

**Effective Limb Length and the Scaling of Locomotor Cost
in Terrestrial Animals**

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Abstract

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 ($\text{J kg}^{-1} \text{m}^{-1}$) 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 was attributable to taxonomic differences in limb design, with birds exhibiting greater residuals than mammals. Differences in COT between semi-aquatic, generalist, and cursorial species also corresponded to differences in leg length between these groups. These results are discussed in light of previous investigations of the limb length and locomotor cost.

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 (Figure 1), drives the scaling of locomotor cost for terrestrial animals.

While numerous within- and between-species studies have reported that larger animals have lower mass-specific locomotor costs, there is little evidence that mass itself is a causal factor underlying the mass-specific cost of transport, COT ($\text{J kg}^{-1} \text{m}^{-1}$), 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 bodyweight (Taylor et al., 1980; Kram and Taylor, 1990; Taylor, 1994; Pontzer, 2005; Pontzer, 2007). 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 and resulting 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). 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), while others shown reported that longer-legged individuals can have a higher COT (Minetti et al., 1994; Griffin et al., 2000) and a greater metabolic cost of generating muscle force (Roberts et al., 1998) during running. The effect of limb length on locomotor cost therefore remains unclear.

A recent biomechanical model linking limb length to COT (Pontzer, 2005; in review) 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 (Figure 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:

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

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, 1974; 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 (Figure 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 due to 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.

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

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). While COT has been measured in many species (ca. 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 for 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,b). 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 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. \log_{10} 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 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. While 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., 1998) 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 ($\text{J kg}^{-1} \text{s}^{-1}$), 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, 2.5ms^{-1} (Froude number ~ 0.38) was deemed more appropriate for comparison in this dataset than that reported for the minimum-COT speed (1.0ms^{-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 trochanter of the femur to the ground while standing. These measurements were taken directly (Pontzer, in review) 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., 2000), 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 Univ. 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). While 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 *T. rugosus* (John-Adler et al., 1986). For all other reptiles, L_E was estimated from reptiles (*D. 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 the regression for limb length presented in (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 gram cockroach ($L_E = 1.9$ cm, Kram et al. 1997) and scaled to match the 4.2 gram cockroaches used for COT analysis (Herreid and Full, 1983) assuming geometric similarity (i.e., that limb length increases as $c \text{ Mass}^{0.33}$, where the constant

determined from Kram et al. 1997 was $c = 13.81$). L_E for tarantulas was estimated from data and description in 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, Figure 2). In the first, most conservative analysis, representing over half of the species analyzed (Table 3: Analysis 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 ($r^2=0.74$, $df=12$, $p<0.001$). In contrast, while 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 ($r^2=0.05$, $df=12$, $p=0.45$). 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, while mass had no effect ($F=0.33$, $p=0.58$); L_E remained the 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 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 ($r^2=0.62$, $df=16$, $p<0.001$). Body mass, while significantly correlated with COT ($r^2=0.89$, $n=19$, $p<0.001$), had no statistically significant independent effect ($r^2=0.14$, $df=16$, $p=0.12$). When taxonomic group (bird or mammal) was considered as a fixed factor in an ANCOVA, with L_E and body mass included as covariates, the independent effect of body mass was removed ($F=0.02$, $p=0.88$), while taxonomic group was a significant factor ($F=6.85$, $p=0.02$) and the independent contribution of L_E remains strongly significant ($F=41.92$, $p<0.001$). These results were consistent with previous work (Roberts et al., 1998a,b) demonstrating differences in COT between birds and mammals.

When reptiles and arthropods were included (Table 4: Analysis 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 ($r^2=0.70$, $df=25$, $p<0.001$). Body mass was strongly correlated with COT ($r^2=0.94$, $n=28$, $p<0.001$), and remained significant effect when controlling for L_E via partial correlation ($r^2=0.23$, $df=25$, $p=0.01$). 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 3), body mass and L_E were strongly correlated ($r = 0.95$, $df=14$, $p<0.001$, Figure 2C), and the direct effect of L_E on COT was strongly significant ($r = -0.88$, $df=12$, $p<0.001$, Figure 2C), but the

direct effect of body mass was not significant ($r = -0.11$, $df=12$, $p=0.73$, Figure 2C). Similar results were obtained for Analysis Group 2 (L_E -COT: $r = -0.75$, $df=16$, $p=0.001$; body mass-COT: $r = -0.24$, $df=15$, $p=0.39$) and Analysis Group 3 (L_E -COT: $r^2=0.53$, $df=24$, $p<0.001$; body mass-COT: $r = -0.27$, $df=24$, $p=0.20$). 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 differences in locomotor cost (Figure 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 ($p=0.97$). Residuals for reptiles were most similar to those of mammals, while arthropods were most similar to birds (Figure 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, while 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, Figure 4A). In 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 (Figure 4C).

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

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. While both body mass and L_E were strongly correlated with COT for the species examined here, 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 3). Further, 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 (Figure 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; see 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 bodyweight (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 , Figure 2A) differs markedly from (-1.0), the value predicted by the LiMb model (eq. 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 $\text{mass}^{-0.10}$ (McMahon, 1975), and may therefore affect the scaling of both ground force production and swing cost (eq. 1, see Pontzer, 2005). The contribution of other size-related variables may explain the marginal effect of body mass seen in Analysis 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. While 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

While 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 on the order of 200 million years (Kumar and Hedges, 1998), and the taxonomic groups included here all fit the L_E -COT trendline well (Figure 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 have a higher COT than expected for their limb length (Figure 3B). This is consistent with previous work (Roberts et al., 1998a,b) demonstrating that birds expend more energy for a given rate of force production due to their longer hindlimb muscle fibers. Still, while 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 (Analyses 3). This suggests that within-group heterogeneity in limb design and gait is substantial, and requires further investigation.

Thus, while limb length appears to be the primary determinant of COT over the wide range of species considered here, 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, and caribou, and lizards (Table 2) are generally consistent with overall interspecific relationship (Figure 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 eq. 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 (Figure 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

Notably, 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), while mean residual COT for cursorial species fell just below that of generalists (Figure 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 (Figure 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, while cursorial species had the longest legs and lowest cost (Figure 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.

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Abbreviations

COT	Cost of Transport ($\text{J kg}^{-1} \text{ m}^{-1}$)
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
k	Cost coefficient relating force production to energy consumption, (J N^{-1})
ϕ	Excursion angle of the limbs
C_{limb}	Energy cost of swinging the limbs during locomotion

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Table 1. Body mass, effective limb length (L_E), and cost of transport (COT).

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

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, 3: least conservative. See text and Table 3.

Table 2. Body mass, effective limb length (L_E), and cost of transport (COT) for different size classes within species.

SPECIES	Common Name	Mass (kg)		L_E (cm)	COT ($J\ kg^{-1}\ m^{-1}$)	Source (L_E , COT)
		COT	L_E			
<i>Canis familiaris</i>	Dog - small	5.60		24.0	6.54	Roberts et al. (1998a), Pontzer (in review)
<i>Canis familiaris</i>	Dog - medium	26.3		39.0	5.63	Pontzer (in review)
<i>Canis familiaris</i>	Dog - large	37.9		56.0	3.12	Pontzer (in review)
<i>Homo sapiens</i>	Human - short	58.8		80.3	2.57	Pontzer (in review)
<i>Homo sapiens</i>	Human - medium	73.6		94.4	2.34	Pontzer (in review)
<i>Homo sapiens</i>	Human - tall	75.2		107	2.40	Pontzer (in review)
<i>Lacerta sicula</i>	lizard	0.006	0.007	3.2	41.21	Irschick & Jayne (1999), John-Adler et al. (1986)
<i>Lacerta sicula</i>	lizard	0.010	0.012	3.4	39.20	Irschick & Jayne (1999), John-Adler et al. (1986)
<i>Rangifer tarandus granti</i>	Caribou - small	25.5		75.0	2.43	Niemen & Helle (1980), Luick & White (1986)
<i>Rangifer tarandus granti</i>	Caribou - medium	54.5		100	1.70	Niemen & Helle (1980), Luick & White (1986)
<i>Rangifer tarandus granti</i>	Caribou - large	103		110	1.71	Niemen & Helle (1980), Fancy & White (1986)
<i>Rangifer tarandus sp.</i>	Reindeer	111		110	1.97	Niemen & Helle (1980), Luick & White (1986)

Table 3. Body mass, skeletal limb length (L_{skel}), and cost of transport (COT).

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

Mass: COT, body mass of subjects used to measure COT; L_{skel} , body mass of subjects used for L_{skel} if different.

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

Table 4. Least squares regression and partial correlation statistics for the three analyses performed comparing 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 Methods for details). LSR equations are for \log_{10} transformed data, with the form $COT = a(\text{Ind.Var}) + b$. SEE: standard error of estimate. ‡ $p = 0.32$ in an ANCOVA with taxonomic group (bird, mammal, reptile, arthropod) as a fixed factor.

Analysis Group	Independent Variable	N	r^2	p	<i>a</i>	<i>b</i>	SEE
1	L_E <i>controlling for Body Mass</i>	15	0.97 0.74	<0.001 <0.001	-0.704	1.854	0.06
	Body Mass <i>controlling for L_E</i>	15	0.89 0.05	<0.001 0.45	-0.268	1.039	0.11
2	L_E <i>controlling for Body Mass</i>	19	0.95 0.62	<0.001 <0.001	-0.720	1.871	0.08
	Body Mass <i>controlling for L_E</i>	19	0.89 0.14	<0.001 0.12	-0.289	1.061	0.13
3	L_E <i>controlling for Body Mass</i>	28	0.98 0.70	<0.001 <0.001	-0.772	1.956	0.08
	Body Mass <i>controlling for L_E</i>	28	0.94 0.23	<0.001 0.01‡	-0.263	1.047	0.13

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

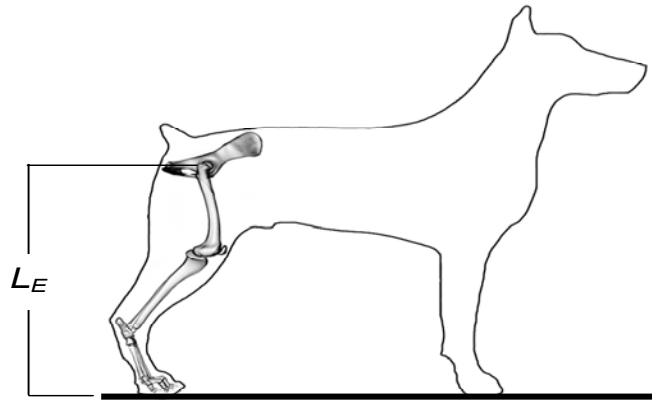


Figure 2. The relationship between **A.** effective limb length, L_E and **B.** body mass and the cost of transport, COT, for all 28 species. **C.** Path analysis indicating the independent effects of L_E and body mass on the mass-specific cost of transport. Results for Analysis 1 species are shown; similar results were obtained for analysis groups 2 and 3. Arrow thickness is proportional to path coefficient. $N = 15$ species, $df = 12$ for all comparisons.

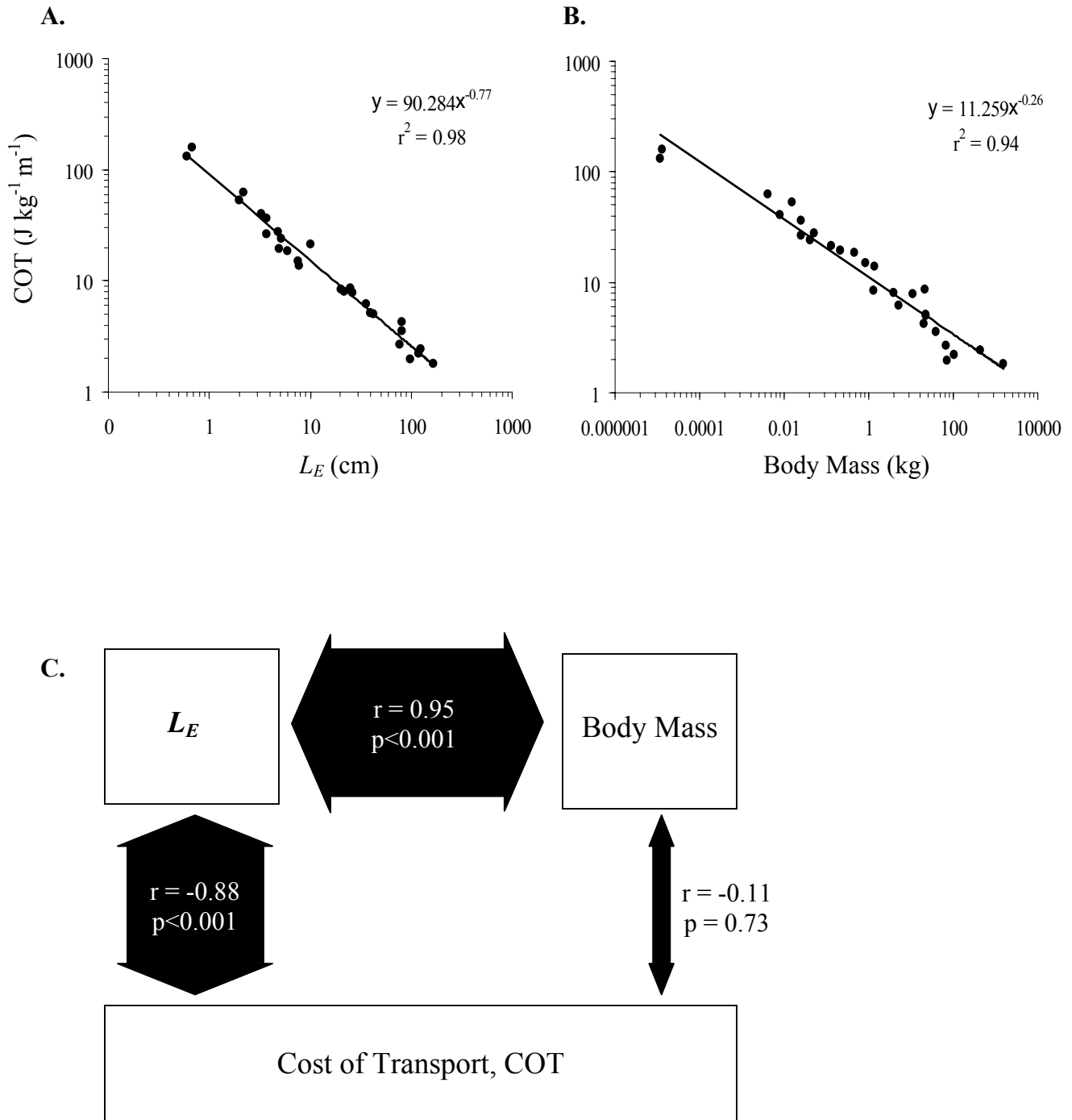


Figure 3. A. The fit of four taxonomic groups to the overall $\log_{10} L_E$ -COT trendline: mammals (red), birds (blue), reptiles (gray), and arthropods (yellow). **B.** Boxplots of \log_{10} COT residuals from the L_E – COT regression for each taxonomic group. * Residuals for Birds are significantly greater than for Mammals ($p < 0.01$, Student's t-test).

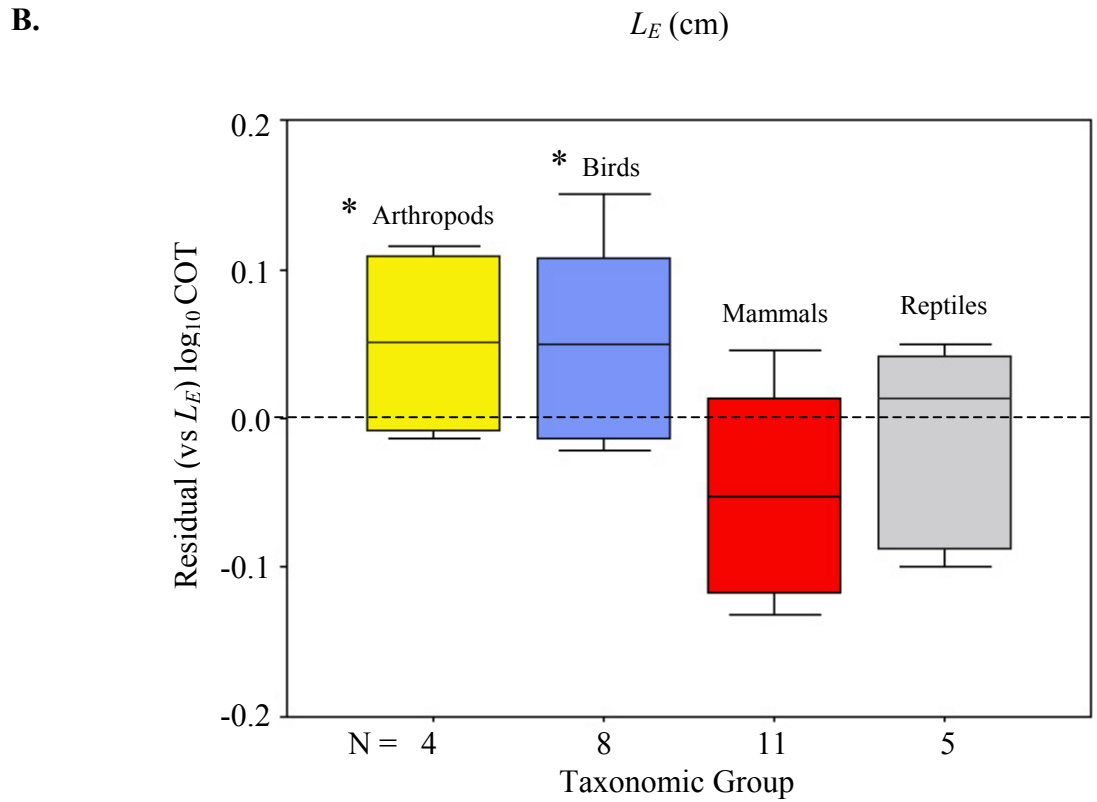
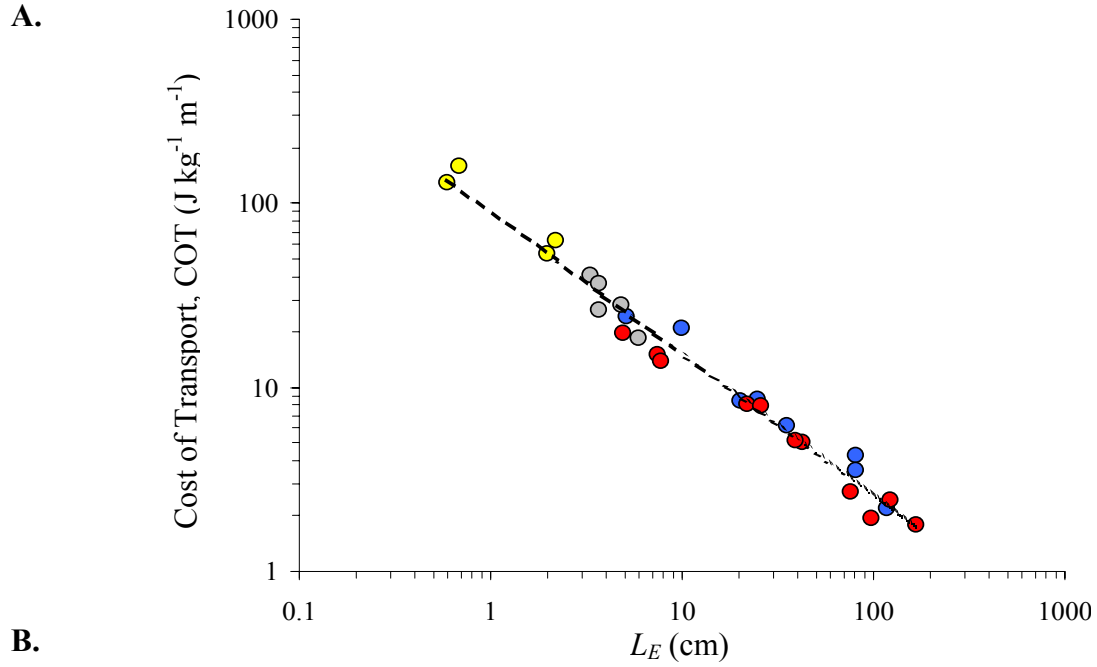


Figure 4. Boxplots of residual \log_{10} COT, controlling for **A.** body mass and **B.** L_E , for semi-aquatic (white), generalist (gray), and cursorial (black) species. Number of species in each locomotor group is shown above each category heading. **C.** \log_{10} residuals of L_E and COT controlling for body mass for each locomotor group. Points indicate group means, error bars indicate standard error.

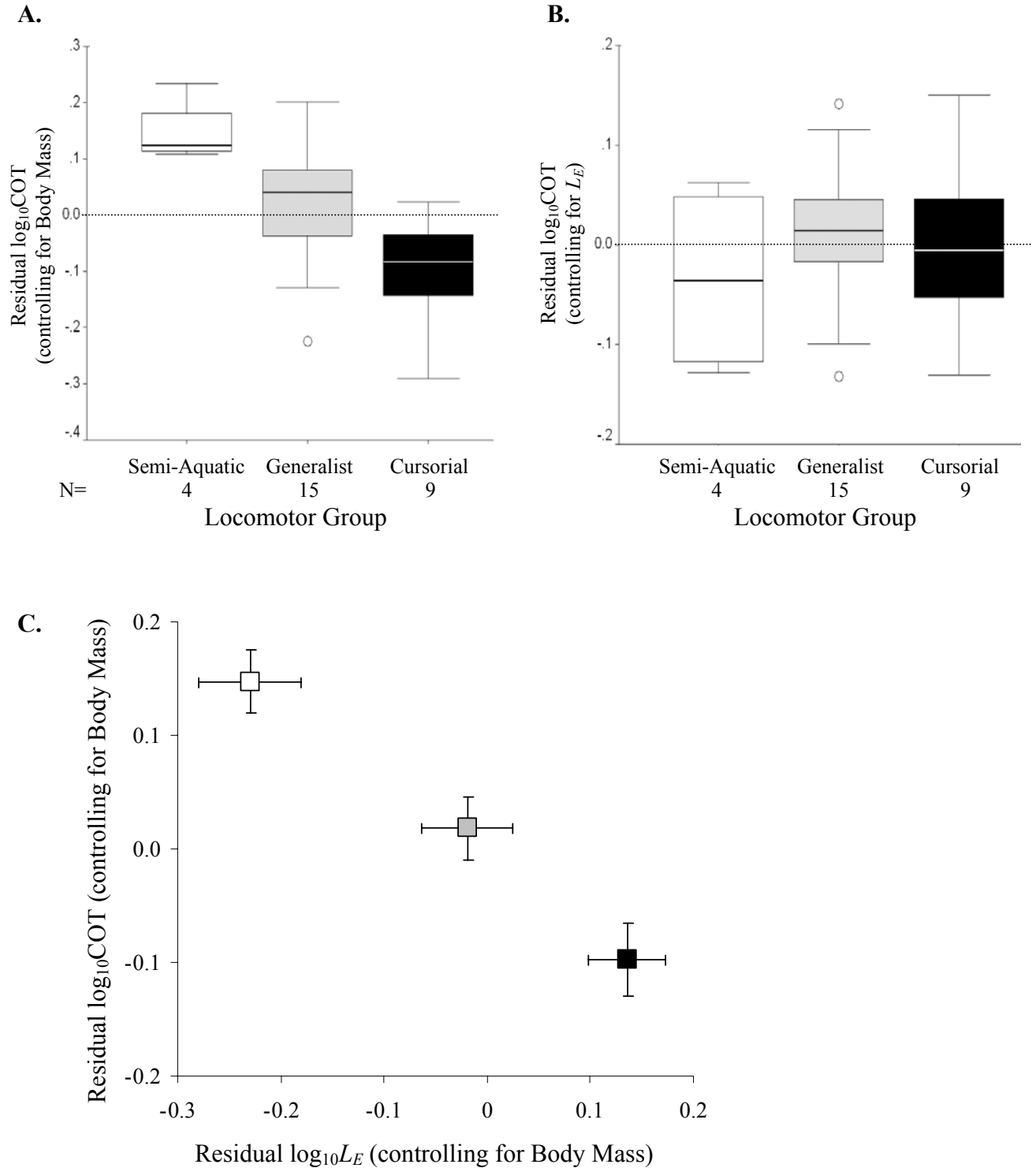


Figure 5. L_E versus COT within species. Circles indicate different size classes (Table 4): lizards (green); dogs (red); humans (white); caribou (blue). Line indicates trendline for all species.

