Effective limb length and the scaling of locomotor cost in terrestrial animals

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Summary

Relative to body size, smaller animals use more energy to travel a given distance than larger animals, but the anatomical variable driving this negative allometry remains the subject of debate. Here, I report a simple inverse relationship between effective limb length (i.e. hip height) and the energy cost of transport (COT; $J\,kg^{-1}\,m^{-1}$) for terrestrial animals. Using published data for a diverse set of terrestrial species including birds, mammals, reptiles and arthropods, I show that between-species differences in locomotor cost are driven by differences in limb length. Notably, there is no independent effect of body mass on cost. Remarkably, effective limb length explains 98% of the observed variance in locomotor cost across a wide range of terrestrial species including mammals, birds, reptiles and arthropods. Variation about the limb-length/COT scaling relationship is attributable to taxonomic differences in limb design, with birds and arthropods exhibiting greater residuals than mammals. Differences in COT between semi-aquatic, generalist and cursorial species also corresponds to differences in leg length between these groups. These results are discussed in light of previous investigations of the limb length and locomotor cost.

Key words: cost of locomotion, LiMb model, limb length, scaling.

Introduction

Relative to body mass, small terrestrial animals use much more energy to travel a given distance than large animals (Taylor et al., 1982). This negative allometry has been recognized for over three decades and demonstrated empirically for a broad range of species (Taylor et al., 1982; Full and Tu, 1991), but its underlying anatomical cause remains elusive (Alexander, 2005). Here, I report data indicating that effective limb length, the length of the leg as a strut (Fig. 1), drives the scaling of locomotor cost for terrestrial animals.

Numerous within- and between-species studies have reported that larger animals have lower mass-specific locomotor costs, but there is little evidence that mass itself is a causal factor underlying the mass-specific cost of transport (COT; $J\,kg^{-1}\,m^{-1}$), the cost to travel a given distance. On the contrary, when mass is modified while holding other aspects of locomotor anatomy constant, as in load-carrying studies, the effect of mass on COT appears to be negligible. Studies of birds, humans and quadrupedal mammals have shown that increasing mass by up to 50% has little effect on COT during running (see Marsh et al., 2006). The independence of COT and body mass in studies that manipulate mass experimentally suggests that some other size-related aspect of locomotor anatomy or gait is responsible for the scaling of COT.

Previous studies have demonstrated that locomotor cost is primarily a function of the muscle force produced to support body weight (Taylor et al., 1980; Kram and Taylor, 1990; Taylor, 1994; Pontzer, 2005; Pontzer, 2007). Kram and Taylor (Kram and Taylor, 1990) noted that, at a given speed, smaller animals use shorter steps and must therefore generate ground forces over shorter amounts of time, thus requiring higher rates of muscle force production, resulting in greater COT. This implies that variation in limb length underlies the scaling of COT, as larger animals with longer limbs will use longer strides and lower rates of force production (Kram and Taylor, 1990; Pontzer, 2005; Pontzer, 2007). However, while such a link between limb length and cost has been favored by some (e.g. Hill, 1950; Kram and Taylor, 1990; Fish et al., 2001; Griffin and Kram, 2000; Pontzer, 2005; Pontzer, 2007), numerous within- and between-species comparisons have found no effect of limb length on COT (Cavanaugh and Kram, 1989; Brisswalter et al., 1994; Steudel and Beattie, 1995), whereas others have reported that longer-legged individuals can have a higher COT (Minetti et al., 1994; Griffin et al., 2004) and a greater metabolic cost of generating muscle force (Roberts et al., 1998a) during running. The effect of limb length on locomotor cost, therefore, remains unclear.

A recent biomechanical model linking limb length to COT (Pontzer, 2005; Pontzer, 2007) suggests the importance of limb length in determining locomotor cost depends upon the scale of comparison. For running gaits, the LiMb model derives the rate of muscular force production during running from effective limb length L_E (Fig. 1), the excursion angle of the limb during

stance phase (φ), and the energy cost of swinging the limb (C_{limb}), and relates these to COT as:

$$\text{COT} = \frac{k[1+\tan(\phi/2)]}{L_E \sin(\phi/2)} + C_{limb}, \qquad (1)$$

where k is a cost-coefficient converting metabolic energy to muscle force (J N^{-1}). This model outperforms other predictors of cost, including contact time, Froude number, and body mass, for both bipeds and quadrupeds, both within- and between-species (Pontzer, 2005; Pontzer, 2007). The success of the LiMb model in linking locomotor anatomy to cost suggests it may be useful for understanding the scaling of locomotor cost with body size. Over a narrow range of body size, variation in k, φ and C_{limb} dominates predicted energy cost, preventing a clear relationship between limb length (L_E) and locomotor cost (Pontzer, 2005; Pontzer, 2007). However, over a wide range of body size, the LiMb model predicts effective limb length to drive the scaling of locomotor cost, since φ, C_{limb}, and k are largely independent of body size (Kram and Taylor, 1990; McMahon, 1975; Hildebrand, 1985). Specifically, the LiMb model predicts that COT is inversely proportional to L_E for terrestrial animals, and that body mass has no independent effect on locomotor cost.

The LiMb model employs L_E, the functional length of the limb as a mechanical strut (Fig. 1), in deriving the relationship between COT and limb length. Many previous studies investigating cost and limb length (e.g. Steudel and Beattie, 1995; Hoyt et al., 2000) have calculated limb length by summing the lengths of the component long bones. This latter approach generally overestimates L_E because of the crouched posture adopted by many species; an effect that is magnified in smaller species (Biewener, 1989). Thus a further prediction for the scaling of COT suggested by the LiMb model is that skeletal limb length, L_{skel}, will not predict COT independently of body mass, since smaller animals, having more crouched postures (Biewener, 1989), will have higher locomotor costs relative to their skeletal limb length than larger animals.

I have tested these predictions using a diverse sample of terrestrial animals. Here I compare measures of COT, L_E, L_{skel} and body mass for a sample of endothermic species (mammals
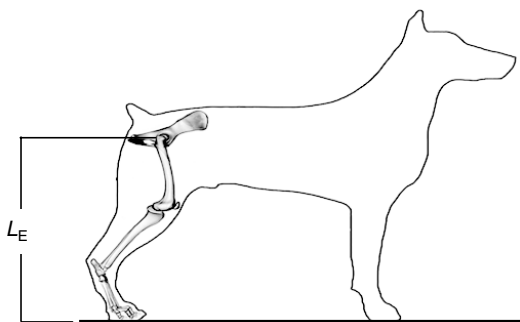

Fig. 1. Effective limb length, L_E. Note that L_E is shorter than the cumulative lengths of the component long bones.

and birds), and in an expanded sample that includes reptiles and arthropods. Taxonomic differences in locomotor cost are also investigated. I then compare these results against previous investigations of limb length and COT, and examine their implications for evolutionary, morphological and ecological studies of locomotor performance.

Materials and methods
Sample composition and statistical analyses

To test the predicted relationship between L_E and COT, I compiled a dataset of body mass, L_E and COT for all terrestrial animals for which all three measures could be found in published sources (Table 1). Whereas COT has been measured in many species (approx. 100), far fewer have associated measures of L_E. Further, the quality of data available differs markedly among species, from direct measurements of L_E, COT and body mass in the same individual to estimates of one or more of these variables. As a result, three separate analyses were performed to assess the effects of L_E and body mass on COT.

The first, most conservative analysis included only species ($N=15$) for which direct measurements of COT and L_E were available. In species for which L_E and COT were measured on different individuals ($N=9$), only species in which body mass of these individuals differed by less than 20% were included in the first analysis; assuming geometric scaling, L_E in these individuals should differ by less than 8%. In order to incorporate a broader range of species, including those in which the link between limb length and locomotor cost has been investigated previously (caribou, platypus and mink), a second, more inclusive analysis ($N=19$) was performed including all endothermic species for which L_E could be reliably estimated. Lastly, to determine whether these relationships between L_E, COT and body mass extend to ectothermic taxa, a third analysis ($N=28$) including reptiles ($N=5$) and arthropods ($N=4$) was performed. For all analyses, where measures were available for multiple individuals within a species (Table 2), species means were calculated and used.

For each analysis, species means for COT were plotted against means for either L_E or body mass, with least square regression used to determine the predictive power of each independent variable. As a first test, partial correlation was used to measure the independent effects of L_E and body mass on COT. Next, to determine whether broad taxonomic differences in limb design affect the second-order relationships between L_E, body mass, and COT an ANCOVA was performed, with taxonomic group (arthropod, bird, mammal or reptile) incorporated as a fixed factor, and L_E and body mass incorporated as covariates. Such taxonomic differences in the scaling of COT have been noted before (Roberts et al., 1998a; Roberts et al., 1998b). A similar approach was also used to investigate differences in cost between cursorial, generalist, and semi-aquatic species. Group assignments (analysis, taxonomic and ecological) are given in Table 1.

Path analysis was also performed to assess the relative

Table 1. *Body mass, effective limb length and cost of transport*

Species	Common name	Mass (kg) COT	Mass (kg) L_E	L_E (cm)	COT (J kg^{-1} m^{-1})	Analysis group	Locomotor group	Source (L_E; COT)
Excalfactoria chinensis	Painted quail	0.04	0.05	5.2	24.12	1	Generalist	(Gatesy and Biewener; 1991; Taylor et al., 1982)
Rattus norvegicus	White rat	0.21	0.20	4.9	19.50	1	Generalist	(Periera et al., 2006; Taylor et al., 1982)
Numida meleagris	Guinea fowl	1.30	1.52	20.3	8.37	1	Cursorial	(Gatesy and Biewener, 1991; Roberts et al., 1998b)
Felis catus	Cat	3.9	4.0	22	8.04	1	Generalist	(Trank et al., 1996; Taylor et al., 1982)
Meleagris gallopavo	Turkey	5.30		35.8	6.19	1	Generalist	(Roberts et al., 1998a)
Lontra canadensis	River otter	11.1		26.1	7.84	1	Semi-aquatic	(Williams et al., 2002)
Rhea americana	Rhea	19.9	20.0	82.0	4.22	1	Cursorial	(Gatesy and Biewener, 1991; Roberts et al., 1998b)
Aptenodytes forsteri	Emperor penguin	21.0		25.0	8.64	1	Semi-aquatic	(Griffin and Kram, 2000)
Capra hircus	Goat	23.0		42.9	5.00	1	Cursorial	(Pontzer, 2007)
Canis familiaris	Dog	26.3		39.0	5.63	1	Cursorial	(Roberts et al., 1998a; Pontzer, 2007)
Dromaius novaehollandiiae	Emu	40.1	40.0	81.6	3.56	1	Cursorial	(Gatesy and Biewener, 1991; Roberts et al., 1998b)
Homo sapiens	Human	73.6		94.4	2.34	1	Cursorial	(Pontzer, 2007)
Struthio camelus	Ostrich	103	90.0	119	2.21	1	Cursorial	(Gatesy and Biewener, 1991; Taylor et al., 1982)
Equus caballus	Horse	431	448	124	2.41	1	Cursorial	(Griffin et al., 2004; Wickler et al., 2000)
Loxondonta africana	Elephant	1542	1632	168	1.80	1	Generalist	(Hutchinson et al., 2006; Langman et al., 1995)
Colinus virginianus	Bobwhite quail	0.13	0.17	10.0	21.07	2	Generalist	(Gatesy and Biewener, 1991; Roberts et al., 1998b)
Mustela vison	N.A. mink	0.87		7.5	14.87	2	Semi-aquatic	(Gingerich, 2003; Williams, 1983)
Ornithorhynchus anatinus	Platypus	1.40		7.8	13.74	2	Semi-aquatic	(Gingerich, 2003; Fish et al., 2001)
Rangifer tarandus granti	Caribou	73.5		98.8	1.95	2	Cursorial	(Niemen and Helle, 1980; Luick and White, 1986)
Camponotus sp.	Carpenter ant	0.000012		0.60	130.00	3	Generalist	(Kaspari and Weiser, 1999; Lipp et al., 2005)
Pogonomyrmex rugosus	Harvester ant	0.000013		0.68	158.00	3	Generalist	(Kaspari and Weiser, 1999; Lighton et al., 1993)
Blaberus discoidalis	Cockroach	0.00418		2.2	62.31	3	Generalist	(Kram et al., 1997; Herreid and Full, 1983)
Lacerta sicula	Lizard	0.008	0.009	3.3	40.20	3	Generalist	(Irschick and Jayne, 2000; John-Adler et al., 1986)
Aphonopelma anax	Tarantula	0.016		2.0	52.66	3	Generalist	(Jackman, 1997; Schilington and Peterson, 2002)
Lacerta viridus	Green lizard	0.026	0.026	3.7	26.13	3	Generalist	(Irschick and Jayne, 2000; John-Adler et al., 1986)
Varanus spp.	Monitor lizard	0.026	0.026	3.7	36.18	3	Generalist	(Irschick and Jayne, 2000; John-Adler et al., 1986)
Dipsosaurus dorsalis	N. desert iguana	0.051	0.060	4.8	27.74	3	Generalist	(Irschick and Jayne, 2000; John-Adler et al., 1986)
Trachydosaurus rugosus	Australian skink	0.47	0.56	6.0	18.51	3	Generalist	(John-Adler et al., 1986)

L_E, limb length; COT, cost of transport.

Mass: COT, body mass of subjects used to measure COT; L_E, body mass of subjects used for L_E if different. Analysis group: 1, most conservative to 3, least conservative. See text and Table 3.

Table 2. *Body mass, effective limb length and cost of transport for different size classes within species*

Species	Common name	Mass (kg) COT	L_E	L_E (cm)	COT (J kg⁻¹ m⁻¹)	Source (L_E; COT)
Canis familiaris	Dog – small	5.60		24.0	6.54	(Roberts et al., 1998a; Pontzer, 2007)
Canis familiaris	Dog – medium	26.3		39.0	5.63	(Pontzer, 2007)
Canis familiaris	Dog – large	37.9		56.0	3.12	(Pontzer, 2007)
Homo sapiens	Human – short	58.8		80.3	2.57	(Pontzer, 2007)
Homo sapiens	Human – medium	73.6		94.4	2.34	(Pontzer, 2007)
Homo sapiens	Human – tall	75.2		107	2.40	(Pontzer, 2007)
Lacerta sicula	Lizard	0.006	0.007	3.2	41.21	(Irschick and Jayne, 1999; John-Adler et al., 1986)
Lacerta sicula	Lizard	0.010	0.012	3.4	39.20	(Irschick and Jayne, 1999; John-Adler et al., 1986)
Rangifer tarandus granti	Caribou – small	25.5		75.0	2.43	(Niemen and Helle, 1980; Luick and White, 1986)
Rangifer tarandus granti	Caribou – medium	54.5		100	1.70	(Niemen and Helle, 1980; Luick and White, 1986)
Rangifer tarandus granti	Caribou – large	103		110	1.71	(Niemen and Helle, 1980; Fancy and White, 1986)
Rangifer tarandus sp.	Reindeer	111		110	1.97	(Niemen and Helle, 1980; Luick and White, 1986)

L_E, limb length; COT, cost of transport.

contributions of body mass and L_E to COT. With path analysis, it is possible to distinguish the direct, independent effects of two related independent variables (L_E and body mass) on a dependent variable (COT), while also calculating the indirect effect of covariance between independent variables (Quinn and Keough, 2002). For example, if the apparent effect of L_E on COT is spurious, and is in fact an indirect effect of body mass, path analysis will show that the direct effect of L_E is negligible. Conversely, if the apparent effect of body mass on COT is solely due to the fact that larger animals have longer legs, the direct effect of mass on COT will be insignificant.

For all analyses, it was predicted that L_E would be a better predictor of COT than body mass, and that L_E would remain a significant predictor of COT when controlling for body mass and taxonomy, whereas body mass would have no effect on COT when controlling for L_E and taxonomic differences. Log₁₀-transformed data were used throughout to reduce the leverage of the smallest and largest species on the overall results.

Determining COT

COT for each species was taken from direct measures of oxygen consumption during treadmill running trials using established methods published elsewhere (Table 1). In each case, the 'net' cost of transport, which excludes resting metabolic rate, was used. These literature values are for running (bipeds) or trotting (quadrupeds) with the exception of COT data for caribou and penguins, which are from walking trials. Although this may underestimate locomotor cost, COT was independent of speed for these species (Fancy and White, 1987; Griffin and Kram, 2000) and has been shown to be independent of gait for most birds (Griffin and Kram, 2000; Roberts et al., 1998b) and at least some large cervids (Parker et al., 1984), and so the inclusion of these walking data was deemed justified. For elephants, COT was calculated at a fast walk because the cost of locomotion, COL (J kg⁻¹ s⁻¹), increased curvilinearly with speed (Langman et al., 1995), and therefore COT could not be determined in a manner similar to other species. Because animals typically run at speeds

equivalent to a Froude number (size-corrected speed) of 0.5 or greater (Alexander and Jayes, 1983), the COT from the fastest reported walking speed, 2.5 m s⁻¹ (Froude number ~0.38) was deemed more appropriate for comparison in this dataset than that reported for the minimum COT speed (1.0 m s⁻¹; Froude number ~0.06).

Measurement and estimation of L_E

For all species included in the most restricted analysis (Table 1), L_E was determined from direct measurements of the distance from the greater trochantor of the femur to the ground while standing. These measurements were taken directly (Pontzer, 2007) or from similar measures (i.e. 'hip height') published elsewhere with two exceptions: for the river otter, L_E was calculated from body proportion measurements (Williams et al., 2002), and for the emperor penguin hip-height was taken from data presented graphically (Griffin and Kram, 2000).

Estimates of L_E for caribou (Table 1) were taken from published estimates of 'shoulder height' (Niemen and Helle, 1980). Note that shoulder height as used here (Niemen and Helle, 1980) refers to the height of the animal's back above the front leg, not the humero-scapular joint, and is therefore similar, although slightly greater than, the actual height of the hip joint. For juvenile and sub-adult caribou, data on shoulder height was combined with growth data for this species reported by the University of Alaska Fairbanks 'Reindeer Research Program' (http://reindeer.salrm.uaf.edu/html/reinFAQ.html) to estimate L_E. For the North American mink and platypus, estimated L_E was calculated as the sum of femur and tibia lengths published for these species (Gingerich, 2003). Although using skeletal elements may overestimate L_E, as argued above, data for semi-aquatic species are relatively rare, and their inclusion was deemed useful in order to investigate the effects of shorter limb lengths in these species (see Fish et al., 2001; Williams et al., 2002). For reptiles, L_E ('hindlimb length') was reported only for the shingle-back lizard *Trachydosaurus rugosus* (John-Adler et al., 1986). For all other reptiles, L_E was estimated using reptiles (*Dipsosaurus dorsalis*) of equivalent mass presented graphically

(Irschick and Jayne, 2000); L_E was measured as the distance from the hindlimb–body junction to the heel at foot-strike. For carpenter and harvester ants, L_E was calculated using a published regression for limb length (Kaspari and Weiser, 1999). L_E for the cockroaches was determined for the middle leg, from published data and description of leg-segment angles for a 2.7 g cockroach (L_E=1.9 cm) (Kram et al., 1997) and scaled to match the 4.2 g cockroaches used for COT analysis (Herreid, II and Full, 1983) assuming geometric similarity [i.e. that limb length increases as c mass$^{0.33}$, where the constant determined from Kram et al. (Kram et al., 1997) was c=13.81]. L_E for tarantulas was estimated from published data and description (Jackman, 1997).

Skeletal versus effective limb length

To assess whether the use of skeletal limb length instead of effective limb length affects the relative predictive power of body mass and limb length, a similar analysis was performed using species (N=21) for which COT and skeletal limb length were available (Table 3).

Results

As predicted, L_E was strongly correlated with COT in all analyses, outperforming body mass as a predictor of locomotor cost (Table 4; Fig. 2). In the first, most conservative analysis, representing over half of the species analyzed (Table 4, Analysis group 1), L_E predicted 97% of the variance in COT (r^2=0.97,

N=15, P<0.001) and remained significant when controlling for body mass *via* partial correlation (r^2=0.74, d.f.=12, P<0.001). By contrast, whereas body mass was significantly correlated with COT (r^2=0.89, N=15, P<0.001), it had no effect on cost when controlling for L_E *via* partial correlation (r^2=0.05, d.f.=12, P=0.45). When taxonomic differences were assessed *via* ANCOVA, taxonomic group (mammal or bird) had a marginally significant effect (F=4.75, P=0.05) on COT, whereas mass had no effect (F=0.33, P=0.58); L_E remained strongly significant (F=45.82, P=0.001). Not surprisingly, L_E was a better predictor of COT [standard error of estimation (SEE)=0.06] than body mass (SEE=0.11). Notably, semi-aquatic species reported to have relatively high COT for their body mass (Griffin and Kram, 2000; Williams et al., 2002) fit the L_E–COT trendline. Removal of the smallest species from the analysis (*Excalfactoria chinensis*) did not affect these results.

Other, more inclusive analyses showed a similar pattern. In the second analysis (Table 4, Analysis group 2), representing all endotherms in the sample, L_E predicted 95% of the variance in COT (r^2=0.95, N=19, P<0.001) and remained significant when controlling for body mass *via* partial correlation (r^2=0.62, d.f.=16, P<0.001). Body mass significantly correlated with COT (r^2=0.89, N=19, P<0.001), but had no statistically significant independent effect (r^2=0.14, d.f.=16, P=0.12). When taxonomic group (bird or mammal) was considered as a fixed factor in an ANCOVA, with L_E and body mass included as covariates, there was no independent effect of body mass

Table 3. *Body mass, skeletal limb length and cost of transport*

| Species | Common name | Mass (kg) | | L_{skel} (cm) | COT (J kg^{-1} m^{-1}) | Source |
		COT	L_{skel}			
Dipodymus merriami	Kangaroo rat	0.032		5.9	22.11	a
Suncus murinus	Musk shrew	0.036	0.038	4.5	32.56	b
Glaucomys volans	Flying squirrel	0.063	0.064	7.9	24.12	b
Tamias striatus	Chipmunk	0.092	0.072	6.7	15.68	b
Tupaia glis	Tree shrew	0.12	0.13	9.9	13.87	b
Setifer setosus	Setifer	0.12	0.12	7.4	13.67	b
Spermophilus tridecemlineatus	Squirrel	0.21	0.19	9.8	24.12	b
Rattus norvegicus	White rat	0.21	0.20	8.6	19.50	b
Mustela nigripes	Ferret	0.54	0.57	13.3	10.45	b
Helogale parvula	Dwarf mongoose	0.58	0.62	13.1	13.47	b
Tenrec ecaudatus	Tenrec	0.68	0.65	11.9	11.66	b
Erinaceus europaeus	Hedgehog	1.05	10.98	10.2	9.25	b
Didelphis virginianus	American opossum	2.70	2.60	17.8	7.24	b
Pedetes capensis	Spring hare	3.00		35.8	6.83	a
Cebus albifrons	Capuchin	3.34	3.50	31.9	5.63	b
Nesotragus moschatus	Suni	3.50	3.10	34.4	10.45	b
Tachyglossus aculeatus	Echidna	3.53	3.80	14.9	7.44	b
Felis catus	Cat	3.90	3.83	30.1	8.04	b
Dasypus novemcinctus	Armadillo	4.07	4.00	19.4	5.03	b
Martes pennanti	Fisher	5.16	5.03	28.8	6.23	b
Canis lupus	Grey wolf	23.1	23.6	54.0	4.62	b
Equus caballus	Pony	141		82.7	3.02	a

Mass: COT (cost of transport), body mass of subjects used to measure COT; L_{skel}, skeletal limb length body mass of subjects used for L_{skel} if different.

Sources: a, Hoyt et al. (Hoyt et al., 2000), Taylor et al. (Taylor et al., 1982); b, Steudel and Beattie (Steudel and Beattie, 1995).

Table 4. *Least squares regression and partial correlation statistics for the three analyses performed comparing limb length and body mass against cost of transport*

Analysis group	Independent variable	N	r^2	P	a	b	SEE
1	L_E	15	0.97	<0.001	–0.704	1.854	0.06
	Controlling for body mass		0.74	<0.001			
	Body mass	15	0.89	<0.001	–0.268	1.039	0.11
	Controlling for L_E		0.05	0.45			
2	L_E	19	0.95	<0.001	–0.720	1.871	0.08
	Controlling for body mass		0.62	<0.001			
	Body mass	19	0.89	<0.001	–0.289	1.061	0.13
	Controlling for L_E		0.14	0.12			
3	L_E	28	0.98	<0.001	–0.772	1.956	0.08
	Controlling for body mass		0.70	<0.001			
	Body mass	28	0.94	<0.001	–0.263	1.047	0.13
	Controlling for L_E		0.23	0.01*			

Limb length (L_E; cm) and body mass (kg) against cost of transport (COT; $J\,kg^{-1}\,m^{-1}$).

Analysis 1 is the most conservative, analysis 3 the most inclusive (see Materials and methods for details). LSR equations are for $\log_{10}$-transformed data, with the form COT=*a*(ind.var)+*b*. SEE, standard error of estimate. *P=0.32 in an ANCOVA with taxonomic group (bird, mammal, reptile, arthropod) as a fixed factor.

(F=0.02, P=0.88), whereas taxonomic group was a significant factor (F=6.85, P=0.02) and the independent contribution of L_E remained strongly significant (F=41.92, P<0.001). These results were consistent with previous work (Roberts et al., 1998a; Roberts et al., 1998b) demonstrating differences in COT between birds and mammals.

When reptiles and arthropods were included (Table 4, Analysis group 3), L_E predicted 98% of the variance in COT (r^2=0.98, N=28, P<0.001) and remained strongly significant when controlling for body mass (r^2=0.70, d.f.=25, P<0.001). Body mass was strongly correlated with COT (r^2=0.94, N=28, P<0.001), and its effect remained significant when controlling for L_E *via* partial correlation (r^2=0.23, d.f.=25, P=0.01). However, when taxonomic differences were considered by including taxonomic group as a fixed factor (mammal, bird, reptile, arthropod) in an ANCOVA, the contribution of body mass was not significant (F=1.04, P=0.32), and was smaller than that of taxonomic group (F=2.51, P=0.09); L_E remained

strongly significant (F=71.38, P<0.001). Least squares regression equations for each analysis are given in Table 4.

Path analysis confirmed these results. For the species in Analysis group 1 (Table 4), body mass and L_E were strongly correlated (r=0.95, d.f.=14, P<0.001; Fig. 2C), and the direct effect of L_E on COT was strongly significant (r=–0.88, d.f.=12, P<0.001; Fig. 2C), but the direct effect of body mass was not significant (r=–0.11, d.f.=12, P=0.73; Fig. 2C). Similar results were obtained for Analysis group 2 (L_E–COT: r=–0.75, d.f.=16, P=0.001; body mass–COT: r=–0.24, d.f.=15, P=0.39) and Analysis group 3 (L_E–COT: r^2=0.53, d.f.=24, P<0.001; body mass–COT: r=–0.27, d.f.=24, P=0.20). These results, as well as those from the partial correlation and ANCOVA analyses, indicate that the relationship between COT and body mass is due solely to the covariance of limb length and body mass. Body mass has no independent effect on COT for the 28 species in this dataset.

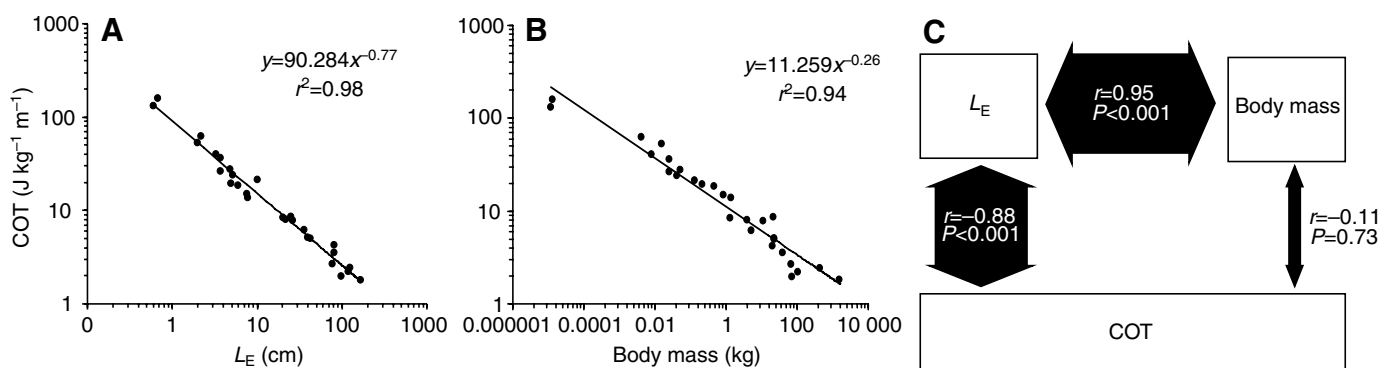Both taxonomy and locomotor ecology were associated with

Fig. 2. The relationship between (A) effective limb length (L_E) and (B) body mass and the cost of transport (COT) for all 28 species. (C) Path analysis indicating the independent effects of L_E and body mass on the mass-specific cost of transport. Results of Analysis group 1 species are shown; similar results were obtained for Analysis groups 2 and 3. Arrow thickness is proportional to path coefficient. N=15 species, d.f.=12 for all comparisons.
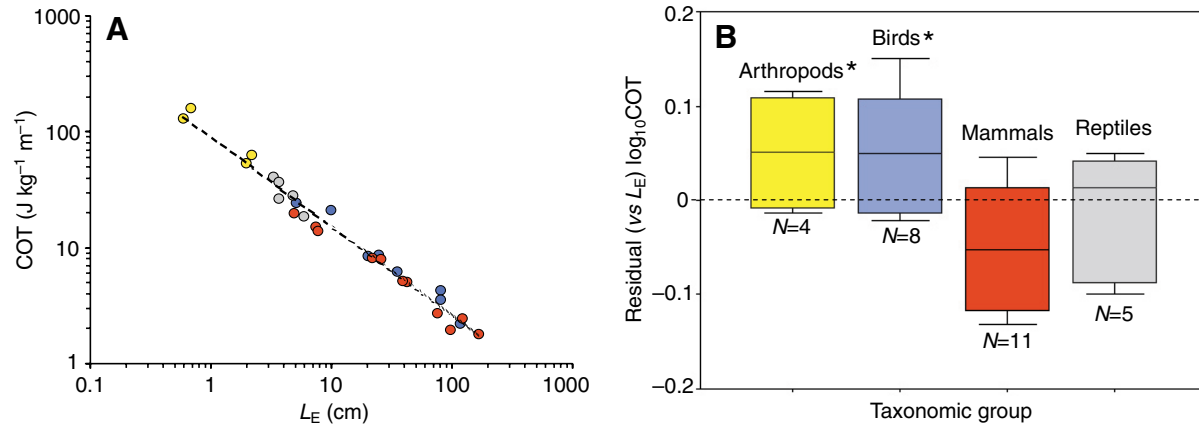
Fig. 3. (A) The fit of four taxonomic groups to the overall $\log_{10}L_E$–COT trendline: mammals (red), birds (blue), reptiles (gray) and arthropods (yellow). (B) Boxplots of $\log_{10}$COT residuals from the L_E–COT regression for each taxonomic group. *Residuals significantly greater than for mammals ($P<0.05$, Student's t-test). COT, cost of transport; L_E, effective limb length.

differences in locomotor cost (Fig. 3). As noted above, when residuals from the L_E–COT regression were compared between taxonomic groups, mean residual COT for birds was significantly greater than that for mammals ($P=0.006$, Student's t-test) and reptiles ($P=0.03$), but not arthropods ($P=0.97$). Similarly, residuals for arthropods were greater than for mammals ($P=0.03$). Residuals for reptiles were most similar to those of mammals, whereas arthropods were most similar to birds (Fig. 3B).

Comparing COT between generalists, cursors and semi-aquatic species revealed a potential link between limb length, locomotor performance, and ranging ecology. When controlling for body mass as a covariate in an ANCOVA, semi-aquatic species had the highest COT and shortest legs, whereas cursors had the lowest COT and longest legs ($F=6.87$ and 8.12 for COT and L_E, respectively, $P<0.01$ both comparisons, Fig. 4A). By contrast, COT did not differ between groups when controlling for L_E via ANCOVA

($F=0.42$, $P=0.66$). That is, semi-aquatic species had higher locomotor cost than expected for their body mass, but not for their limb length. Indeed, residual COT was proportional to residual L_E, with long-legged cursors having low cost, and short-legged semi-aquatic species having high cost, with respect to their body mass (Fig. 4C).

As expected, when using skeletal limb length, L_{skel}, to predict COT, body mass remained a significant factor. L_{skel} was significantly correlated with body mass ($r^2=0.78$, $N=22$, $P<0.001$), but it did not remain significant when controlling for body mass via partial correlation ($r^2=0.004$, d.f.=19, $P=0.80$). By contrast, body mass was significantly correlated with COT ($r^2=0.88$, $N=22$, $P<0.001$) even when accounting for L_{skel} ($r^2=0.46$, d.f.=19, $P=0.001$). As predicted, COT was negatively correlated with body mass when controlling for skeletal limb length ($r^2=-0.68$). These results are similar to those of Steudel and Beattie (Steudel and Beattie, 1995), who reported that skeletal limb length had no independent effect on COT.
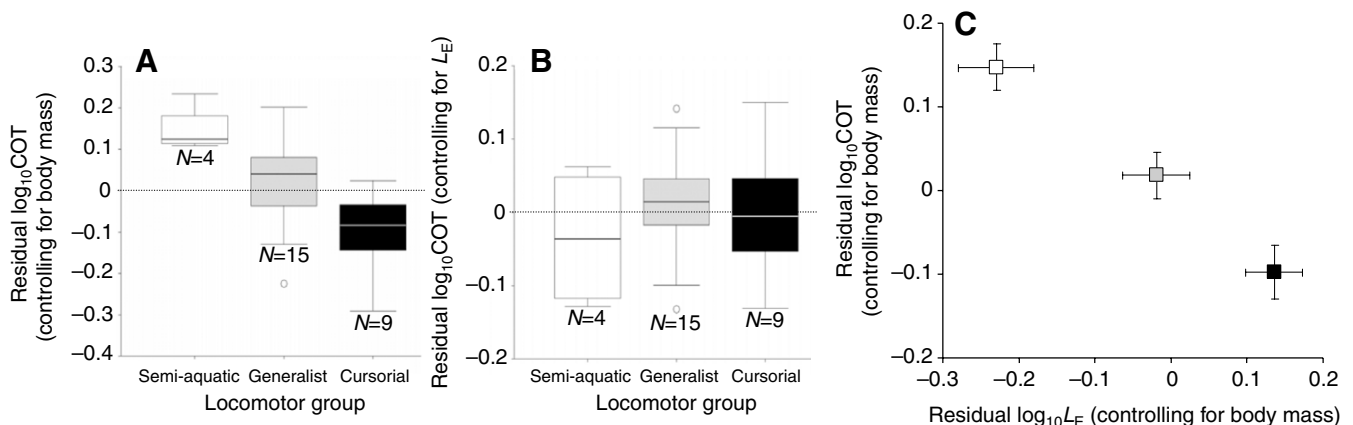

Fig. 4. Boxplots of residual $\log_{10}$COT, controlling for (A) body mass and (B) L_E, for semi-aquatic (white), generalist (gray) and cursorial (black) species. Number of species in each locomotor group is shown below each category heading. (C) $\log_{10}$ residuals of L_E and COT controlling for body mass for each locomotor group. Squares indicate group means, error bars indicate standard error. Shading indicates locomotor group as in A. COT, cost of transport; L_E, effective limb length.
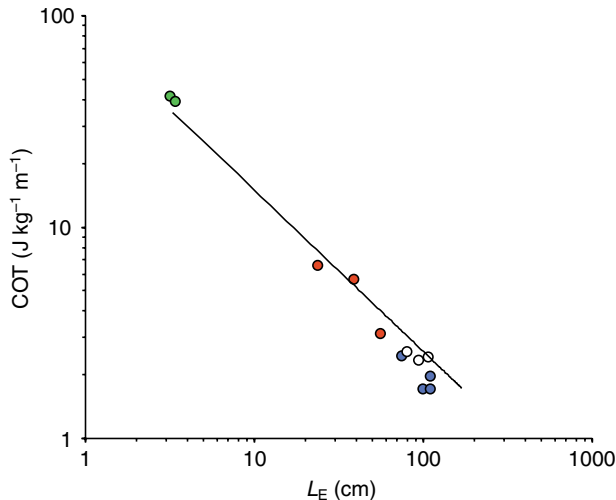
Fig. 5. Effective limb length (L_E) *versus* cost of transport (COT) within species. Circles indicate different size classes (see Table 4): lizards (green), dogs (red), humans (white), caribou (blue). Line indicates trendline for all species.

Discussion

The scaling of locomotor cost

The results of this study strongly suggest that effective limb length drives the scaling of locomotor cost in terrestrial animals. Both body mass and L_E were strongly correlated with COT for the species examined here, but L_E was the better predictor for all three sets of analyses, explaining a greater portion of the variance in COT, with nearly half the error of estimation, than body mass (Table 4). Furthermore, when controlling for L_E and broad taxonomic differences in locomotor anatomy, body mass had no effect on COT, and path analysis revealed no significant independent contribution of body mass to COT (Fig. 3). This supports the predictions of the LiMb model for broad interspecific comparisons (Pontzer, 2005; Pontzer, 2007). The lack of an independent effect of body mass on cost is also consistent with load-carrying studies, which have shown that the mass-specific energy consumed to run a given distance does not change substantially when mass is added to a subject (Taylor et al., 1980; Marsh et al., 2006). In the context of the LiMb model, these results support the hypothesis that effective limb length drives locomotor cost *via* its role in determining the magnitude and frequency of muscle force generated to support body weight (Kram and Taylor, 1990; Pontzer, 2005; Pontzer, 2007).

Limb length predicted over 95% of the variance in COT, but this does not rule out the possibility that other size-related aspects of locomotor anatomy or gait contribute to the scaling of COT. In fact, the observed exponent for the L_E–COT regression (–0.77; Fig. 2A) differs markedly from (–1.0), the value predicted by the LiMb model (Eqn 1) if L_E were the sole determinant of cost. Other variables, such as those identified by the LiMb model (ϕ, C_{limb} and k) or others, may change with body size and thus affect the scaling of COT. For example, excursion angle, ϕ, scales as mass$^{-0.10}$ (McMahon, 1975), and

may therefore affect the scaling of both ground force production and swing cost [Eqn 1 (see Pontzer, 2005)]. The contribution of other size-related variables may explain the marginal effect of body mass seen in Analysis group 3. Identifying the independent contribution and covariance of such size-related variables affecting COT will require more complete datasets for large interspecific comparisons.

As with most interspecific studies of COT (e.g. Taylor et al., 1982), this study focused on running gaits. Although the LiMb model predicts that limb length will also drive the scaling of cost during walking (Pontzer, 2005; Pontzer, 2007), more data on walking COT for a wide range of species is needed to test this prediction. Load-carrying studies have shown that COT changes more with added mass during walking than during running (see Marsh et al., 2006), which may indicate that the effect of mass on aspects of gait, such as stride frequency or excursion angle, are relatively more important in determining the scaling of walking cost than for running.

Taxonomic and individual differences in COT

Although uncertain divergence times for such a wide taxonomic range preclude a reliable phylogenetic contrasts analysis, it is unlikely that phylogenetic inertia is responsible for the strong relationship between L_E and COT shown here: average divergence time between species in this dataset is in the order of 200 million years (Kumar and Hedges, 1998), and the taxonomic groups included here all fit the L_E–COT trendline well (Fig. 3A). Taxonomic differences in limb design do appear to have an effect on cost, however. Residuals from the L_E–COT trendline indicate that birds and arthropods have a higher COT than expected for their limb length (Fig. 3B). This is consistent with previous work (Roberts et al., 1998a; Roberts et al., 1998b) demonstrating that birds expend more energy for a given rate of force production due to their longer hindlimb muscle fibers. Still, whereas results from ANCOVA indicated that taxonomic differences have a greater effect on COT than body mass, differences between broad taxonomic groups were not always statistically significant (Analysis group 3). This suggests that within-group heterogeneity in limb design and gait is substantial, and requires further investigation.

Thus, limb length appears to be the primary determinant of COT over the wide range of species considered here, but other aspects of limb design and gait are clearly important in determining locomotor cost. Indeed, over a narrow range of body size, differences in L_E may not correspond to differences in COT. For example, different size classes of humans, dogs, caribou and lizards (Table 2) are generally consistent with overall interspecific relationship (Fig. 5), but the longest-legged classes did not always exhibit the lowest COT (Table 2). This is similar to a recent study of horses (Griffin et al., 2004), in which the tallest breed included in the analysis did not exhibit the lowest COT, as well as a recent human study (Pontzer, 2005) in which between-subjects differences in ϕ, C_{limb}, and k (see Eqn 1) prevented a clear relationship between L_E and COT. Other factors are clearly critical for predicting cost within species or between similarly sized species, as suggested by previous studies

that found no effect of limb length. As with most broad scaling relationships, the utility of L_E as the sole predictor of cost is dependent on the scale of analysis.

Skeletal limb length

The comparison of skeletal limb length to COT highlights a second caveat in using limb length to predict COT. As expected, body mass remained significantly negatively correlated with COT even when controlling for L_{skel}, eliminating the utility of skeletal limb length as a predictor of cost. Skeletal limb length fails as a useful predictor of COT in this sample presumably because it is not the biomechanically relevant measure of limb length. For most species, effective limb length – the length of the leg as a strut – is not equal to the summed lengths of the component long bones (Fig. 1). Further, the difference between skeletal and effective limb lengths is related to body size, as smaller animals adopt more crouched postures (Biewener, 1989). Using skeletal limb length to predict COT is therefore problematic, since body mass will have a strong effect on the relationship between L_{skel} and COT. Distinguishing between effective and skeletal limb length may, therefore, be critical for large-scale comparisons of locomotor anatomy (e.g. Steudel and Beattie, 1995; Gingerich, 2003).

Limb length, locomotor cost and ecology

Differences in limb length and cost appear to correspond to broad differences in locomotor ecology. Corrected for body mass, semi-aquatic species had the highest residual COT of the three groups analyzed ($P<0.05$ all comparisons, Student's t-test), whereas mean residual COT for cursorial species fell just below that of generalists (Fig. 4A). However, the same was not true for residuals from the L_E–COT regression; all three groups fit this trendline equally well, with mean residual COT values near zero (Fig. 4B). Notably, deviations from the body mass–COT regression were proportional to deviations from the body mass–L_E regression: when controlling for body mass, semi-aquatic species had the shortest legs and highest cost, whereas cursorial species had the longest legs and lowest cost (Fig. 4C). This supports previous work that has used limb length, relative to body mass, as a gross measure of locomotor performance and ecological niche (Gingerich, 2003), and suggests relative limb length might be useful in quantifying some tradeoffs in locomotor performance (see Fish et al., 2001; Pontzer and Wrangham, 2004).

These results shed new light on the relationship between body size and locomotor cost (Taylor et al., 1982). Studies of locomotor cost across wide ranges of body size may therefore benefit by correcting for L_E rather than body mass. Similarly, estimates of COT, such as for extinct species, should employ L_E rather than body mass when possible, since this decreases the error of estimation substantially. Finally, the link between effective limb length and locomotor cost has broad potential application in ontogenetic and ecological studies, as limb lengths and ranging strategies vary with age and between species. The relationship between L_E and COT may enable ecologists and morphologists to test relationships between travel cost, limb length and ranging behavior quantitatively, improving our understanding of the selection pressures shaping limb design in terrestrial species.

List of abbreviations

C_{limb}	Energy cost of swinging the limbs during locomotion
COT	Cost of transport (J kg^{-1} m^{-1})
k	Cost coefficient relating force production to energy consumption (J N^{-1})
L_E	Effective limb length, the length of the limb as a mechanical strut
L_{skel}	Skeletal limb length, the summed lengths of the limb's long bones
ϕ	Excursion angle of the limbs

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