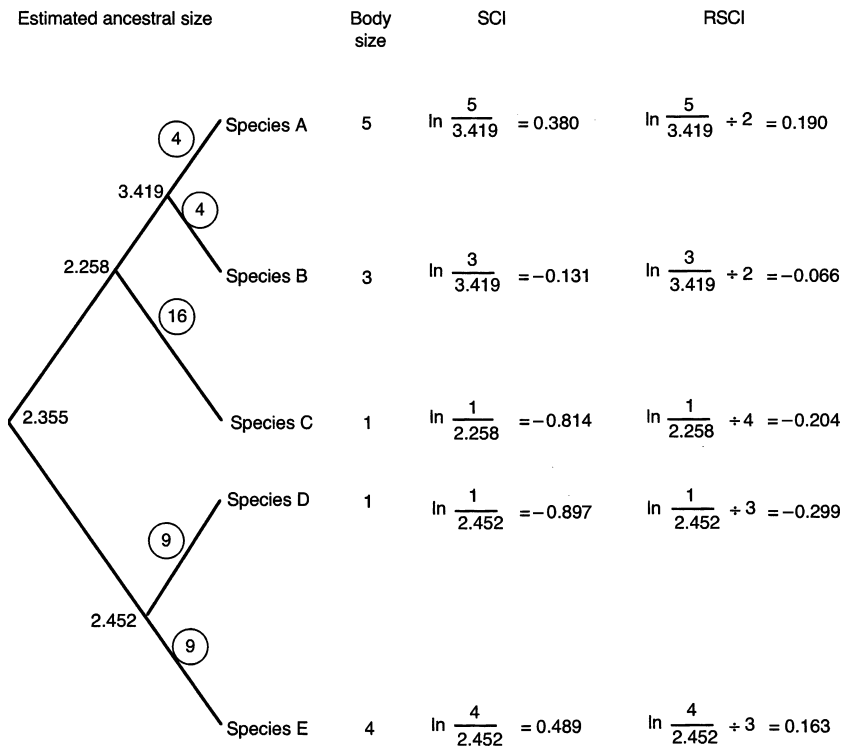


Fig. 2 Example of how size change index and relative size change index are calculated. Numbers at nodes are estimates of ancestral values; numbers in circles are branch lengths.

body size has undergone a recent reduction. Similarly, when RSCI is the measure of size change, a positive correlation indicates that increases in the body size-independent value of the life history trait are associated with a recent, rapid body size increase, a negative correlation with a recent, rapid body size reduction.

All regression analyses were performed over the carnivore phylogeny as a whole; earlier work (Webster, 2001) showed further division of the phylogeny for analysis (into the seven individual clades shown in Fig. 1, for example) revealed no obvious patterns in differences among clades. Scaling of independent contrasts to give them common variance is very sensitive to imprecision in the species data, because the scaling assumes all differences among species values to have arisen through evolution rather than through sampling error. Imprecision in the data can therefore cause heteroscedasticity in the contrasts (Purvis & Webster, 1999), which may lead to either type I or type II errors depending upon the position of the most influential observations. We therefore assessed the robustness of all regression analyses to unusually influential points: observations with a Studentized residual greater than ± 3 were removed from each analyses and the regression recalculated (following Jones & Purvis, 1997). We report results both before and after the removal of such points.

Island living correlates of the size change indices

We used the BRUNCH algorithm of CAIC (Purvis & Rambaut, 1995) to make independent contrasts between

island endemics and their closest relatives not restricted to islands, to assess whether island endemics had atypical values of SCI when body size effects on SCI were controlled for.

Results

The body size, ancestral body size and SCI value for each species are given in Table 1, Fig. 3a shows that species lie along a continuum of size change when measured using SCI. Species at the extremes of the distribution include species whose status as dwarf or giant species has already been recognized, such as *Helogale parvula* (the dwarf mongoose), *Mustela nivalis* (the least weasel), *Pteroneura brasiliensis* (the giant otter) and *Genetta victoriae* (the giant genet).

Life history correlates of the size change indices

Two of the five traits correlate significantly with SCI independently of body size whether or not contrasts having extreme influence are removed (Table 2a): for a given body size, species that have undergone recent size increase mature earlier (Fig. 4a) and have litters at shorter intervals. The predictive power is increased considerably by using SCI as well as current body size as a predictor: r^2 for the contrasts regressions rises from 15.7 to 25.6% for age at sexual maturity, and from 1.4 to 8.1% for inter-birth interval. Two further traits correlate

Table 1 Current body mass [Ln (kg)], estimated ancestral body mass [Ln (kg)] and size change index (SCI) value for each species.

Species	Current body mass [Ln (kg)]		Ancestral body mass [Ln (kg)]		SCI	Current body mass [Ln (kg)]		Ancestral body mass [Ln (kg)]		SCI	Current body mass [Ln (kg)]		Ancestral body mass [Ln (kg)]		SCI
	mass	[Ln (kg)]	mass	[Ln (kg)]		mass	[Ln (kg)]	mass	[Ln (kg)]		mass	[Ln (kg)]	mass	[Ln (kg)]	
<i>Act. jub</i>	3.880	2.205	1.676	Gal. kuj	0.487	0.707	-0.221	Mar. zib	0.160	0.285	-0.125	Par. sel	0.513	0.064	0.448
<i>Alo. lag</i>	1.200	1.007	0.193	Gal. ele	-0.210	-0.152	-0.058	Mel. cap	2.081	0.177	1.904	Par. zey	0.936	1.138	-0.202
<i>Amb. cin</i>	1.400	2.175	-0.775	Gal. vit	0.890	0.707	0.183	Mep. mac	-0.127	0.412	-0.539	Pho. cas	4.007	4.317	-0.310
<i>Aon. cap</i>	2.763	2.499	0.264	Gen. aby	0.180	0.564	-0.384	Mep. mep	0.799	0.412	0.388	Pho. fas	4.396	5.026	-0.630
<i>Aon. con</i>	2.760	2.499	0.261	Gen. ang	0.740	0.757	-0.017	Mir. ang	7.726	7.301	0.425	Pho. gro	5.042	5.026	0.016
<i>Arc. aus</i>	4.718	4.703	0.015	Gen. gen	0.645	0.626	0.019	Mir. leo	7.485	7.301	0.184	Pho. his	4.317	4.317	0.068
<i>Arc. gal</i>	3.818	4.703	-0.885	Gen. mac	0.916	0.757	0.159	Mon. mon	5.635	5.456	0.179	Pho. hoo	5.753	5.514	0.239
<i>Arc. pus</i>	5.481	4.759	0.722	Gen. ser	0.270	0.589	-0.319	Mon. sch	5.250	5.349	-0.099	Pho. lar	4.443	4.638	-0.195
<i>Arc. tow</i>	4.913	4.759	0.154	Gen. tig	0.701	0.626	0.076	Mon. tro	5.298	5.349	-0.051	Pho. vit	4.650	4.638	0.012
<i>Arc. tri</i>	0.888	1.238	-0.350	Gen. vic	0.920	0.589	0.331	Mun. dec	-0.320	-0.152	-0.168	Poi. ric	-0.553	-0.084	-0.468
<i>Bde. cra</i>	0.404	0.665	-0.261	Gul. gul	2.553	0.843	1.710	Mun. gem	0.590	0.200	0.390	Pri. ben	1.056	1.373	-0.317
<i>Bde. nig</i>	1.100	0.665	0.435	Hel. gry	5.377	4.788	0.589	Mun. mun	0.187	0.200	-0.013	Pri. lin	-0.359	-0.274	-0.085
<i>Can. adu</i>	2.257	2.211	0.046	Hel. hir	-1.241	-0.924	-0.317	Mus. alt	1.737	-1.654	-0.084	Pri. par	-0.510	-0.274	-0.236
<i>Can. aur</i>	2.231	2.211	0.020	Hel. par	-1.355	-0.924	-0.431	Mus. erm	-1.615	-1.654	0.038	Pri. pla	0.679	1.105	-0.425
<i>Can. lup</i>	3.511	3.241	0.270	Hem. der	0.772	1.087	-0.314	Mus. kat	-1.273	-1.264	-0.009	Pri. rub	0.316	1.097	-0.780
<i>Can. mes</i>	2.029	2.211	-0.182	Her. edw	0.215	0.129	0.085	Mus. nig	-0.125	-0.396	0.271	Pri. viv	2.164	1.373	0.791
<i>Can. ruf</i>	3.307	3.241	0.066	Her. jav	-0.253	0.129	-0.383	Mus. nud	-0.693	-0.361	-0.332	Pro. aur	2.480	2.191	0.289
<i>Car. car</i>	2.377	1.735	0.643	Her. yag	1.842	2.823	-0.981	Mus. put	0.076	-0.396	0.472	Pse. cul	2.077	1.639	0.438
<i>Cat. bad</i>	0.920	1.927	-1.007	Hyd. lep	6.109	5.888	0.221	Mus. str	0.405	-0.361	0.766	Pse. gri	1.433	1.639	-0.206
<i>Cat. tem</i>	2.464	1.927	0.537	Ich. alb	1.415	0.321	1.094	Mus. vis	-0.062	0.024	-0.086	Pse. vet	1.160	1.579	-0.419
<i>Chr. ows</i>	1.189	1.087	0.103	Leo. par	2.465	1.828	0.638	Nan. bin	0.980	1.202	-0.221	Pum. con	3.950	2.823	1.127
<i>Civ. civ</i>	2.493	1.875	0.617	Leo. wie	1.218	1.828	-0.609	Neo. cin	5.247	5.514	-0.267	Spi. put	-0.423	0.647	-1.070
<i>Con. chi</i>	0.613	0.948	-0.335	Lep. ser	2.388	2.205	0.183	Neo. neb	2.815	2.502	0.314	Sur. sur	-0.307	0.321	-0.629
<i>Con. feu</i>	1.220	0.948	0.272	Lep. wed	5.934	5.812	0.122	Odo. ros	6.824	5.507	1.317	Uhc. unc	3.581	3.736	-0.155
<i>Con. sem</i>	1.200	0.948	0.252	Lob. car	5.442	5.888	-0.446	Omm. ros	5.481	5.812	-0.331	Uro. cin	1.317	1.058	0.259
<i>Cro. ale</i>	0.410	0.095	0.315	Lon. can	1.996	1.786	0.210	Onc. cal	1.607	1.672	-0.065	Uro. lit	0.720	1.058	-0.338
<i>Cro. ans</i>	0.000	0.095	-0.095	Lon. fel	1.458	1.744	-0.286	Onc. geo	1.291	1.381	-0.090	Viv. civ	2.490	2.124	0.366
<i>Cry. fer</i>	2.250	1.311	0.939	Lon. lon	1.822	1.744	0.078	Onc. gui	0.920	1.381	-0.461	Viv. ind	1.034	1.875	-0.841
<i>Cyn. ben</i>	1.419	1.143	0.276	Lut. lut	2.131	2.000	0.131	Ore. jac	1.976	1.672	0.304	Viv. meg	2.183	2.124	0.060
<i>Cyn. pen</i>	-0.423	0.064	-0.488	Lut. sum	1.869	2.000	-0.131	Osb. pls	0.340	0.313	0.027	Viv. tan	1.550	1.871	-0.321
<i>Cys. cri</i>	5.907	5.249	0.658	Lyn. can	2.328	2.650	-0.322	Ota. byr	5.447	5.536	-0.089	Viv. zib	2.184	1.871	0.313
<i>Eir. bar</i>	1.406	0.843	0.563	Lyn. lyn	2.975	2.650	0.325	Oto. man	1.179	1.735	-0.555	Vul. ben	0.820	1.000	-0.180
<i>Eri. bar</i>	5.511	5.513	-0.002	Lyn. par	2.824	2.622	0.202	Oto. meg	1.401	1.120	0.282	Vul. can	0.033	0.371	-0.338
<i>Eum. jub</i>	6.456	5.657	0.799	Lyn. ruf	2.214	2.527	-0.313	Pag. lar	1.508	1.779	-0.271	Vul. cor	0.953	0.907	0.047
<i>Eup. gou</i>	0.740	0.994	-0.254	Mec. mus	1.440	1.250	0.190	Pan. leo	5.047	4.386	0.661	Vul. fer	0.850	0.907	-0.057
<i>Fel. ble</i>	1.700	1.761	-0.061	Mar. ame	-0.150	-0.042	-0.108	Pan. onc	4.370	4.386	-0.016	Vul. pal	1.114	1.000	0.115
<i>Fel. cha</i>	1.832	1.761	0.071	Mar. fla	0.813	0.766	0.047	Pan. par	3.764	4.386	-0.622	Vul. rue	0.504	1.029	-0.525
<i>Fel. mar</i>	0.923	0.851	0.072	Mar. foi	0.590	0.285	0.305	Pan. tig	5.058	4.384	0.674	Vul. vel	0.833	1.007	-0.174
<i>Fel. nig</i>	0.357	0.851	-0.494	Mar. gwa	0.710	0.766	-0.056	Par. her	1.071	1.175	-0.104	Vul. vul	1.607	1.029	0.578
<i>Fel. sil</i>	1.422	1.075	0.347	Mar. mar	0.343	0.285	0.058	Par. jer	1.277	1.138	0.139	Vul. zer	0.302	0.371	-0.069
<i>Fos. fos</i>	0.704	0.994	-0.289	Mar. mel	0.000	-0.042	0.042	Par. mar	0.995	2.502	-1.506	Zal. cal	5.187	5.621	-0.434

Species names abbreviated to the first three letters of each name.

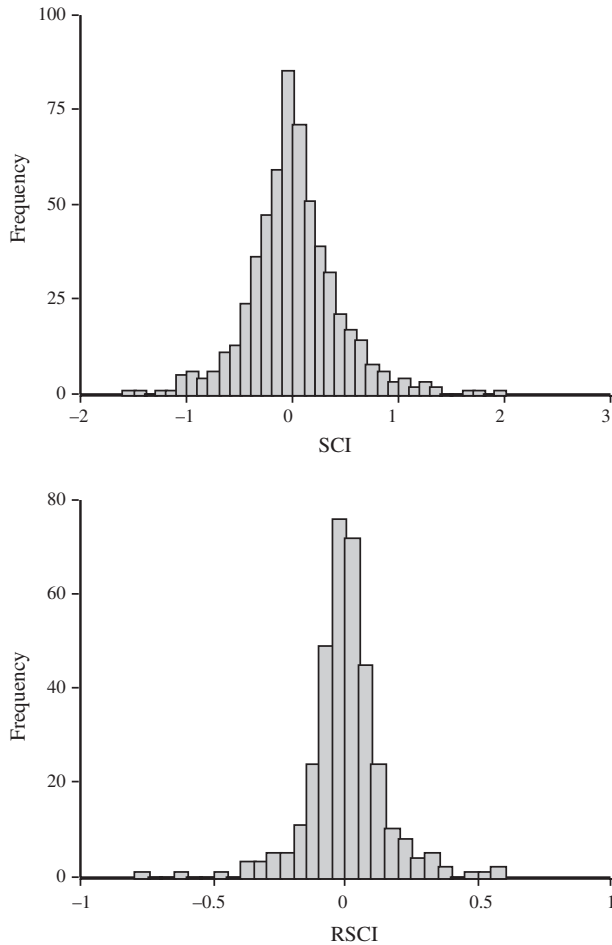


Fig. 3 Histogram of (a) size change index (SCI) and (b) relative size change index (RSCI).

with SCI when influential points are removed (Table 2a): phyletic giants have large litters (Fig. 4b) of small neonates, compared with other species of the same body size.

The distribution of RSCI has longer tails than that of SCI, with more extreme outliers (see Fig. 3). This made the results harder to interpret. We therefore considered it more conservative to use the SCI results for any further analysis and discussion, although the RSCI results were largely similar. We provide the results gained using RSCI in Table 2b for comparison.

Island living correlates of the size change index

Island endemics had more positive values of relative SCI in four of the nine comparisons, and more negative values in the other five. There is no significant trend within these results indicating island endemics have atypical values of SCI when body size effects on SCI are controlled for [using the sign-test, an eight to one split would be required for a trend to be confirmed ($P < 0.05$)].

Discussion

Macroevolutionary trends

Recent changes in body size predict present-day life history in carnivores independently of present-day body size. Although the allometric relationships of life history variables are often tight (e.g. Western, 1979; Read & Harvey 1989; Purvis & Harvey, 1995), we find that significant additional variance is explained by considering ancestral, as well as present, body size. Put another way, lineages that have recently undergone marked size change tend to lie away from the overall allometric relationships.

	Including influential points				Influential points removed			
	d.f.	Coefficient	<i>t</i>	<i>P</i> -value	d.f.	Coefficient	<i>t</i>	<i>P</i> -value
(a)								
Litter size	106	+0.176	1.44	0.154	104	+0.324	3.86	0.000
Gestation length	82	-0.049	-1.44	0.155	81	-0.040	-1.31	0.195
Interbirth interval	77	-0.222	-2.36	0.021	75	-0.182	-2.20	0.031
Age at sexual maturity	66	-0.282	-2.79	0.007	65	-0.268	-2.87	0.005
Neonatal mass	41	-0.431	-1.99	0.054	40	-0.344	-2.11	0.041
(b)								
Litter size	108	+0.112	1.59	0.129	105	+1.480	4.05	0.000
Gestation length	84	-0.124	-2.30	0.024	83	-0.126	-2.30	0.024
Interbirth interval	79	-0.393	-2.21	0.030	77	-0.364	-2.36	0.021
Age at sexual maturity	68	-0.382	-1.95	0.055	67	-0.377	-2.09	0.040
Neonatal mass	43	-1.750	-2.20	0.033	42	-1.360	-1.75	0.088

Table 2 Results of regression of life history and ecological traits against (a) size change index (SCI) and (b) relative size change index (RSCI).

Other columns refer to the regression of change index on the variable named in the first column, with body size factored out by multiple regression. *P*-values significant at the 0.05 level are in bold.

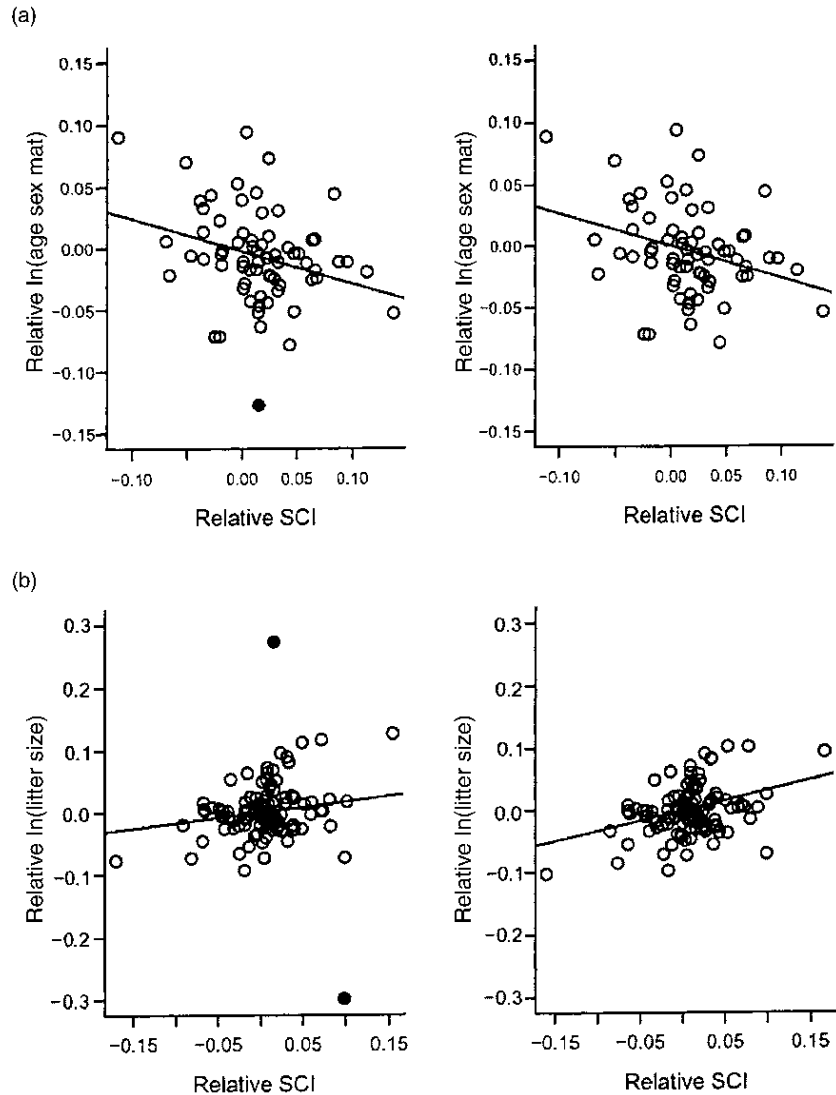


Fig. 4 Relationship between two life history traits and size change index (SCI), with body size effects removed by multiple regression through the origin. (a) Age at sexual maturity; (b) litter size. Left-hand graphs show the regression through all contrasts. Solid circles indicate contrasts with Studentized residuals greater than ± 3 . Right-hand graphs show the results of repeating the multiple regression after excluding those contrasts.

Life history variables are known to correlate strongly with one another across mammalian lineages, even when body size differences are controlled for: early sexual maturity is associated with large litters, small neonates, short intervals between litters and short gestations (e.g. Harvey *et al.*, 1989). As a result, mammalian species lie on a 'fast-slow continuum' (Read & Harvey, 1989; Promislow & Harvey, 1990; Oli & Dobson, 2003). Our results indicate that phyletic giants tend to be 'faster', and phyletic dwarfs 'slower', than average species of the same body size. These results largely agree with the less rigorous analysis by Purvis & Harvey (1996), whose data set spanned most mammalian families. They found that presumed phyletic dwarfs (identified by being in the smallest quartiles of their taxonomic family) had relatively small litters of relatively large neonates after relatively long gestations, but did not

have atypical ages at sexual maturity; inter-birth interval was not in their data set. Purvis & Harvey (1996) noted that an artefact (a nonlinear relationship with body mass) might have been responsible for their gestation length result; in an analysis designed to overcome this artefact, phyletic dwarfs did not have unusual gestation lengths. The two studies used very different methods and largely different mammalian taxa, the similarity in results gives weight to the genuine importance of recent body size change in predicting life history characteristics of lineages.

Why might life histories of extant carnivoran species reflect inferred ancestral, as well as current, body size? We envisage two possible mechanisms, both of which predict our observed patterns in the comparative relationships among body size, ancestral body size and life history. We outline possible ways in which the

mechanisms might be distinguished, but have only weak evidence on which to prefer one over the other.

Mechanism 1: Lag

Where body size change has been described in the literature, body size is often the first obvious trait to shift, with other morphological traits lagging behind (Lande, 1979; Roth, 1992; Lister, 1996; Wikelski & Trillmich, 1997; but see Deaner & Nunn, 1999). Fossil evidence suggests that body size can change markedly and quickly – up to 20–30% in only thousands of years for species ranging in size from *Vulpes vulpes* (red fox) to *Ursus arctos* (brown bear) (Kurten, 1968). If life history variables are unable to evolve as quickly as body size, they will lag behind. Although the reduction of body size may (and presumably does) result in a better-adapted species than the larger ancestor, the lagging life history traits may mean that, until the life history catches up with body size, the species is suboptimally adapted to the environment (Stanley, 1973). This prediction leads to a possible test, the lack-of-fit, and the reduced reproductive output that results, may reduce a species' global population size, perhaps even to the point of extinction. This mechanism predicts that ancestral body size predicts life history independently of current body size, and that species whose life history lags furthest behind its body size should have smaller geographic ranges and global population sizes. We used geographic range data from Purvis *et al.* (2000) to test whether geographic range was largest for species with SCI close to zero, using second-order polynomial regression across the species data (Fig. 5a) (independent contrasts assumes a linear relationship between the variables, Felsenstein, 1985). Neither the linear nor the squared term was significant (both $P > 0.1$) and both had positive coefficients, indicating that geographic range may increase with SCI rather than being largest for SCI near zero.

Mechanism 2: Optimization

Whereas lag is based on the idea that species are suboptimal, the second mechanism views departures from the typical allometric relationship as the results of optimization. Kozłowski & Weiner's (1997) model of mammalian life history views body size as being optimized by a trade-off between survivorship to reproduction (higher for small species that reproduce early) and adult reproductive effort (higher for large species that mature late). In their model, altering the rate at which animals acquire energy changes adult size by much more than reproductive rate, leaving species with reproductive rates that are those more typically encountered in species with the ancestral body size. Species whose rate of energy acquisition is increased evolve relatively high reproductive rate for their new larger size. Like the first, this mechanism predicts that ancestral body size predicts life history independently of current body size; however, if species whose rates of energy acquisition increase also

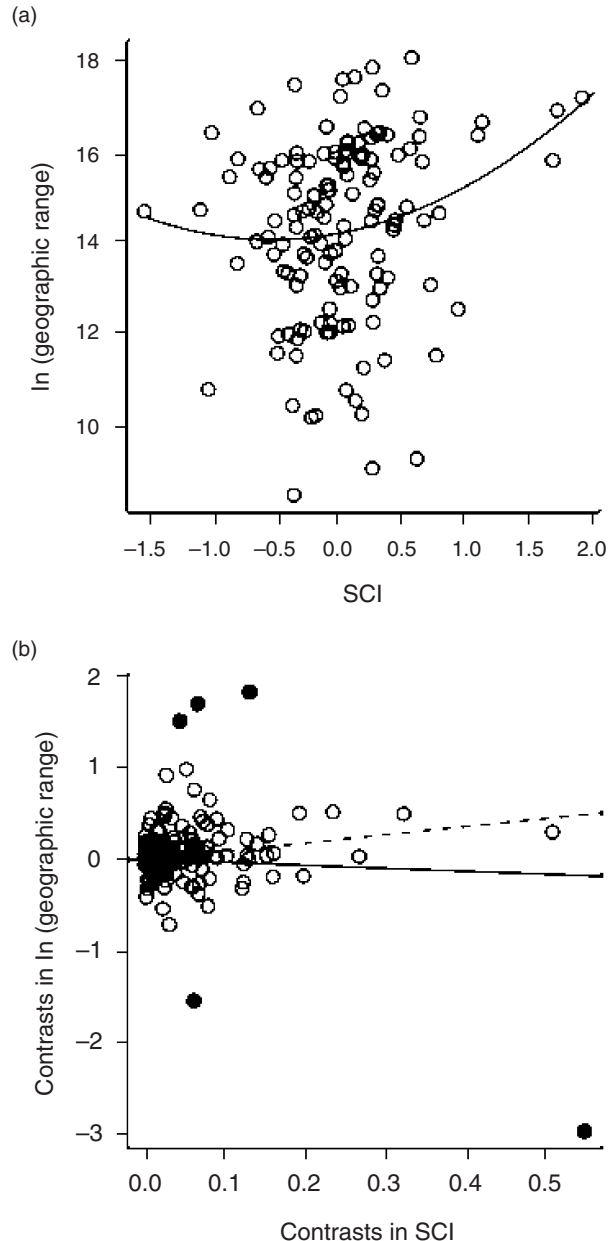


Fig. 5 (a) Relationship between geographic range and size change index (SCI) assessed across species and (b) relationship between geographic range and SCI, assessed across contrasts. Solid line: regression line for all contrasts ($t = -0.804$, ns). Solid circles indicate contrasts with Studentized residuals greater than ± 3 . Dashed line: regression line excluding these contrasts ($t = 3.367$, $P = 0.001$).

expand their geographic ranges (in response to favourable changes in habitat), then species whose body size has increased will tend to have large geographic ranges. SCI and geographic range are positively correlated across species ($t_{135} = 2.113$, $P = 0.037$) and, if influential contrasts are removed, across contrasts (all contrasts

$t_{135} = -0.840$, $P > 0.4$; removing influential observations $t_{130} = 3.367$, $P < 0.001$, Fig. 5b). These results give some support for the optimization mechanism, but are not particularly robust – deletion of the influential observations changes the sign of the relationship.

As a general ecological mechanism, resource availability is thus a potential candidate for a cause of size and life history changes in carnivores. Data on the six parameters in Kozłowski and Weiner's model are frustratingly unavailable, precluding a direct test. However, the scenario makes one further interesting prediction. If habitat changes occur that enable some species to assimilate energy at a more rapid rate, those species will become larger and also will presumably have a decreased risk of extinction; this leads to an indirect tendency for phyletic giants to persist for longer than phyletic dwarfs. This mechanism alone cannot explain the historical trend of increased body size termed Cope's rule, because resources cannot increase indefinitely, but it may be a contributory factor.

Comparative methods

Estimation of ancestral body sizes is clearly central to our study, but we recognize that the estimates may not be accurate. Estimates will be biased if there is an evolutionary trend over time (Oakley & Cunningham, 2000; Webster & Purvis, 2002b). Such a trend has been identified in Cenozoic mammals. Ancestral body sizes used in the calculation of the two size change indices were inferred as the ML state under a Brownian motion model of evolution. Polly (2001) found this method to be the most accurate in predicting molar size for a group of fossil carnivorans, when compared with other available methods. However, where there is a trend in a data set, the accuracy of the ML reconstructions can be extremely poor, although it still provides a better estimate of ancestral body size than most other methods (Webster & Purvis, 2002b). Cenozoic mammals show a trend towards increasing body size, Alroy (1998) made ancestor-descendant comparisons within genera and found an average rate of size increase of 9.1% over the lifetime of a genus (about 1 g/Myr on average, although many of his taxa were smaller than ours). We therefore designed our study to minimize the effect of this bias, by estimating body sizes only for nodes that are directly ancestral to extant species: most such nodes lie within the same genera as their extant descendants. Furthermore, even where a trend makes ancestral estimates biased, they are strongly correlated with the true values (Webster & Purvis, 2002b). Thus, the changes inferred along the branches leading to extant species may still bear the right relation to one another – all our method requires – even if they are incorrect in absolute terms.

Many of the statistical methods for estimating ancestral values of continuous variables are based on Brownian motion. We have chosen to use one of these Brownian

motion based models because of the results of the limited number of studies that compare estimated ancestral characters with fossil data (e.g. Oakley & Cunningham, 2000; Polly, 2001; Webster & Purvis, 2002a,b). However, having no complete fossil record of the carnivores, it is difficult to determine whether or not Brownian motion is an adequate model of evolution for reconstructing ancestral characters. As explained above, some violation of the assumptions of the Brownian motion model will not affect the outcome of this particular analysis, and by splitting the phylogeny into clades where evolutionary rates are not significantly different (see method), we attempt to minimize any rate heterogeneity that would break the model's assumptions. However, in the future it will be helpful to know how robust our approach is to assumption violation in general, something that could be achieved with computer simulation.

A second methodological issue is whether or not to remove extremely influential points from the regression analyses. As outlined in the Introduction, contrasts may be heteroscedastic, increasing the likelihood that a small number of very influential contrasts can skew the result of an analysis. Figure 4, especially Fig. 4b, shows that some contrasts do have extreme influence, justifying our approach (following Jones & Purvis, 1997) of exploring the effect of their removal. However, where influential points are caused by species known to be phyletic dwarfs or giants (species already highlighted for their unusual traits with respect to their body size), these are the very points most likely to display a signal of biological interest, making their removal harder to justify. Each regression analysis should therefore be assessed separately, as we have done above.

We have focused on continuous characters in this study for methodological reasons, but covariance with categorical traits might also be important. One of particular interest for the study of body size evolution is island endemism. The 'island rule' is a well-known generalization in macroecology, whereby species on islands evolve body sizes which are often far removed from the body size they possessed on arrival; large bodied species tend to evolve towards a smaller body size whereas small species increase in size (Foster, 1964; Heaney, 1978). In our analysis island endemics had more positive values of relative SCI in four of the nine comparisons, and more negative values in the other five, suggesting that any effect must be weak. We are therefore confident that our results are not attributable to differences between island and mainland lineages.

Although the mechanism remains uncertain, our results clearly indicate that evolutionary body size changes cast a lasting shadow over the life history of carnivore species. Looking at the evolutionary context of traits clearly increases the scope of comparative investigation. Parallel studies on other groups, particularly those with divergent size classes and life histories, are required to assess the generality of our results; studies of

other characters, such as ecological traits, would also be useful. More generally, our results demonstrate how a more dynamic view of character change can open up a new angle for comparative studies of mammalian ecology and life history.

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