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Differential scaling of locomotor performance in small and large terrestrial mammals

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Summary

It has been observed that the relationship between locomotor performance and body mass in terrestrial mammals does not follow a single linear trend when the entire range of body mass is considered. Large taxa tend to show different scaling exponents compared to those of small taxa, suggesting that there would be a differential scaling between small and large mammals. This pattern, noted previously for several morphological traits in mammals, has been explained to occur as a result of mechanical constraints over bones due to the differential effect of gravity on small and large-sized forms. The relationship between maximum relative running speed (body length s^{-1}) and body mass was analysed in 142 species of terrestrial mammals, in order to evaluate whether the relative locomotor performance shows a differential scaling depending on the range of mass analysed, and whether the scaling pattern is consistent with the idea of mechanical constraints on locomotor performance. The scaling of relative locomotor performance proved to be non-linear when the entire range of body masses was considered and showed a differential scaling between small and large mammals. Among the small species, a negative, although nearly independent, relationship with body mass was noted. In contrast, maximum relative running speed in large mammals showed a strong negative relationship with body mass. This reduction in locomotor performance was correlated with a decrease in the ability to withstand the forces applied on bones and may be understood as a necessary stress reduction mechanism for assuring the structural integrity of the limb skeleton in large species.

Key words: body length, body size, locomotion, mammal, running speed, scaling.

Introduction

Locomotor performance has been widely studied and quantified in a variety of organisms. Among terrestrial vertebrates, these studies have focused mainly on reptiles (for example, Garland, 1984; Losos, 1990a; Bauwens et al., 1995; Farley, 1997; Bonine and Garland, 1999; Irschick and Jayne, 1999; Miles et al., 2000). In contrast, information on locomotor performance among mammals is much less common (Garland, 1983; Djawdan and Garland, 1988; Garland et al., 1988; Djawdan, 1993).

Based on geometric similarity models, maximum running speed has been predicted to be independent of body size (Hill, 1950; McMahon, 1975a). Other similarity models (i.e. elastic, static stress and dynamic similarity) predict that running speed must increase in larger animals (see Garland, 1983). Alternatively, it has been proposed that the relationship between body mass (M_b) and running speed is simpler and more intuitive than these similarity models imply. Biomechanical models predict a positive relationship between limb length and body size (see Losos, 1990b), which has been observed empirically in lizards (Garland and Losos, 1994 and references therein). However, in a study on mammal running speeds, Garland (1983) showed that the relationship between maximum running speed and M_b was curvilinear rather than linear. After analysing the relationship within taxonomic groups, he found that orders containing the largest animals (i.e. Artiodactyla and Carnivora) showed negative or mass-independent scaling exponents, while orders of small animals (i.e. Rodentia, Lagomorpha) had mass-independent or positive relationships. A similar pattern was found in skeletal allometry of the limb long bones in mammals, where small and large body-sized groups yielded different scaling exponents (McMahon, 1975b; Alexander, 1977; Alexander et al., 1977, 1979; Biewener, 1983a). Economos (1983) and Bou and Casinos (1985) suggested that the different results could be explained by a differential scaling of the long bones of large *versus* small-sized mammals owing to the greater effects of gravity on the larger animals (Biewener, 1990). Differential scaling of morphological characters, including bone length and width (Bertram and Biewener, 1990; Christiansen, 1999), bone curvature (Bertram and Biewener, 1992) and body length (Economos, 1983), and of ecological characteristics (e.g. Silva and Downing, 1995; Marquet and Taper, 1998), have been described previously.

Several studies have shown that bone properties are extremely conservative regardless of phylogenetic and mass considerations (Biewener, 1990 and references therein). Among mammals, compressive failure strength ranges from 180 to 220 MPa (Biewener, 1990), and ultimate bending strength ranges from 170 to 300 MPa (Biewener, 1982). If mammals were designed according to geometric similarity, the static pressure stress (force per area) should increase in proportion to $M_b^{0.28}$ (see Biewener, 1982), indicating that the ratio of failure stress (i.e. mechanical strength) to static stress should decrease as M_b increases. If we assume that peak locomotor forces exerted on the ground are constant multiples of M_b, then peak locomotor stresses should scale with M_b in the same way as static stress. However, *in vivo* measurements of bone strain (Biewener and Taylor, 1986; Biewener et al., 1988; Rubin and Lanyon, 1984; Taylor, 1985), and calculations of bone stress from force platforms using high speed cameras (Alexander and Vernon, 1975; Alexander et al., 1984; Biewener, 1983b; Biewener and Blickhan, 1988), in different sized terrestrial species during strenuous activities, such as running or jumping, indicate that, rather than increasing with M_b, peak bone stress is mass-independent. Thus, the ratio of peak locomotor bone stress and static bone stress, defined as stress scope, which indicates how much stress can be resisted by a loaded bone, would decrease in proportion to $M_b^{-0.28}$ and $M_b^{-0.27}$, for compressive and bending stress, respectively. Experimental measurements of limb bone stress in a variety of mammals during locomotion have shown that, within each gait, the forces applied over bones increase proportionally with speed (Biewener, 1983b; Biewener and Taylor, 1986; Biewener et al., 1988). Farley and Taylor (1991) showed that the transition from trot to gallop in horses occurs at the same level of peak stress on muscles and tendons, suggesting that the gait transition might be triggered when musculoskeletal forces reach a critical level as a mechanism to reduce the chance of injury. It has been shown that maximum running speed recorded during gallop reaches similar peak bone stress values to those observed during the trot-gallop transition (Biewener and Taylor, 1986), indicating that those animals with greater stress scope values should be able to attain greater speeds than animals with a lower stress scope.

Locomotor performance has been considered an 'ecologically relevant' trait because of its effect on an animal's ability to escape from predators or to catch prey (Huey and Stevenson, 1979). However, when we wish to compare locomotor performance among organisms of different body size we are confronted with the problem of scale because body size affects nearly all physiological functions (Schmidt-Nielsen, 1984). Therefore, because (1) the amount that an animal's muscle shortens, and (2) the distance travelled with one step, both vary directly with body length, a body length-dependent scale (relative running speed) might be more appropriate when characterising the performance of animals (Jones and Lindstedt, 1993). Accordingly, through a computer simulation, Van Damme and Van Dooren (1999) showed that animals with higher relative speeds (in body length s^{-1}) would be less likely to be caught than relatively slower animals, and that the relationship between running speed and catchability might be size dependent. Therefore, a relative measurement of performance might be an important factor that would predict the outcome of a predator-prey interaction.

In this paper, I analysed the effect of body weight on a length-dependent measurement of maximum locomotor performance in terrestrial mammals. Based on the geometric similarity model, the relative running speed should scale as $M_b^{-0.33}$. Alternatively, if relative speed scales with limb length according to biomechanical predictions, the relationship should be mass independent. It is hypothesised that gravity would be playing a differential role on locomotor performance across different size ranges, and large species would be more affected than small ones. Therefore, it is expected that small mammals would show an allometric exponent similar to that predicted by either geometric similarity or biomechanical analysis. In contrast, if locomotor performance in large mammals is constrained by the ability of musculoskeletal structures to withstand forces during activity, it is expected that absolute maximum running speed would be proportional to stress scope and therefore would scale according to $M_b^{-0.27}$. Consequently, a length-based measurement of performance would scale in proportion to $M_b^{-0.60}$. On the other hand, if locomotor performance was not constrained by body weight, a monotonic relationship between maximum relative speed and body mass should be observed in all ranges of body mass. In order to test this hypothesis, I worked with a sample spanning a wide range of body sizes as well as taxonomic groups, analysing the differences in patterns observed between large and small-sized mammals.

Materials and methods

Morphological and running speed data

Data on running speed and M_b of 142 terrestrial mammals, spanning a wide range of M_b (from 9 g to 6 tons) and belonging to the orders Proboscidae (N=2), Perissodactyla (N=7), Artiodactyla (N=37), Primata (N=3), Carnivora (N=21), Rodentia (N=50), Lagomorpha (N=8) and Marsupialia (N=14), were gathered from the literature (Garland, 1983; Djawdan and Garland, 1988; Garland et al., 1988; Garland and Janis, 1993) (Table 1). Maximum running speeds have been obtained using a wide variety of methodologies that are of highly variable quality (see Garland, 1983). There are potentially some errors associated with the analyses due to the fact that some values have been estimated or measured with poor-precision methods (e.g. car chasing for absolute speed). The magnitude of these errors will be dependent on the range analysed (larger errors in small allometric ranges of M_b than in large ranges). Most recompiled data were included, necessarily sacrificing precision for completeness. Assuming there is no systematic bias in measurements, the analyses would underestimate the real relationships between relative speed and M_b. When more than one value had been reported for the same species, the single fastest running speed documented was chosen in an

Table 1. *Maximum relative running speed (V_{max}/L_b), body mass (M_b), and body length (L_b) of the 142 mammal species used in this study*

Species	Body mass (kg)	Body length (m)	Maximum relative running speed (body length s^{-1})	References
Proboscidae				
Loxodonta africana	6000	6.75	1.40	2,7
Elephas maximus	4000	5.95	1.18	1,2
Perissodactyla				
Ceratotherium simum	2000	3.78	1.79	5,7
Diceros bicornis	1200	3.38	3.60	5,7
Equus caballus	350	2.50	7.56	5,7
Equus zebra	300	2.35	7.35	2,7
Tapirus bairdii	250	2.08*	5.18	5,6
Equus burchelli	235	2.32	8.16	5,7
Equus hemionus	200	2.25	8.40	5,7
Artiodactyla				
Hippopotamus amphibius	3800	3.98	1.70	2,7
Giraffa cameolopardalis	1075	4.27	3.80	5,7
Bison bison	865	2.80	5.40	5,7
Bos sauveli	800	2.16	3.62	2,7
Syncerus caffer	620	2.75	5.60	5,7
Camelus dromedarius	550	2.85	3.03	5,7
Taurotragus oryx	511	2.63	7.20	5,7
Alces alces	384	2.77	5.47	5,7
Cervus elaphus	300	2.15	9.04	2,7
Connochaetes gnu	300	2.21*	10.97	2,6
Hippotragus equinus	226.5	2.28	6.65	5,7
Connochaetes taurinis	216	1.98*	10.88	5,6
Alcelaphus buselaphus	136	1.98	10.94	5,7
Damaliscus lunatus	130	1.63	11.63	5,7
Oreamnos americanus	113.5	1.40	6.36	5,7
Rangifer tarandus	100	1.70	12.71	5,7
Lama guanacoe	95	1.73	8.77	5,7
Ovis canadensis nelsoni	85	1.45	8.96	1,5
Phacochoerus aethiopicus	85	1.20	12.38	2,7
Odocoileus hemionus	74	1.39*	11.87	5,6
Capra caucasia	70	1.58	7.71	2,7
Ovis ammon	65	1.50	10.80	2,7
Gazella granti	62.5	1.31*	16.67	5,6
Odocoileus virginianus	57	1.27*	13.59	5,6
Dama dama	55	1.53	11.51	5,7
Aepyceros melampus	53.25	1.30	9.76	5,7
Antilocapra americana	50	1.25	21.60	2,5,7
Capreolus capreolus	50	1.23	13.17	2,7
Rupicapra rupicapra	50	1.10	9.82	2,7
Antilope cervicapra	37.5	1.20	23.63	5,7
Saiga tatarica	35	1.20	18.00	5,7
Antidorcas marsupialis	34	1.30	20.15	2,7
Gazella subgutturosa	30	1.03*	25.51	2,6
Procapra gutturosa	30	1.22	17.78	2,7
Capra aegagrus	30	1.40	8.68	2,7
Gazella thomsonii	20.5	0.904*	24.19	5,6
Madoqua kirki	5	0.620	18.29	5,7
Carnivora				
Ursus maritimus	265	2.35	4.60	1,7
Ursus arctos	251.3	2.25	5.76	5,7
Panthera tigris	161	2.10	7.20	5,7
Panthera leo	155.8	1.95	8.17	5,7

Table 1. *Continued*

Species	Body mass (kg)	Body length (m)	Maximum relative running speed (body length s^{-1})	References
Carnivora				
Ursus americanus	93.4	1.65	7.85	1,5
Acinonyx jubatus	58.8	1.31	22.67	5,7
Panthera pardus	52.4	1.41	11.49	5,7
Crocuta crocuta	52	1.30	13.46	5,7
Canis lupus	35.3	1.22	14.13	5,7
Hyaena hyaena	26.8	1.11	12.13	5,7
Canis familiaris	25	0.966*	18.73	2,6
Lycaon pictus	20	0.940	20.11	2,7
Canis latrans	13.3	0.875	20.06	5,7
Meles meles	11.6	0.736	11.01	5,7
Canis aureus	8.8	0.830	18.22	5,7
Procyon lotor	7	0.508	12.77	5,7
Canis mesomelas o adustus	7	0.631*	25.66	2,6
Vulpes fulva	4.8	0.678	28.69	5,7
Nasua narica	4.4	0.540	13.50	5,7
Urocyon cinereoargenteus	3.7	0.584	29.59	5,7
Mephitis mephitis	2.5	0.330	13.09	5,7
Primates				
Gorilla gorilla	127	1.66*	5.20	2,6
Homo sapiens	70	1.36	7.93	2,7
Presbytis	13	0.515	19.40	2,7
Rodentia				
Marmota monax	4	0.450	9.60	2,7
Uromys caudimaculatus	1.18	0.270	16.63	4,7
Sciurus niger	1.078	0.338*	19.17	4,6
Spermophilopsis leptodactylus	0.6	0.278*	34.98	2,6
Spermophilus undulatus	0.6	0.278*	19.43	2,6
Spermophilus citellus	0.5	0.261*	18.59	2,6
Sciurus carolinensis	0.5	0.261*	30.98	4,6
Sciurus vulgaris and persicus	0.4	0.243*	22.25	2,6
Spermophilus beldingi	0.3	0.220*	15.92	2,6
Rattus	0.25	0.190	13.78	2,7
Spermophilus saturatus	0.222	0.199*	30.06	4,6
Tamiasciurus hudsonicus	0.22	0.198	20.51	2,7
Spermophilus tridecemlineatus	0.125	0.164*	20.02	4,6
Spermophilus tereticaudus	0.1126	0.159*	25.82	3,6
Neotoma lepida	0.1106	0.190	24.30	3,7
Mesocricetus brandti	0.11	0.175	13.89	2,7
Tamias striatus	0.1	0.323	14.21	2,7
Dipodomys deserti	0.0976	0.152*	26.73	3,6
Ammospermophilus leucurus	0.0759	0.153	30.45	3,7
Pseudomys nanus	0.061	0.130*	30.02	4,6
Zymomys argurus	0.0605	0.131	25.56	4,7
Dipodomys microps	0.056	0.126*	45.05	2,6
Tamias amoenus	0.051	0.122	42.94	1,4
Microtus pennsylvanicus	0.05	0.121*	24.51	2,6
Pseudomys australis	0.05	0.121*	36.54	4,6
Heteromys dasmarestianus	0.05	0.148	22.88	4,7
Dipodomys ordii	0.0478	0.119*	31.89	3,6
Lyomis pictus	0.042	0.116	40.03	4,7
Chaetodipus baileyi	0.0391	0.112*	29.99	3,6
Dipodomys merriami	0.035	0.108*	80.31	2,6
Notomys cervinus	0.035	0.108*	35.14	4,6
Pitymys pinetorum	0.03	0.102*	17.97	2,6
Tamias minimus	0.0293	0.101*	44.74	3,6

Table 1. *Continued*

Species	Body mass (kg)	Body length (m)	Maximum relative running speed (body length s^{-1})	References
Rodentia				
Zapus trinotatus	0.0285	0.100*	38.44	4,6
Peromyscus leucopus	0.025	0.0961*	30.89	2,6
Napeozapus insignis	0.025	0.0900	25.80	2,7
Notomys alexis	0.0245	0.0955*	37.04	4,6
Perognathus parvus	0.0244	0.0954*	35.39	3,6
Peromyscus eremicus	0.0198	0.0889*	39.77	3,6
Peromyscus truei	0.0193	0.0882*	43.78	3,6
Onychomys torridus	0.0193	0.115	24.29	3,1
Peromyscus maniculatus	0.0182	0.0865*	41.84	3,6
Chaetodipus fallax	0.018	0.0862*	40.12	3,6
Zapus hudsonicus	0.018	0.0862*	27.89	2,6
Pseudomys hermannbergensis	0.018	0.0862*	39.49	4,6
Mus musculus	0.016	0.0800	43.88	2,7
Leggadina forresti	0.0155	0.0820	41.51	4,7
Peromyscus crinitus	0.0137	0.0786*	39.14	3,6
Microdipodops megacephalus	0.0123	0.0759	38.79	3,7
Perognathus longimembris	0.0089	0.0681*	39.26	3,6
Lagomorpha				
Lepus arcticus	4.6	0.549*	31.49	2,6
Lepus alleni	4.4	0.541*	35.96	2,6
Lepus europeus	4	0.524	37.12	1,2
Lepus townsendii	3.5	0.501*	30.19	2,6
Lepus californicus	2	0.415	41.59	1,2
Oryctolagus cuniculus	1.9	0.400	37.80	2,7
Lepus americanus	1.5	0.377	35.77	1,2
Sylvilalagus	1.5	0.343	31.49	2,7
Marsupialia				
Macropus spp	50	1.22*	14.42	4,6
Macropus eugenii	4	0.477	22.64	1,4
Bettongia penicilata	1.1	0.365	18.35	4,7
Potorus tridactylus	0.998	0.329	17.56	4,7
Isoodon obesulus	0.718	0.320	12.07	4,7
Dasyuroides byrnei	0.12	0.225	31.68	4,7
Monodelphis brevicaudata	0.0745	0.159	19.86	4,7
Antechinus flavipes	0.052	0.155	29.03	1,4
Antechinus stuardii	0.0315	0.123*	39.26	4,6
Antechinomys laniger	0.025	0.104*	38.76	4,6
Sminthopsis macroura	0.02	0.0961*	40.54	4,6
Sminthopsis crassicaudata	0.017	0.0892*	34.82	4,6
Cercatetus concinnus	0.015	0.0845	15.92	4,7
Myrmecobius fasciatus	0.48	0.0950	39.60	4,7

*Values obtained from Silva's (1998) allometric equation.

Body mass and body length estimates correspond to those of average adult specimens.

Source of data on body mass, body length, and maximum running speed are indicated for each species: 1, Eisenberg (1981); 2, Garland (1983); 3, Djawdan and Garland (1988); 4, Garland et al. (1988); 5, Garland and Janis (1993); 6, Silva (1998); 7, Nowak (1999).

attempt to reduce the effect of differences in procedure and/or motivation among studies (Garland, 1983; Garland et al., 1988). Species with highly specialised habits and limb morphologies, such as arboreal and fully fossorial species, were excluded from the analysis (i.e. *Erithizon*, *Didelphis*, *Bradypus*, *Talpa* and *Scalopus*).

Data on body length (L_b), measured as the length of the head and body (excluding tail length), were obtained mainly from Eisenberg (1981) and Nowak (1999). Data reported correspond to mean values for adult individuals. If mean values were unavailable, the midpoint of ranges was used. Where specific values were unavailable, values were obtained from Silva's (1998) allometric equation for terrestrial non-flying mammals $L_b=0.330\ M_b^{0.334}$ ($r^2=0.98$).

An estimation of bending stress scope for mammals analysed in this study was obtained using the equation

$$\text{stress scope} = 10.47M_b^{-0.27}, \quad (1)$$

calculated using an arbitrary stress scope value of 1 for *Loxodonta* (M_b=6000 kg).

Statistical analysis

The relationship between M_b and maximum relative speed (V_{max}/L_b) was obtained through linear regression on log-transformed data to yield estimates of the parameters of the allometric equation

$$y = ax^b, \quad (2)$$

where y is V_{max}/L_b in body length s^{-1}, and x is M_b in kg. Scaling equation parameters were obtained through ordinary least-squares regression analysis (OLS). As neither relative maximum running speed nor M_b can be considered errorless, a model II regression (reduced major axis, RMA) is more appropriate for estimating parameters (LaBarbera, 1989; Swartz and Biewener, 1992). In this study, both OLS and RMA are shown, but analyses and discussions are mainly based on OLS estimations in order to be able to compare exponent values with previously existing data reported in the literature, and also for the purposes of comparing linear with non-linear regression results.

Non-linearity in the relationship between maximum relative running speed and M_b was suggested by the LOWESS method (robust *lo*cally *we*ighted *s*catterplot *s*moother; Cleveland, 1979), a non-parametric technique of sequential smoothing that does not attempt to fit a simple model over the entire range of data, but fits a series of local regression curves using restricted sets of data near the area of interest (Efron and Tibshirani, 1991). This procedure is used for revealing distribution patterns that are difficult to identify in a scatterplot (Ellison, 1993). I used polynomial regression analysis to test for statistical significance of non-linearity indicated by LOWESS. Differential scaling can be modelled by a continuous linear relationship with different slopes on either side of a critical point (k), generating a broken line. If there is only one critical point, there will be two domains with their own linear regressions (bilinear model). If there are two critical points, three domains will appear (trilinear model). Comparisons between regression models were conducted by comparing the resulting Error Mean Squares under the different models (polynomial, bilinear, and trilinear) to calculate the F-statistic from their ratio and applying the sequential Bonferroni test using the Dunn–Šidák method to avoid inflating the type I error (Sokal and Rohlf, 1995). This approach was used rather than comparing coefficients of determination because it considers the reduction in degree of freedom by fitting additional parameters to the regression model.

Comparisons of estimated slopes with slopes obtained from the literature were made by t-test. Analysis of covariance (ANCOVA) was used to test the equality of slopes of different taxa or size ranges. When more than two slopes were compared, multiple comparisons of slopes were carried out through a Bonferroni test (Zar, 1996). All analyses were made with α=0.05.

Results

Overall, maximum relative running speed was found to decrease with increasing M_b (Fig. 1). A scaling exponent of –0.17 was obtained through linear regression on the complete sample of mammals (Table 2). The heteromyid rodent *Dipodomys merriami* proved to be the mammalian species with the fastest relative running speed. LOWESS analysis suggested that the relationship between relative running speed and M_b was non-linear (Fig. 1) with polynomial regression yielding higher coefficient of determination (r^2=0.798) and fit than simple linear regression, as indicated by a significant quadratic coefficient (P<0.001). Three body mass ranges over which allometric exponents differed were identified using LOWESS analysis, giving rise to a trilinear model (r^2=0.813): below 10 kg, between 10 and 100 kg, and over 100 kg, with scaling exponents of –0.09±0.04 (mean ± 95% confidence interval), –0.34±0.20 and –0.51±0.10, respectively. Allometric slopes differed significantly among these size groups (ANCOVA, P<0.001), being significantly different in small *vesus* large-sized mammals (Bonferroni test, P<0.05). Intermediate-sized mammals did not differ from large (Bonferroni test, P>0.05, power=0.96) or small mammals (Bonferroni test, P>0.05, power=1.00). This pattern of differential scaling may also be modelled through a bilinear model. The critical body mass

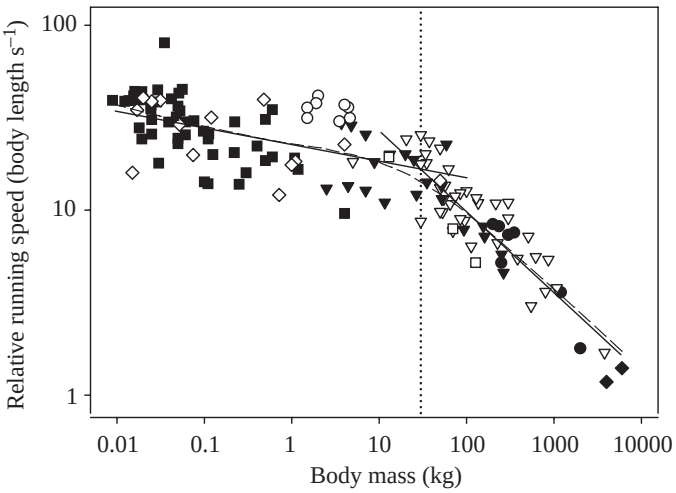

Fig. 1. Maximum relative running speed of 142 species of mammals. Dashed line represents the LOWESS non-parametric smoothed regression fit (sampling proportion=0.6). Dotted line indicates the point of slope change (k=30 kg) in the one point-change regression model. Solid lines represents the fit under the ordinary least-squares method (OLS) for small and large mammals. Filled squares, Rodentia; open squares, Primata; filled diamonds, Proboscidae; open diamonds, Marsupialia; filled triangles, Carnivora; open triangles, Artiodactyla; filled circles, Perissodactyla; open circles, Lagomorpha.

Table 2. *Linear regression parameters of maximum relative running speed on body mass estimated from ordinary least-squares (OLS) and reduced major axis regression (RMA)*

		Linear regression estimates of V_{max}/L_b=log a+b log (M_b)				
			b			
Data set	N	a	OLS	RMA	r^2	S.E.E.
All mammals	142	21.52	–0.17* (–0.19, –0.15)	–0.21* (–0.23, –0.19)	0.692	0.190
>30 kg	56	88.64	–0.46* (–0.53, –0.40)	–0.52* (–0.58, –0.45)	0.808	0.131
<30 kg	86	24.21	–0.09* (–0.12, –0.06)	–0.17* (–0.20, –0.14)	0.271	0.153

*P<0.001.
Values are shown as means with 95% confidence limits given in parentheses.
Values of scaling coefficient a were corrected following Sprugel (1983).
S.E.E., standard error of estimates.

breakpoint, where the change in slope between small and large mammals occurs, was positioned at M_b=30 kg, around the interception between linear regressions for mammals below 10 kg and above 100 kg (see Fig. 1). The scaling exponent of small mammals (below 30 kg) differed significantly from that of larger mammals (Table 2). However, despite the fact this bilinear model presents the highest coefficient of determination (r^2=0.815), there were no significant differences in the fit between the models (Bonferroni test, P>0.05).

When plotted against stress scope, maximum relative speed showed a similar pattern to that observed against body mass. The group of small-sized mammals showed a significant positive correlation between these traits (r=0.548; P<0.01; Fig. 2A), and the group of large mammals showed an even stronger correlation (r=0.803; P<0.001; Fig. 2B).

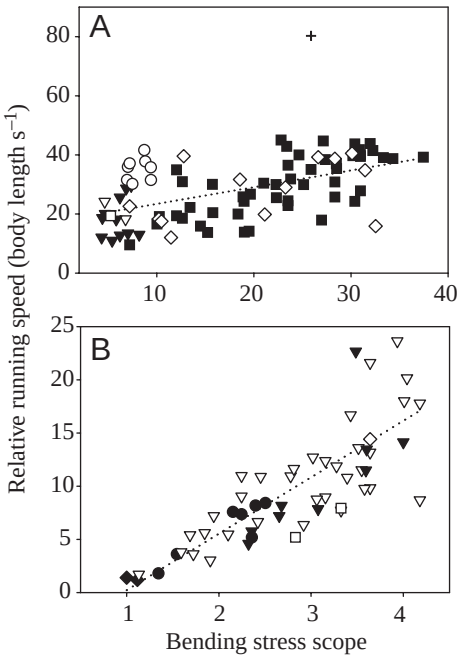

Fig. 2. Relationship between bending stress scope and maximum relative running speed for (A) small (below 30 kg) and (B) large-sized mammals (above 30 kg). The cross corresponds to *Dipodomys merriami*. Symbols as in Fig. 1.

Separate analyses on taxonomic groups for which adequate data sets were available (N≥7) suggested more negative scaling exponents in large body-sized orders of mammals than in small body-sized ones (see Table 3). There were differences in allometric exponents among the best represented taxonomic groups: Artiodactyla, Carnivora and Rodentia (ANCOVA, P<0.01). The slope of Artiodactyla differed significantly from that of Rodentia (Bonferroni test, P<0.05). Consistently, the allometric exponent of Carnivora, an intermediate body sized group (2.5–265 kg), was intermediate between that of Artiodactyla and Rodentia, and did not differ significantly from them (Bonferroni test, P>0.05; Table 3; power, 0.870 and 0.369, respectively). The only slope that did not differ significantly from zero was that of lagomorphs, while the scaling exponents of rodents and marsupials proved to be slightly less than zero.

Discussion

Body mass seems to be more highly correlated with maximum relative speed (r^2=0.69, this study) than with maximum absolute running speed (r^2=0.44, from Garland, 1983). This higher correlation might be a simple consequence that some body-length data were obtained from a single allometric equation. However, when analyses were carried using Silva's (1998) equation only, the correlation was not significantly improved, indicating that the way as data were expressed would not have a significant effect on the results. The scaling exponent found for all pooled mammals does not differ from that predicted by the dynamic similarity hypothesis ($M_b^{-0.16}$; Alexander and Jayes, 1983). However, this result must be taken cautiously as geometric similarity in general morphology is an implicit assumption in dynamic similarity models (Alexander and Jayes, 1983), which is not true for all mammals (McMahon, 1975a,b; Bou et al., 1987;

Table 3. *Linear regression parameters for maximum relative running speed on body mass, of separate taxonomic groups, estimated from ordinary least-squares regression (OLS) and reduced major axis regression (RMA)*

		Linear regression estimates of V_{max}/L_b=log a+b log (M_b)				
			b			
Data set	*N*	*a*	OLS	RMA	r^2	S.E.E.
Perissodactyla	7	200.8	–0.59** (–0.86, –0.32)	–0.64** (–0.91, –0.37)	0.863	0.101
Artiodactyla	37	65.04	–0.39*** (–0.47, –0.31)	–0.46*** (–0.54, –0.37)	0.735	0.138
Carnivora	21	32.66	–0.26*** (–0.38, –0.15)	–0.36*** (–0.47, –0.24)	0.542	0.155
Rodentia	50	17.76	–0.19*** (–0.26, –0.13)	–0.29*** (–0.36, –0.23)	0.446	0.129
Lagomorpha	8	37.06	–0.05 (–0.26, 0.16)	–0.23* (–0.43, –0.02)	0.055	0.050
Marsupialia	14	21.86	–0.10* (–0.19, –0.01)	–0.18*** (–0.27, –0.08)	0.320	0.158

*P<0.05, **P<0.01, ***P<0.001.
Values are shown as means with 95% confidence limits given in parentheses.
Values of scaling coefficient *a* were corrected following Sprugel (1983).
S.E.E., standard error of estimates.

Christiansen, 1999). Furthermore, the non-linear relationship between body mass and maximum running speed was evident, both in terms of absolute as well as relative speed. In the case of relative speed, the relationship between M_b and running speed behaved differently over different ranges of body mass.

Three domains (small, intermediate and large-sized mammals), each with different scaling exponents, were identified through LOWESS analysis. This may be reflecting a pattern of two extreme regimes with different slopes and a transitional zone of gradual exponent change, although it needs to be considered in terms of the taxa that comprise this zone in order to evaluate potentially evolutionary or taxonomic effects (see below). In this particular case, these domains may be modelled by gravitational effect over organisms. For simplification, the data set was modelled as if there were only two domains with one critical or break point distinguishing small and large-sized mammals. This model yielded a similar fit to the two-point change model, but makes interpretations easier. There was no difference between scaling exponents of mammals below 10 and 30 kg, and between mammals above 30 and 100 kg. The power analyses showed very low values (approx. 0.1) for these comparisons, but these should be considered cautiously. The values obtained from retrospective power analysis are dependent on the observed differences between treatments, so if the difference is close to zero, the power of the test will be extremely low. In this case, the differences observed in slope between below 10 and 30 kg groups and above 30 and 100 kg groups and the associated errors are small. Besides, the differences between the large groups and between the small-sized groups using the different models are also small in terms of number of species. For example, the below 30 kg and below 10 kg groups differed in only seven species, yielding, as expected, few differences in the estimated slopes. This would indicate that the distinction between two or three domains would have no effects on parameter estimation.

The scaling exponent of small-sized mammals (below 30 kg) did not differ from that which would be expected under elastic similarity ($M_b^{-0.08}$; McMahon, 1975a). However, Bou et al. (1987) reported a significantly different allometric exponent for the limb bones dimensions (diameter and length) of rodents and insectivores from those expected under elastic similarity, mainly due to limb adaptations to their habitat (e.g. fossorial and arboreal mammals). On the other hand, linear dimensions in large mammals scale to M_b in agreement with elastic or static stress similarity, depending on the range of M_b analysed (Prothero and Sereno, 1982; Bertram and Biewener, 1990; Biewener, 1990). However, in this study it was found that the scaling exponent of relative locomotor performance of large mammals cannot be predicted by any particular similarity model, although geometric similarity is the model that predicts the closer exponent (b=–0.33).

The discrepancies between morphological and speed scaling, as noted by Günther (1975), show that there is no single criterion that provides a satisfactory explanation for qualitatively different characters such as limb proportions and locomotor performance. Furthermore, the non-correspondence between morphology and performance based on expectations from similarity models might be due to a lack of knowledge of the factors that contribute towards determining maximum locomotor performance. Predictions obtained might be based on erroneous assumptions yielding spurious results. For example, predicted values of scaling exponents from geometric similarity

are derived from the assumption that absolute maximum performance is determined by maximum mechanical power developed by limb muscles (for derivation, see McMahon, 1975a). However, among lizards, some evidence has been gathered suggesting that the mechanical power developed by limb muscles is not a determinant of maximum running speed (Farley, 1997). Also, the absence of correlation between power output and running speed might be a mass-dependent phenomenon of this methodology, where larger lizards would be more affected in their performance by mechanical power output, as Farley (1997) pointed out. In addition, other factors could be affecting maximum locomotor performance, such as muscle energetics, neuromuscular coordination, dynamic constraints and efficiency (for a review, see Jones and Lindstedt, 1993). There is some evidence suggesting that mechanical impositions over musculoskeletal structures could be constraining locomotor performance (Biewener, 1990), although this hypothesis has not been tested directly.

The steeper reduction in locomotor performance with increasing M_b in large mammals observed in this study is consistent with the hypothesis of differential scaling between large and small-sized species, and it could be explained to occur as a result of mechanical constraints imposed on the skeletal structure, as pointed out by Biewener (1990). If mammals scale following geometric similarity, bone peak stress would increase faster than the ability to resist it, making organisms mechanically unviable over determined M_b (Biewener, 1990). Fariña et al. (1997), in an allometric study of bending resistance of long bones of birds, mammals and dinosaurs, showed that the ability of limb bones to withstand forces decreases with M_b. This is in agreement with previous laboratory studies that reported that small mammals can resist more gravity than large ones (Economos, 1981). Nevertheless, it has been observed that mammals keep relatively constant values of safety factors (i.e. the ratio between the bone's failure stress and stress experienced during functional activities; Alexander, 1981) in a wide range of M_b (Biewener, 1990 and references therein). Thus, as M_b increases, mammals must carry out several postural, morphologic, and behavioural modifications in order to keep the structural integrity of the skeletal support, such as more upright postures (Biewener, 1983a, 1989), more robust skeletons in larger organisms (Bertram and Biewener, 1990; Christiansen, 1999) and reductions in locomotor performance (Biewener, 1990). This is noted in the correlation between relative performance and stress scope, where very large mammals (i.e. those having very low stress scope values within the large mammal group) show little variation around the regression line. This variation, however, increases concomitantly with stress scope, in agreement with the idea that very large species are more restricted in their performance by mechanical constraints over support structures than smaller species. Nevertheless, when the group of small-sized species is analysed, correlation between stress scope and performance becomes weaker, showing great variation around the regression line, apparently independent of stress scope, which may be the product of factors other than M_b, such as morphological adaptations to habitat and modes of locomotion (Bou et al., 1987; Garland et al., 1988).

Locomotor performance in large mammals is more highly correlated with M_b and stress scope than in small ones (see Fig. 2). The small amount of variation around the regression line could reflect the fact that almost all mammals above 10 kg are 'cursorial' (*sensu* Alexander and Jayes, 1983), which means that they stand and run with the femur and humerus upright and have conservative locomotor modes (Bertram and Biewener, 1990). In addition, it has been noted that the values of speed tend to be independent of locomotor adaptations as M_b increases (Bou et al., 1987). Thus, M_b alone could be responsible for the variation in locomotor performance.

In regression analyses within restricted taxonomic groups, Perissodactyla and Artiodactyla, the largest groups of mammals analysed, showed the highest allometric exponents (see Table 3). Both exponents were not different from those previously described for large mammals overall (over 30 kg), suggesting that exponent estimation does not seem to be affected when phylogenetic relationships among species included in the analyses are taken into account. The low retrospective power of these tests (0.168 and 0.418, respectively) seems to be a product of the small differences in slope estimations between the groups rather than an actual low power of test, at least in the case of artiodactyls. For perisodactyls, the slope estimation would not be reliable due to the large error associate caused by the small sample size (N=7). Artiodactyls possess a greater scaling exponent than the small-sized group Rodentia, whereas the medium-sized Carnivora have an intermediate exponent, although this value is not significantly different from that of large and small-sized taxonomic groups. However, the value of this exponent should be considered cautiously. The group of carnivores has the smallest sample size and the greatest error estimates when compared to rodents and artiodactyls, and would be expected to have the least sensitivity to the differences in slope. Moreover, Carnivora is the only well-represented group that is present on both sides of critical point. In residual analysis, the carnivores of the small mammals group are evenly distributed throughout the regression line (Fig. 3A), whereas all the large-sized carnivores (except one, the cheetah) are grouped as negative residuals (Fig. 3B). This pattern is explained by the fact that small and large-sized carnivores do not follow a monotonic relationship with M_b, but have a differential scaling as observed in the pooled-sample of all mammals (nearly mass independent in small species, and strongly negative in large ones). Therefore, the observed scaling exponent of Carnivora would be spurious.

Lagomorpha is a group of species with fast running speeds and spanning a narrow body mass range. All species in this group fall above the regression line of the pooled small-sized mammals (Fig. 3A), generating a high leverage over parameter estimation. When lagomorphs are excluded from the analysis, the regression slope becomes steeper, but still significantly different from that of rodents (P<0.05).

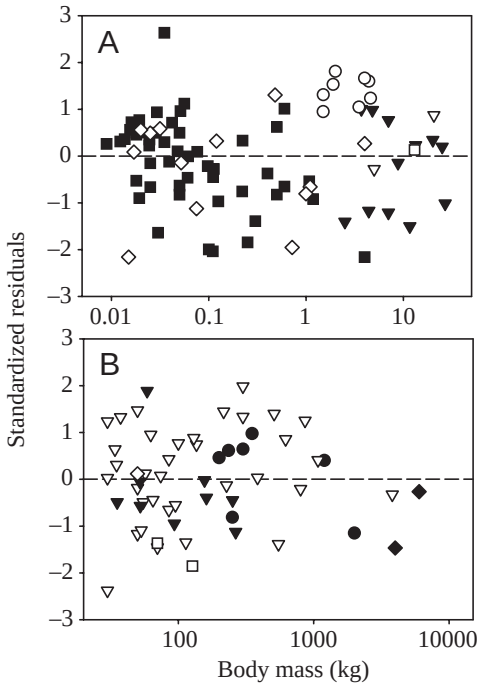

Fig. 3. Residual analyses for maximal relative running speed against M_b for (A) small mammals (below 30 kg) and (B) large-sized mammals (above 30 kg). Symbols as in Fig. 1.

The differential scaling observed in mammals would have ecological implications also. Small mammals are commonly prey for animals that use surprise attacks as hunting techniques (e.g. raptors, snakes, and felines). In these cases, the predators are usually bigger and faster (in absolute terms) than the prey, which escape by running to a suitable refuge. In this type of predation technique, where the attacks are quick and discrete, the success of an attack might be dependent of the size of the prey. It is intuitively logical that in a choice between two prey of different size moving at the same absolute speed, the predator has more chance if it chases the larger one, as shown by Van Damme and Van Dooren (1999). Another important factor in predator–prey interactions is the manoeuvrability of the organism. Many animals are able to escape a predator that is, in absolute terms, faster, thanks to the ability to make a tighter turn than predator. This escape strategy, called the 'turning gambit' (sensu Howland, 1974), has been observed in different species spanning from small moths to large mammals. The turning gambit has been shown to be a size-dependent characteristic (Webb, 1976; Witter et al., 1994; Domenici, 2001), but few works have evaluated the effect of shape and size of the body on turning performance in terrestrial vertebrates (Eilam, 1994; Carrier et al., 2001; Lee et al., 2001). Turning performance is dependent on the rotational inertia of the body (i.e. the sum of differential elements of mass multiplied by the square of the perpendicular distance from the axis of rotation) and, therefore, larger animals should have a higher rotational inertia and a poorer turning performance than smaller ones. This work shows that the largest species of the small-sized group should be more susceptible to predation because of their reduced relative performance and reduced manoeuvrability. According to this, Hedenström and Rosén (2001) suggested that selection of large-sized prey by sparrowhawks over small-sized ones could be due to the higher manoeuvrability of the latter; it could also be an energy-based decision, because larger prey are more profitable.

On the other hand, large mammals are chased by large predators (e.g. lions) using maintained persecutions (Emerson et al., 1994). In this type of hunting, the absolute running speed seems to be more important in determining the success of an attack. However, manoeuvrability plays an important role in the escape strategy of prey and as pointed out above, this depends on body length. The poor performance (absolute and relative) observed in large mammals indicates that they would be easily susceptible to individual predation. Thus, the life in groups observed in some large mammals (e.g. some artiodactyls) has been explained as an antipredation protective mechanism (Jarman and Jarman, 1979) in order to compensate their poor running ability. Some morphological adaptations to rapid locomotion in some large species of mammals have been described (Taylor et al., 1971; Lindstedt et al., 1991), but these adaptations might be a secondary acquisition, where the initial selection would be the reduction in transport costs and the increase of home range (Janis and Wilhelm, 1993). The strong diminution in relative performance as M_b increases in large mammals supports the idea that running speed, either absolute or relative, has not been a selected characteristic in mammalian evolution.

This study showed that an analysis of scaling of maximum locomotor performance over a broad range of M_b might yield spurious results. As observed in several traits, the relationship between maximum locomotor performance and body size changes depending on the range of M_b studied. Locomotor performance of small mammals seems to be nearly independent of M_b, which agrees with previous studies conducted in rodents (Garland, 1983; Djawdan and Garland, 1988; Garland et al., 1988). However, when large-sized mammal species are analysed, the relationship between relative locomotor performance and M_b becomes more negative. The reduction in locomotor performance in large mammals is consistent with the hypothesis of mechanical constraints and may be understood as a stress reduction mechanism. Nevertheless, despite the fact that this idea had been mentioned previously in the literature (Garland, 1983; Biewener, 1990), it has not been tested.

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