Oikos

Appendix 1

Previously untabulated species for allometric analyses

These species, together with those already presented in online appendices to Pereira and Daily (2006) and Duncan et al. (2007) comprise the complete set of species analyzed in this paper.

Scientific name	Family	Population growth rate (year $^{-1}$)	Standardized biomass (g)
From Thompson 1987 (reporting ρ)			
Aepyceros melampus	Bovidae	0.35	45150
Aepyprymnus rufescens	Potoroidae	0.87	2500
Antechinus stuartii	Dasyuridae	1.62	22
Antechinus swainsonii	Dasyuridae	1.60	47
Antidorcas marsupialis	Bovidae	0.56	27900
Antilocapra americana	Antilocapridae	0.41	44240
Arctocebus calabarensis	Loridae	0.38	265
Bassaricyon gabbii	Procyonidae	0.49	1235
Bassariscus astutus	Procyonidae	1.05	870
Bettongia lesueur	Potoroidae	1.02	1300
Blarina brevicauda	Soricidae	12.73	17
Cephalophus maxwelli	Bovidae	0.55	8000
Choloepus hoffmanni	Megalonychidae	0.18	6250
Cryptotis parva	Soricidae	16.74	5
Dasycercus cristicauda	Dasyuridae	1.37	95
Dasyprocta leporina	Dasyproctidae	0.47	3265
Dasyurus geoffroii	Dasyuridae	1.41	880
Dasyurus hallucatus	Dasyuridae	1.61	378
Dasyurus maculatus	Dasyuridae	1.23	2438
Dasyurus viverrinus	Dasyuridae	1.66	843
Didelphis marsupialis	Didelphidae	3.26	1280
Didelphis virginiana	Didelphidae	3.26	1850
Eira barbara	Mustelidae	0.47	3950
Elephantulus rufescens	Macroscelididae	3.65	60
Eulemur fulvus	Lemuridae	0.32	2276
Gazella dorcas	Bovidae	0.45	12950
Gazella thomsoni	Bovidae	0.47	20900
Glaucomys volans	Sciuridae	1.41	79
Isoodon macrourus	Peramelidae	3.45	1050
Lagidium peruanum	Chinchillidae	0.60	1252
Lagostomus maximus	Chinchillidae	1.02	3311

Lemur catta	Lemuridae	0.31	2333
Macropus agilis	Macropodidae	0.55	11000
Macropus eugenii	Macropodidae	0.38	5500
Macropus fuliginosus	Macropodidae	0.32	21750
Macropus giganteus	Macropodidae	0.32	26100
Macropus parma	Macropodidae	0.65	3775
Macropus parryi	Macropodidae	0.34	11000
Macropus robustus	Macropodidae	0.34	16733
Macropus rufogriseus banksianus	Macropodidae	0.38	16200
Macropus rufogriseus rufogriseus	Macropodidae	0.37	16200
Macropus rufus	Macropodidae	0.42	27667
Madoqua kirki	Bovidae	0.65	5377
Marmosa robinsoni	Didelphidae	6.54	58
Monodelphis domestica	Didelphidae	4.35	85
Muntiacus reevesi	Cervidae	0.43	12733
Mustela frenata	Mustelidae	3.23	153
Mustela nivalis	Mustelidae	3.84	57
Mustela putorius	Mustelidae	1.05	745
Myoprocta acouchy	Dasyproctidae	1.04	910
Onychomys leucogaster	Macropodidae	4.56	33
Onychomys torridus	Macropodidae	4.45	22
Perameles nasuta	Peramelidae	4.18	859
Petaurus breviceps	Petauridae	1.10	109
Petrogale penicillata	Macropodidae	0.41	6300
Phascogale tapoatafa	Dasyuridae	2.52	156
Phascolarctos cinereus	Phascolarctidae	0.31	6024
Planigale gilesi	Dasyuridae	3.99	7
Planigale maculata	Dasyuridae	2.55	10
Potorous tridactylus	Potoroidae	1.06	876
Pseudocheirus peregrinus	Pseudocheiridae	0.88	885
Pudu pudu	Cervidae	0.47	8200
Redunca fulvorufula	Bovidae	0.34	29300
Sarcophilus harrisii	Dasyuridae	0.66	8000
Setonix brachyurus	Macropodidae	0.76	3250
Sminthopsis crassicaudata	Dasyuridae	3.98	15
Sminthopsis macroura	Dasyuridae	5.69	20
Suncus murinus	Soricidae	7.90	39
Sylvicapra grimmae	Bovidae	0.54	16993
Taxidea taxus	Mustelidae	1.01	6385
Thylogale billardierii	Macropodidae	0.51	3900
Tragelaphus scriptus	Bovidae	0.40	31100
Tragulus javanicus	Tragulidae	0.52	1460
Trichosurus caninus	Phalangeridae	0.25	2933
Trichosurus vulpecula	Phalangeridae	0.67	2433
Tupaia glis	Tupaiidae	3.00	148

From Global Population Dynamics Database (used in Fagan et al. 2001) (reporting r_m)

Apodemus flavicollis	Muridae	0.35	27
Apodemus sylvaticus	Muridae	1.39	23

Arctocephalus pusillus	Otariidae	0.09	76667
Blarina brevicauda	Soricidae	1.10	17
Canis latrans	Canidae	0.35	9700
Canis lupus	Canidae	0.23	31100
Castor canadensis	Castoridae	0.47	13000
Cervus elaphus	Cervidae	0.25	203625
Chaetodipus penicillatus	Heteromyidae	1.16	17
Connochaetes	Bovidae	0.27	177300
Dipodomys merriami	Heteromyidae	0.42	37
Dipodomys ordii	Heteromyidae	0.59	51
Dipodomys spectabilis	Heteromyidae	0.69	130
Enhydra lutris	Mustelidae	0.48	22950
Halichoerus grypus	Phocidae	0.44	167250
Hydrochaeris hydrochaeris	Hydrochaeridae	0.33	41204
Lepus americanus	Leporidae	0.25	1600
Lepus europaeus	Leporidae	0.25	3750
Lepus timidus	Leporidae	0.43	2988
Lycaon pictus	Canidae	0.35	22200
Lynx canadensis	Felidae	0.26	8590
Lynx lynx	Felidae	0.16	17800
Lynx rufus	Felidae	0.33	5200
Macaca fuscata	Cercopithecidae	0.19	8672
Macaca sylvanus	Cercopithecidae	0.26	10838
Marmota flaviventris	Sciuridae	0.43	3515
Martes americana	Mustelidae	0.56	716
Martes pennanti	Mustelidae	0.32	2375
Microtus agrestis	Muridae	1.32	22
Microtus arvalis	Muridae	0.43	28
Microtus montanus	Muridae	1.08	49
Microtus oregoni	Muridae	1.16	20
Microtus pennsylvanicus	Muridae	0.47	37
Mirounga sp.	Phocidae	0.66	668833
Mustela erminea	Mustelidae	0.55	126
Mustela nivalis	Mustelidae	0.52	57
Mustela vison	Mustelidae	0.32	605
Myodes gapperi	Cricetidae	1.39	21
Myodes glareolus	Cricetidae	1.12	20
Myodes rufocanus	Cricetidae	1.42	18
Napaeozapus insignis	Dipodidae	0.26	23
Neotoma albigula	Muridae	1.02	195
Ondatra zibethicus	Muridae	0.38	1461
Onychomys leucogaster	Macropodidae	1.22	33
Onychomys torridus	Macropodidae	0.87	22
Oryctolagus cuniculus	Leporidae	0.29	1439
Pagophilus groenlandicus	Phocidae	0.77	180000
Pan troglodytes schweinfurthi	Hominidae	0.74	44984
Panthera leo	Felidae	0.14	135500
Peromyscus eremicus	Muridae	0.81	21
Peromyscus maniculatus	Muridae	1.03	19
Phoca vitulina	Phocidae	0.24	74167

Pteronura brasiliensis	Mustelidae	0.25	24000
Puma concolor	Felidae	0.34	39600
Rattus norvegicus	Muridae	0.17	248
Reithrodontomys megalotis	Muridae	1.25	13
Sciurus vulgaris	Sciuridae	0.74	376
Sorex cinereus	Soricidae	0.66	4
Stenella attenuata	Delphinidae	0.02	112500
Syncerus caffer	Bovidae	0.47	488750
Tamias striatus	Sciuridae	1.40	96
Taxidea taxus	Mustelidae	0.22	6385
Tupaia glis	Tupaiidae	0.96	148
Urocyon cinereoargenteus	Canidae	0.50	3300
Ursus americanus	Ursidae	0.43	97000
Ursus arctos	Ursidae	0.25	111857
Ursus maritimus	Ursidae	0.38	272500
Vulpes lagopus	Canidae	0.49	5200
Vulpes vulpes	Canidae	0.49	3900
Wallabia bicolor	Macropodidae	0.37	13000
Zapus hudsonius	Dipodidae	0.77	19
Zapus sp.	Dipodidae	0.54	22

Appendix 2

Detailed discussion of alternative regression analyses

Our full analysis included four different methods for analyzing the allometric scaling slope between population growth rate and biomass. These methods represent the four-way cross between two methods of accounting for regression error (ordinary least squares [model I error] versus standardized major axis regression [model II error; sometimes called reduced major axis regression]) and the inclusion or exclusion of phylogenetic information in the regression model. These two modeling issues are addressed here, and the results of all four analyses presented. We feel that the combination of standardized major axis regression and phylogenetic information provides the best possible representation of the true allometric slope, and we have presented those results in the main text.

Ordinary least squares versus standardized major axis regression
When describing the relationship between two variables, the most popular model of error structure is to assume that the variable along the x-axis contains no error, and the best-fit line is chosen as that line which minimizes the mean squared error along the y-axis. This approach is known as ordinary least squares (OLS), and it is the standard approach for regression used by statistical software. In situations where the x-axis variable is used to predict the value of the y-axis variable, OLS will provide the best prediction and in many practical cases is the most appropriate line-fitting method. However, there are several situations in which OLS is inappropriate. In their comprehensive review of line-fitting methods, Warton et al. (2006) cite three scenarios in which OLS is inappropriate, all three of which are variants on the problem of allometric scaling, where the goal is to summarize the relationship between two variables. Considering alternatives to OLS is particularly important when the measured slope is to be compared against a theoretical prediction (Warton et al. 2006). The approach we use in our analysis, standardized major axis regression (SMA) minimizes the sum-of-squares of the shortest distance between the data (standardized in x and y) and the line. The best-fit line resulting from SMA regression represents the principal component of the correlation matrix of the x and y variables (for more details see Warton et al. 2006, Sokal and Rohlf 1995). In our analysis, where the goal is to estimate the scaling relationship between two variables measured with error and compare this slope to a theoretical prediction, SMA is more appropriate than OLS (Warton et al. 2006). In these cases, SMA will always predict a more positive (or negative) slope than OLS, and this correction increases as the quality of the fit decreases. This effect is reflected in the comparison in Table S1.

Phylogenetic comparative methods
Life-history traits, compared across a sample of all organisms, are constrained to some extent by the evolutionary history shared by organisms in the sample. In this analysis, we are comparing analyses on different sets of organisms sampled from all possible organisms, and it is important to consider the possibility that our analysis will be biased by correlations between species deriving from a shared evolutionary history. Incorporating phylogenetic information into a generalized least squares analysis is one way of addressing this concern (Garland and Ives 2000, Ives et al. 2007). Despite the potential for phylogenetic correlations to impact allometric scaling relationships between life-history variables, phylogenetic comparative methods have not traditionally been used. One recent exception is the analysis by Duncan et al. (2007) in which results using both OLS and phylogenetic generalized least squares are reported. For our analysis, we constructed a phylogeny of all the species in our analysis, subsets of which were used to compare different published results (see main text). Our phylogeny extended to the level of family, except in the case of the rodent family Muridae which was resolved to the level of subfamily (based on Jansa and Weksler 2004). The eutherian and marsupial phylogenies were based on the work of Liu et al. (2001) and Cardillo et al. (2004) respectively. We have constructed our phylogeny assuming the Monotremes represent an early divergence from the other mammals, with a subsequent divergence occurring between eutherian (placental) mammals and the marsupials (the theria hypothesis as supported by van Rheede et al. 2006). We calculated the phylogenetic correlation matrix using the vcv.phylo function of the R package 'ape' (Paradis et al. 2004).

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Appendix 3

Analyses of the influence of individual species on phylogenetically corrected SMA regressions

The best-fit line in Fig. 3C (main text) represents the standardized major axis (SMA) regression line corrected for phylogenetic correlations as applied to the data available for the estimation of r_m from time series data. This line appears skew to the cloud of points, and here we describe in detail the source of this apparent discrepancy. The magnitude of the SMA+phylogeny slope is given by:

$$\left| \hat{\beta} \right| = \left[\frac{(y - \hat{a}_y)'C^{-1}(y - \hat{a}_y)}{(x - \hat{a}_x)'C^{-1}(x - \hat{a}_x)} \right]^{1/2} \tag{A1}$$

where $\hat{a}_x$ and $\hat{a}_y$ are the phylogenetically corrected means of x and y, and $\hat{C}^{-1}$ is the inverse of the covariance matrix associated with the phylogenetic structure. Here we are using the terminology and symbology of Ives et al. (2007), where further details on the procedure may be found. Phylogenetic correlations among the points in Fig. 3C mean that not all points will have equal leverage on the fit of the line. Different species exert different amounts of leverage on the slope of the best fit line by virtue of both their position in the space of the scatterplot, and also by virtue of their distance phylogenetically to the other points in the sample. Whereas the former operates even in traditional (non-phylogenetically corrected) SMA, the latter is specific to our correcting for phylogenetic correlations between the species in the sample. We note in Fig. A1 that the SMA only best-fit line does fall through the bulk of points in the scatterplot, and therefore we would like to investigate which points are most strongly associated with the change in slope between the SMA only fit and the SMA+phylogeny fit. We will use the term 'phylogenetic leverage' to describe the extent to which individual points impact the addition of phylogenetic correlations to the SMA only analysis.

For the sample of species with r_m estimates, phylogenetic leverage is most strongly associated with the magnitude of the numerator in Eq. A1, and we can rank species by their influence on this component of the final SMA+phylogeny slope. In Fig. A1 we have replotted Fig. 3C to illustrate the influence of phylogenetic correction on the regression fit. Although the best-fit line does not fall through the bulk of the points in the scatterplot, it does closely track those points which have the highest phylogenetic leverage on the slope. The traditional scatterplot of Fig. 3C does not include this additional information, and this explains why the best-fit SMA+phylogeny line is correct even though visually it appears skew to the data.

The strong effect of phylogeny evident in Fig. A1 appears to occur because there are, by chance, many species in the r_m dataset that possess high growth rates that also are closely related. In a phylogenetically corrected regression, those species are disproportionately downweighted because they happen to be closely related. This can be checked by examining the mean C^{-1} value (i.e. the phylogenetic correlation matrix) for all the high growth rate species ($r > 5$) in each of the three datasets. The r_m dataset (i.e. Count) had a mean relatedness among these high growth rate species of 0.60, where the ρ data (i.e. Cole) average was 0.40 and the $\hat{r}$ (Pereira) dataset had a mean of 0.36.
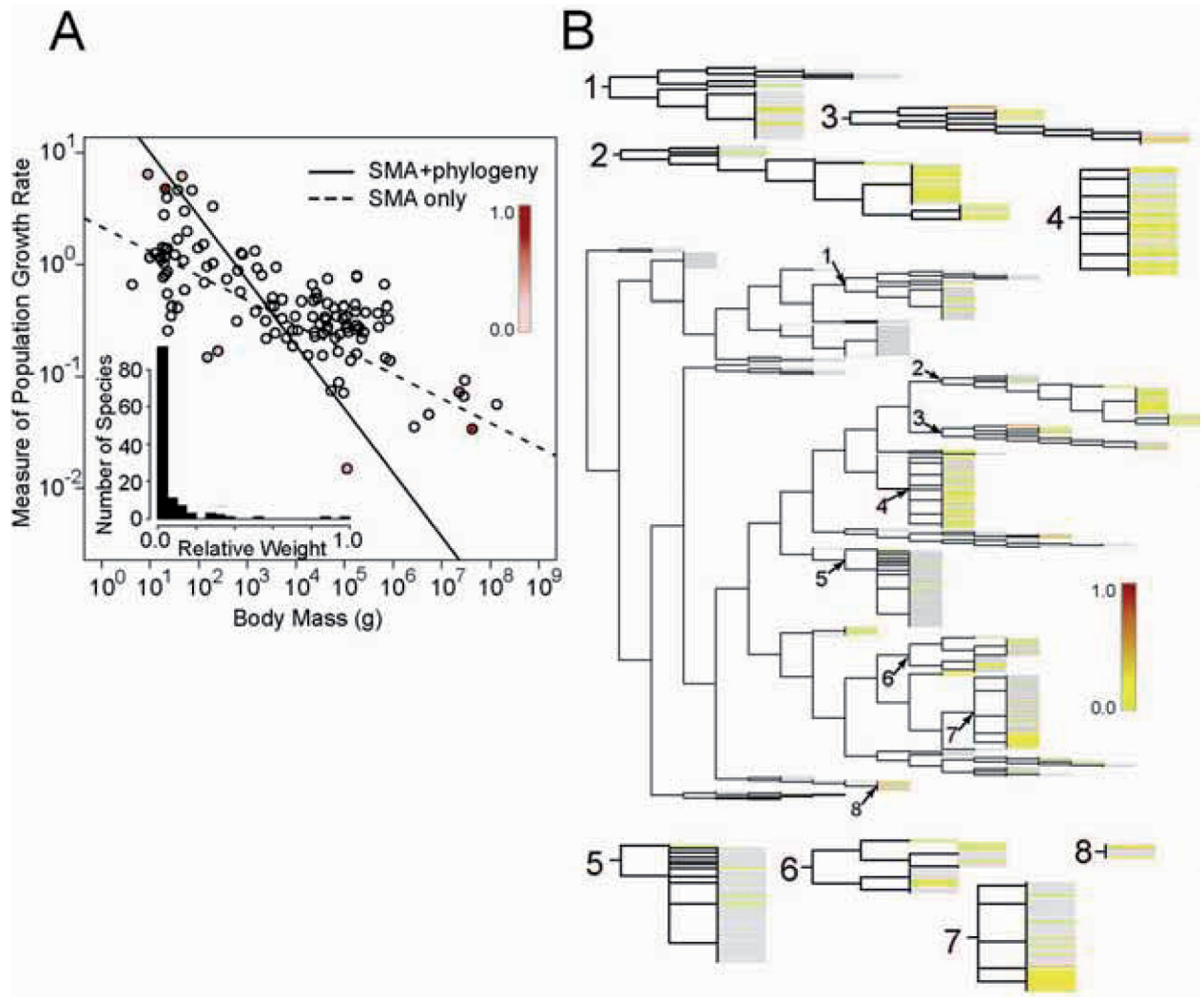
Figure A1. (A) Influence of phylogenetic leverage on the best fit of SMA regression to the allometric scaling of r_m, the density-independent per capita population growth rate obtained from time series analysis. This figure re-plots Fig. 2C from the main text with the symbol fill color proportional to the relative phylogenetic leverage of each data point (white = 0.0 to red = 1.0). As illustrated in the histogram inset, most points have relatively low phylogenetic leverage while a few points (toward the red end of the scale) are predominantly responsible for driving the change in slope when phylogenetic correlations are included. (B) Phylogenetic tree representing the relationship among all of the mammals used in this analysis. Branch lengths do not reflect phylogenetic distance. The tips of the tree are color coded according to phylogenetic weight. Gray lines represent those species that appear elsewhere in our analyses, but for which r_m values were not reported; these species are not represented by the scatterplot in (A). The remaining tip colors range from 0.0 (yellow) to 1.0 (red) giving the relative phylogenetic 'leverage' as plotted in the inset to panel (A). Note that, although our analysis did not assume equal branch lengths between all nodes, the tree has been drawn assuming equal branch lengths so that branch tips, and their relative phylogenetic weightings, may be more easily compared.

Appendix 4

Although we have focused on allometric scaling properties across all mammals, here we focus our analysis on scaling within specific Orders. Although the former is overwhelmingly represented in the literature, the latter question of allometric scaling within certain taxonomically related groups of organisms has received less attention (examples include Schmitz and Lavigne 1984, Zammuto 1987, Ross 1992). Here we report on allometric scaling within three Orders (Carnivora, Primates and the Rodentia) for which sufficient data was available. Within each Order, we estimated both ordinary least squares (OLS) and standardized major axis regression (SMA) estimates for the relationship between r (which was either r_m, ρ, $\hat{r}$) and biomass (Tables D1–D3). Note that our estimate of the OLS allometric scaling coefficient for ρ among primates is consistent with Ross' (1992) estimate of –0.37.

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Table D1. Allometric slopes (± 95% CI) of three measures of population growth rate as estimated by ordinary least squares (OLS) and standardized major axis regression (SMA) for the Carnivora.

Population growth estimator	Regression technique	
	OLS	SMA
$\hat{r}$	–0.194 (–0.412,0.024) (n = 24)	–0.557 (–0.834,–0.372) (n = 24)
ρ	–0.318 (–0.377,–0.259) (n = 38)	–0.366 (–0.432,–0.310) (n = 38)
r_m	–0.199 (–0.299,–0.099) (n = 33)	–0.347 (–0.467,–0.258) (n = 33)

Table D2. Allometric slopes (± 95% CI) of three measures of population growth rate as estimated by ordinary least squares (OLS) and standardized major axis regression (SMA) for the Primates. Note that there were insufficient data for r_m among the Primates to obtain estimates.

Population growth estimator	Regression technique	
	OLS	SMA
$\hat{r}$	–0.277 (–0.737,0.183) (n = 8)	–0.638 (–1.433,–0.284) (n = 8)
ρ	–0.388 (–0.440,–0.336) (n = 72)	–0.447 (–0.504,–0.398) (n = 72)
r_m	NA	NA

Table D3. Allometric slopes (± 95% CI) of three measures of population growth rate as estimated by ordinary least squares (OLS) and standardized major axis regression (SMA) for the Rodentia.

Population growth estimator	Regression technique	
	OLS	SMA
$\hat{r}$	–0.305 (–0.396,–0.214) (n = 88)	–0.528 (–0.628,–0.443) (n = 88)
ρ	–0.263 (–0.431,–0.095) (n = 14)	–0.397 (–0.626,–0.252) (n = 14)
r_m	–0.166 (–0.305,–0.027) (n = 38)	–0.457 (–0.623,–0.335) (n = 38)