Predicting the energy cost of terrestrial locomotion: a test of the LiMb model in humans and quadrupeds

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Summary

The energy cost of terrestrial locomotion has been linked to the muscle forces generated to support body weight and swing the limbs. The LiMb model predicts these forces, and hence locomotor cost, as a function of limb length and basic kinematic variables. Here, I test this model in humans, goats and dogs in order to assess the performance of the LiMb model in predicting locomotor cost for bipeds and quadrupeds. Model predictions were compared to observed locomotor cost, measured *via* oxygen consumption, during treadmill trials performed over a range of speeds for both walking and running gaits. The LiMb model explained more of the variation in locomotor cost than other predictors, including contact time, Froude number and body mass. The LiMb model also accurately predicted the magnitude of vertical ground forces. Results suggest the LiMb model reliably links locomotor anatomy to force production and locomotor cost. Further, these data support the idea that limb length may underlie the scaling of locomotor cost for terrestrial animals.

Key words: terrestrial locomotion, locomotor energetics, limb length, biomechanics.

Introduction

What determines the energetic cost of walking and running? Over a century ago, Zuntz proposed that the cost of locomotion in terrestrial animals is a function of body size: larger animals use less energy, per g body mass, to travel a given distance or at a given speed (Zuntz, 1897). This negative allometry has been demonstrated over a wide range of species and body plans, from arthropods to mammals (Taylor et al., 1982; Full, 1989), but the mechanism underlying this relationship remains a matter of some debate (see Alexander, 2005; Ruina et al., 2005). In particular, a link between anatomy and performance that can explain both between- and within-species differences has not been identified.

Physiological studies have shown that the metabolic cost of locomotion, COL, typically measured as the mass-specific rate of oxygen consumption (ml O_2 kg^{-1} s^{-1}), derives primarily from the muscle force generated to support body weight (Taylor et al., 1980; Kram and Taylor, 1990; Kram, 1991; Taylor, 1994; Roberts et al., 1998a; Roberts et al., 1998b; Wickler et al., 2001; Griffin et al., 2003; Pontzer, 2005). Indeed, the rate of muscle force production, estimated from the inverse of contact time, t_c (stance duration), predicts changes in COL with body size and speed better than other predictors of cost such as the mechanical work performed to move the body's center of mass and limbs (Heglund et al., 1982; Kram and Taylor, 1990; Cavagna and Kaneko, 1977; Willems et al., 1995).

While broadly supported by empirical studies of locomotor cost, some aspects of this Force Production Hypothesis have been challenged by recent studies. For example, focusing on muscle force generated to support body weight ignores the cost of swinging the limbs and, while many previous studies have argued that leg swing costs are negligible (Taylor et al., 1974; Taylor et al., 1980; Kram and Taylor, 1990; Taylor, 1994; Griffin et al., 2003), more recent experiments have demonstrated that these costs can account for 10–25% of COL (Marsh et al., 2004; Doke et al., 2005; Modica and Kram, 2005; Gottschall and Kram, 2005). Similarly, focusing on vertical forces (i.e. opposing gravity) ignores horizontal forces (i.e. braking and propulsion), which may account for as much as 40–50% of COL (Chang and Kram, 1999; Gottschall and Kram, 2003). Further, while the Force Production Hypothesis predicts that animals with longer legs will use longer contact times (Kram and Taylor, 1990; Hoyt et al., 2000) and therefore have lower locomotor cost, numerous studies, mostly in humans, have reported no relationship between leg length and cost in walking humans (Censi et al., 1998), running humans (Ferretti et al., 1991; Cavanagh and Kram, 1989; Brisswalter et al., 1996) or between species (Steudel and Beattie, 1995). Finally, some have suggested that collisional energy losses may determine COL, rather than muscle force generation associated with 'inverted pendulum' or 'mass-spring' models of walking and

running mechanics (Donelan et al., 2002; Collins et al., 2005; Ruina et al., 2005).

The recently proposed LiMb model (Pontzer, 2005) links limb length to locomotor cost and addresses some of these issues by incorporating horizontal forces and leg swing cost as predictors of COL. This model estimates the muscle force produced to accelerate the center of mass (including both vertical and horizontal forces) and swing the limbs as functions of forward speed U, effective limb length (i.e. hip height) L, excursion angle ϕ, and stride frequency f. A mass-specific rate of force generation, calculated as the mean mass-specific force generated by the limb per step, can then be used to predict COL for running (COL_{run}) and walking (COL_{walk}) as:

$$COL_{run} = kgU[2L\sin(\phi/2)]^{-1} [1+\tan(\phi/2)] + C_{limb} , \quad (1)$$

and

$$COL_{walk} = 8kfU^2L^{-1} [1+\cos(\phi/2)]^{-1} [1+\tan(\phi/2)] + C_{limb} , (2)$$

where k is a constant relating muscle force to oxygen consumption (ml O_2 N^{-1}), g is gravitational acceleration, and C_{limb} is the metabolic cost of swinging the limb (Pontzer, 2005). Note that a stride is defined here as the period between two heel-strikes of the same foot, i.e. one complete cycle; step frequency is twice stride frequency, $2f$. This model suggests limb length, leg swing and kinematic variables (U, f, ϕ) all contribute to COL, but that their relative importance depends upon the scale of analysis. Over narrow ranges of body size where differences in L are small, variation in kinematic variables or leg-swing costs may dominate COL. Conversely, over a large range of body size, variation in L will largely determine COL. While the LiMb model effectively predicts COL in humans during walking and running (Pontzer, 2005), it has yet to be tested over a broad range of body size or in quadrupeds.

Here, I test the LiMb model in an interspecific sample of goats, dogs and humans to determine the effectiveness of the model for bipeds and quadrupeds. In addition, I examine other predictors of cost, including contact time, Froude number, body mass and limb length in order to determine their relative effectiveness both within- and between-species. Finally, forces predicted by the model are compared to observed ground forces and published values for leg swing forces. Results are discussed in light of current approaches to estimating cost and accounting for body size in comparisons of locomotor performance.

Materials and methods

Humans *Homo sapiens* L. (N=10), dogs *Canis familiaris* L. (N=4), and goats *Capra hircus* L. (N=4) (Table 1) performed sets of walking and running (humans) or trotting (dogs, goats) trials over a range of speeds on a large, custom-built treadmill. All subjects were healthy adults with no apparent gait abnormalities. Of the ten humans in this study, two had also participated in the previous test of this model (Pontzer, 2005). All were all recreationally fit, engaging in running or other aerobic exercise at least twice per week. Informed consent was obtained for all human subjects, who were paid for their participation in accordance with institutional guidelines. Dogs were pets in good physical condition; each dog owner gave their informed consent, and was paid in accordance with institutional guidelines. Goats were pastured at the Concord Field Station in large paddocks, and were allowed to graze and range freely. Human subjects committee and IACUC approvals were obtained prior the study.

Kinematic and energy expenditure data were collected at each speed as previously described (Pontzer, 2005). For humans, walking and running speeds were chosen such that the fastest walking speed exceeded the subject's habitual walk–run transition speed, and the slowest running speed was less than the walk–run transition speed. A minimum of four walking and three running speeds were examined for each human subject. For all goats and one dog, a minimum of three walking and three trotting speeds were examined, while for three dogs, only trotting speeds were examined.

For all subjects, a set of anatomical measurements was collected, including body mass, hip height (greater trochanter to floor while standing) and, for quadrupeds, shoulder height (humeral head to floor). Infrared-reflective markers were adhered to the skin overlying skeletal landmarks and joint centers, including: iliac crest, greater trochanter, calcaneal tuber (humans), distal fifth phalange (hindlimb and, for quadrupeds, forelimb) and, for quadrupeds, the proximal–caudal tip of the scapula, and humeral head. Humans performed trials in their personal running shoes, and so foot markers were placed on the shoe. Marker position was tracked using a Qualisys Motion Capture System (Gothenburg, Sweden) at 240 Hz. Kinematic data were used to calculate excursion angle, contact time, stride period and stride frequency as described previously (Pontzer, 2005).

Kinematic variables, with speed, hip height and (for quadrupeds) shoulder height, were used to calculate predicted locomotor cost *via* the LiMb model (Pontzer, 2005). For quadrupeds, LiMb model predictions were calculated separately for the forelimb and hindlimb, and the mean value was used for subsequent analyses. Using predictions based solely on the hindlimb or forelimb had a negligible effect on the results.

To predict the cost of leg-swing, the LiMb model treats the limb as a pendulum with a radius of gyration, D, and natural period, T_0. Following Pontzer (Pontzer, 2005), C_{limb} is estimated as the mass-specific oxygen consumed to drive this pendulum, based on the mean force required to swing the limb at stride frequency, f:

$$C_{limb} = 2kBfgM_LD\phi|1 - T^2 T_0^{-2}| , \quad (3)$$

where $T=f^{-1}$, M_L=(limb mass)/(body mass), k is cost coefficient relating oxygen consumption per unit force produced (ml O_2 N^{-1}) as in Eqn 1 and Eqn 2, and B is a dimensionless scaling factor relating leg-swing force production to force generated to accelerate the body's center of mass. Note that this formulation differs from the original (Pontzer, 2005), as the term kB replaces the cost coefficient b

Table 1. *Sample size, body mass and limb length for each species*

Species	N (m, f)	Body mass (kg)		Hindlimb L (cm)		Forelimb L (cm)	
		Mean	Range	Mean	Range	Mean	Range
Humans	10 (6, 4)	71.3	52.5–94.8	93.1	76.0–108.5	–	–
Dogs	4 (2, 2)	23.0	5.6–38.0	40.0	28.0–56.0	31.5	22.5–46.5
Goats	4 (1, 3)	22.7	19.0–28.1	43.1	43.0–43.5	32.6	32.0–33.5

m, male; f, female; L, length.

(Pontzer, 2005). Parsing the b term into kB does not alter the model mathematically, but has the advantage of explicitly incorporating the cost coefficient k into the cost of leg swing. This allows k to be estimated properly as the slope of the force production–oxygen consumption regression line (e.g. Fig. 3), since both ground-forces and leg-swing forces are incorporated into total force production (Eqn 1, Eqn 2). That is, calculating the cost coefficient k as the slope of the regression line implicitly assumes k modifies each term in Eqn 1 and Eqn 2, and therefore incorporating k explicitly into C_{limb} is appropriate. A value of $B=30$ was used for all species, just as $b=30$ was used previously (Pontzer, 2005) to scale leg-swing cost to the cost of generating ground forces. As discussed previously (Pontzer, 2005), B subsumes the moment arm of the idealized leg swing muscle, such that C_{limb} is derived *via* the muscle force required to provide the torque for leg swing.

The natural period of the limb and its mass relative to body mass, required for Eqn 3, were estimated from limb length using regression equations reported for humans (Dempster, 1955; Plagenhoef, 1966) or, for quadrupeds, dogs (Myers and Steudel, 1997). Using the dog equation to estimate these variables for goats likely overestimates relative mass and natural period, since ungulate limbs exhibit a greater reduction of the distal elements (Hildebrand, 1985). However, while the absence of similar regression equations for ungulates required the use of the dog-equation, the contribution of swing forces to overall force production for quadrupeds was low (~15% total force, see below), and thus this overestimation is likely to have minimal effect on the overall fit of the model. To assess the effect of this likely overestimation, the fit of the model was also compared with leg swing costs for goats decreased by 50%; this reduction had negligible effect on the fit of the model reported below, and is not considered further. The insensitivity of the model's fit to this change in swing cost does not suggest swing costs are unimportant: 15% represents a significant, though small, portion of total cost. Instead, the insensitivity of the model in this case indicates that decreasing the small (~15%) contribution of leg swing does not substantially affect the regression statistics for the overall fit of the model.

Energy expenditure was calculated from observed oxygen consumption using standard open-flow techniques (Fedak et al., 1981). Oxygen consumption was measured using a Sable Systems PA-1B (Sable Systems, Las Vegas, NV, USA) analyzer, with mass-flow rates between 150 and 300 l min^{-1}, allowing real time assessment of consumption. Treadmill trials lasted 4–7 min, until at least 2 min of steady-state oxygen

consumption data were collected. Oxygen consumption rates for all quadrupeds and most humans ($N=6$) were measured at least twice at each speed on separate days. Least squares regression (LSR) of day-1 *versus* day-2 measures of COL indicated low day-to-day variability ($r^2=0.97$, $N=36$, $P<0.001$, slope=0.98), and so inclusion of human subjects for whom only one measurement was available was deemed justified. Resting oxygen consumption, measured while standing prior to treadmill trials, was calculated for each subject, and this was subtracted from the rate of oxygen consumption at each speed to calculate net rate of oxygen consumption. Dividing net rate of oxygen consumption by body mass yields the mass-specific cost of locomotion, COL (ml O$_2$ kg^{-1} s^{-1}). Dividing COL by forward speed yields the mass-specific cost of transport, COT (ml O$_2$ kg^{-1} m^{-1}). Thus COL is the energy expended per second, and COT is the energy expended per meter. Mean COL and COT, calculated for each subject at each speed, were used for all analyses. Each subject–speed–gait combination was treated as one trial.

For human trials, vertical ground reaction force, GRF, was also collected at 1000 Hz *via* a custom-built force plate embedded under the tread of the treadmill (Kram and Powell, 1989). Mass-specific mean of the vertical GRF (N kg^{-1}) for each stance period (i.e. the mean of the vertical GRF during stance phase; Fig. 1) was calculated by integrating the GRF trace and dividing by contact time and body mass. Three steps for each subject at each running speed were analyzed, and the mean was used for comparison with the vertical force component of the LiMb model to test the agreement between predicted and observed ground force production. Similarly, mass-specific mean of the vertical GRF for each step was also calculated using the LiMb model by dividing the rate of vertical force production during running [eqn 4 in Pontzer (Pontzer, 2005)] by step frequency, $2f$. The mean of the vertical GRF is what the LiMb model uses to estimate the vertical component of force production (see Pontzer, 2005) in predicting the rate of force production as (mean force per step×step frequency). Dividing the rate of vertical force production by step frequency gives:

$$\text{GRF} = gU[4fL\sin(\phi/2)]^{-1} . \qquad (4)$$

Vertical GRF estimates generated by the model were compared to those measured *via* the force plate to test the accuracy of the LiMb model in predicting ground forces. To assess the validity of predicted horizontal and leg swing forces, LiMb model predictions were compared to reported values
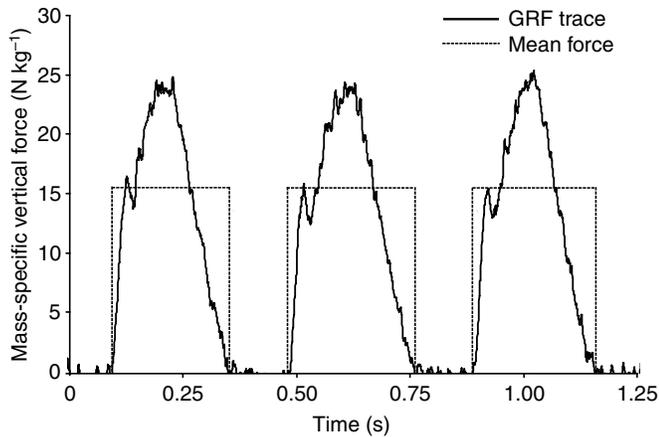
Fig. 1. Representative vertical GRF traces for three steps of a human running trial at 2.5 m s^{-1}. Solid line: raw vertical GRF trace. Note the noise imposed by the treadmill. Dotted line: mean vertical force of the GRF.

from studies designed to isolate these forces (Chang and Kram, 1999; Gottschall and Kram, 2003; Marsh et al., 2004; Doke et al., 2005; Modica and Kram, 2005; Gottschall and Kram, 2005).

Predictions of the LiMb model, as well as t_c^{-1}, Froude number (Alexander and Jayes, 1983) and other predictors of cost, were plotted against observed COL and COT, and least squares regression (LSR) was used to assess the explanatory power of each predictor. The percentage of the variation in observed cost explained by each predictor (i.e. the r^2 value of the LSR) was then used to compare their relative performance.

Results

Kinematic and energetic data

As expected, the rate of oxygen consumption increased with speed for all subjects (Fig. 2A), consistent with previous studies (Taylor et al., 1982). In humans, excursion angle increased with speed during walking and running, but was markedly greater during walking (Fig. 2B). In contrast, excursion angle changed little with speed in goats and dogs, and the difference between gaits was much smaller (Fig. 2B). Stride frequencies for goats and dogs were approximately twice those of humans (Fig. 2C), reflecting the longer limb length of humans.

Estimated mean muscle force per step, calculated by dividing Eqn 1 and Eqn 2 by step frequency, $2f$, increased with speed for all species (Fig. 2D). This was expected, since the mean magnitude of the GRF (see Fig. 1), the primary predictor of muscle force per step *via* the model (see Pontzer, 2005), has been shown to increase with speed in numerous studies. This increase in estimated muscle force with speed is also consistent with a recent study showing a regular increase in active muscle volume with speed in humans (Biewener et al., 2004). Multiplying this estimated force-per-step by step-frequency gives the rate of force production as estimated by the LiMb

model. This estimated rate of force production reliably predicts the rate of oxygen consumption within and between individuals, species and gaits (Fig. 2E), as discussed in greater detail below.

Predicting COL and COT

The LiMb model explained a significant portion of the variance in observed COL and COT both within- and between-species. In humans, the model explained over 90% of the variance in COL$_{walk}$ (r^2=0.92, N=40 trials, P<0.001) and over 70% of the variance in COL$_{run}$ (r^2=0.75, N=38 trials, P<0.001) (Fig. 3). Comparisons of LSR equations indicated that k, the cost coefficient relating oxygen to force (ml O$_2$ N^{-1}), measured as the slope of the LSR, was similar for walking and running. Both the slope (0.0038) and intercept (0.0256) of the LSR for walking were within the 95% confidence interval of the slope (0.0037, CI: 0.0029–0.0044) and intercept (–0.0015, CI: –0.0610–+0.0641) for running. Combining running and walking trials, the LiMb model accounted for over 90% of the variance in COL (r^2=0.92, N=78 trials, P<0.001) (Fig. 3). The fit of the model for running (r^2=0.75) was better than reported in the first test of the LiMb model (r^2=0.43) (Pontzer, 2005), possibly due to decreased between-subjects differences in k, or to the wider ranges of speeds used in the present study. Otherwise, the fit of the LiMb model for walking, running and combined trials was similar to the previous test of the model in humans (Pontzer, 2005).

The small sample size for goats combined with variability in k affected the power of the model for predicting COL$_{run}$ in that species. While the LiMb model accounted for over 70% of the variance in COL$_{walk}$ (r^2=0.74, N=12 trials, P<0.001), it predicted only 20% of the variance in COL$_{run}$ (r^2=0.20, N=38, P=0.047). However, this was likely due to between-subjects differences in k, the economy with which oxygen is converted into muscle force. While the fit of the model for each goat was excellent (mean r^2=0.90, range 0.80–0.97, 6+ speeds per subject, see Fig. 2E), there was marked variation in k (mean k=0.0036, range 0.0028–0.0041). Such variation has been noted before in humans (Weyand et al., 2001; Pontzer, 2005). Correcting for individual differences in k following Pontzer (Pontzer, 2005), the fit of the model for COL$_{run}$ (r^2=0.55, N=15, P<0.001) was more similar to that for COL$_{walk}$ (r^2=0.84, N=12, P<0.001). The number of walking trials for dogs (N=3 speeds, 1 subject) was insufficient to compare the fit of COL$_{walk}$ and COL$_{run}$ for that species.

Walking and running trials were pooled within each species in order to assess between-species differences in model performance. As in the combined (walking + running) human data, the LiMb model accounted for over 75% of the variance in COL for goats (r^2=0.76, N=27 trials, P<0.001) and over 95% of the variance in COL for dogs (r^2=0.96, N=18 trials, P<0.001). In addition, k, measured as the slope of the LSR for combined walking and running trials, was similar for goats (k=0.0036, CI: 0.0028–0.0044), dogs (k=0.0035, CI: 0.0031–0.0038) and humans (k=0.0033, CI: 0.0031–0.0035). To determine the fit of the model across species, data from a
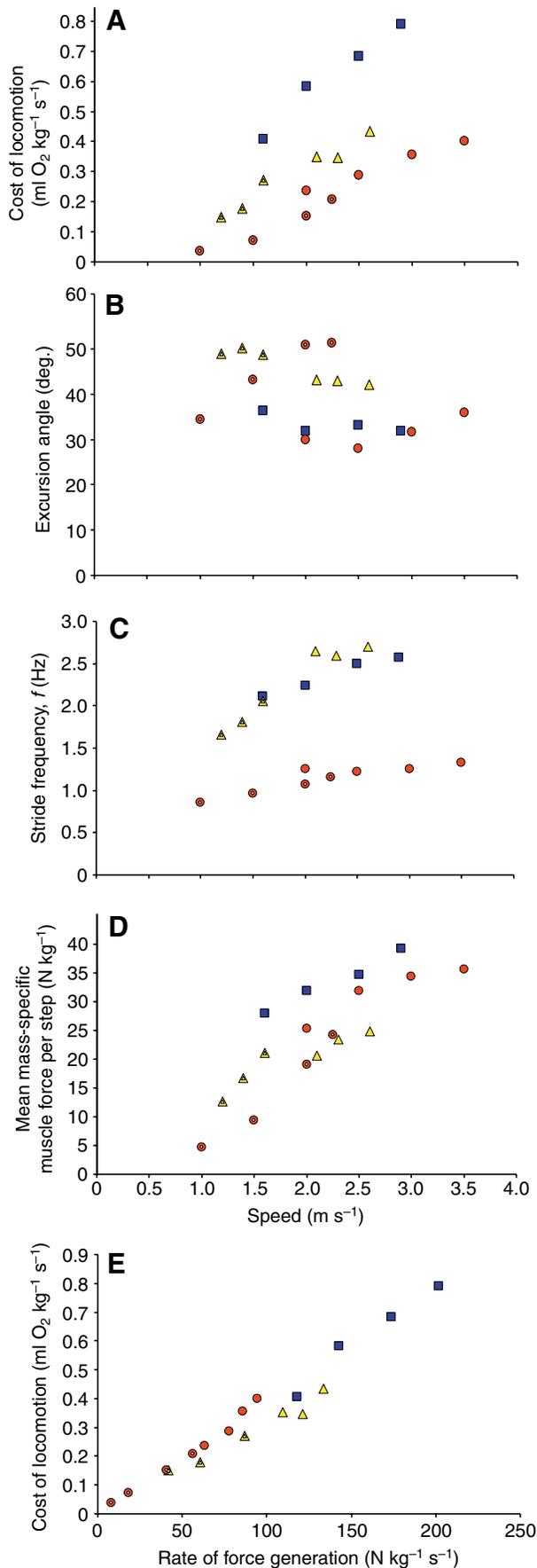
Fig. 2. Kinematic, energetics and estimated force data for three subjects: one human (M_b=69.0 kg, hindlimb L=95cm, red circles), one goat (M_b=23, L=43.5, yellow triangles), and one dog (M_b=26.3, L=39, blue squares). Each point represents one subject at one speed. Open-centered points indicate walking trials, while filled points represent running trials. (A) The rate of oxygen consumption (i.e. COL), (B) excursion angle ϕ, (C) stride frequency f and (D) mean muscle force generated per step, as estimated by the LiMb model, *versus* speed. (E) The rate of muscle force generation, predicted by the LiMb model, *versus* the observed rate of oxygen consumption. The estimated rate of force production is a product of mean muscle force per step (D) and step frequency (2f; C).

representative subset of four humans (L=76, 85, 95 and 108.5 cm) was combined with the dog and goat data. The LiMb model predicted 90% of the variance in COL for this interspecific dataset (r^2=0.90, N=76 trials, P<0.001), while k was similar to that within-species (k=0.0035, CI: 0.0033–0.0038) (Fig. 4).

The LiMb model consistently outperformed other predictors of cost, including contact time, Froude number and body mass (Fig. 5), both within- and between-species. For example, the LiMb model predicted 96%, 76% and 92% of the variance in COL in dogs, goats and humans, respectively, while t_c^{-1} accounted for 88%, 47% and 79% (Fig. 5A). For the combined-species dataset, the LiMb model accounted for 89% of COL, while t_c^{-1} and Froude number accounted for 75% and 77%, respectively. By comparison, UL^{-1}, a limb length-corrected speed, performed as well or better than contact time or Froude number, predicting 84% of the variance in COL interspecifically (Fig. 5A). Performance differences were greater for COT (energy/distance). The LiMb model-predicted COT, calculated by dividing Eqn 1 or Eqn 2 by U, accounted for 85%, 29% and 59% of the variance in COT within dogs, goats and humans, respectively, and 86% of the variance in COT for the combined-species dataset (Fig. 5B). In contrast, while COT predicted *via* contact time ($t_c^{-1}U^{-1}$) predicted 82% of the variance in COT for dogs, it accounted for only 4% of the variance in goats and humans, and 67% of the variance in the combined dataset. Here again, the inverse of limb length, L^{-1}, performed as well or better as a predictor. L^{-1} also consistently outperformed body mass, commonly used to predict or account for differences in COT allometrically (Fig. 5B).

Predicting GRF and leg-swing forces

Comparing predicted and observed vertical GRF highlighted the potential effect of foot length on force production. While predicted mean vertical force per step was strongly correlated with observed mean vertical GRF (r^2=0.67, N=36 trials, P<0.001), the slope of the LSR (slope=0.71, intercept set at 0) differed markedly from unity. This difference was likely due to the effect of foot length. The LiMb model treats the leg as a strut with length L that has a constant point of foot–ground contact during stance phase. However, humans strike the ground with the heel but leave the ground from the toe, and this
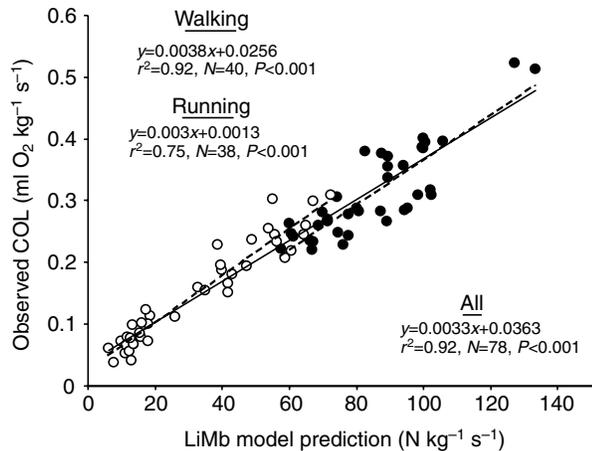
Fig. 3. LiMb model-predicted rate of force production (N kg^{-1} s^{-1}) *versus* observed COL$_{walk}$ (open circles) and COL$_{run}$ (ml O$_2$ kg^{-1} s^{-1}) (filled circles) for humans (N=10 subjects). This pattern is similar to that reported previously for a different group of humans (Pontzer, 2005). Broken lines indicate LSR for COL$_{walk}$ and COL$_{run}$, solid line indicates LSR for all trials. LSR equations and coefficients of determination are given in the figure.

Fig. 4. LiMb model-predicted rate of force production (N kg^{-1} s^{-1}) *versus* observed COL (ml O$_2$ kg^{-1} s^{-1}) for 4 humans (red circles), 4 goats (yellow triangles) and 4 dogs (blue squares). Walking and running trials are combined; symbols with open centers indicate walking trials. Broken line indicates LSR for all data (y=0.0035x+0.0433, r^2=0.90, N=76 trials, P<0.001).

forward shift of the point of foot–ground contact effectively increases the length of the limb (Fig. 6A). This increase in effective length was calculated trigonometrically from foot length and excursion angle, and then added to the length of the hindlimb (greater trochanter–heel) at heelstrike to give effective hindlimb length, L' (Fig. 6A). As expected, when using L' to estimate vertical GRF *via* Eqn 4, the fit of the predicted–observed relationship improved (r^2=0.79, N=36 trials, P<0.001), and the slope of the LSR was 1.00 (intercept set at 0) (Fig. 6B).

Predicted contributions of vertical and horizontal forces and leg-swing force to COL were similar to those measured empirically elsewhere. For all species, both walking and running (or trotting), vertical forces constituted the majority of predicted force production, accounting for 57–61% during walking and 60–67% in running (Fig. 7), in line with previous studies suggesting that supporting body weight accounts for the majority of COL (Taylor et al., 1980; Kram and Taylor, 1990; Kram, 1991; Griffin et al., 2003). Leg-swing forces accounted for 19% of predicted COL for humans during walking, and 23% during running. This compares well with estimates of 10–30% for walking and 20–26% of running cost from studies measuring the metabolic cost of leg swing in humans [walking (Doke et al., 2005; Gottschall and Kram, 2005), running (Modica and Kram, 2005)] and guinea fowl (Marsh et al., 2004). It must be noted, however, that in walking, predicted leg-swing costs were dependent upon speed; the value of 19% here is for speeds (1.5 m s^{-1}) near the subjects' preferred speed, but this increases to 33% at speeds near the walk–run transition (2.0–2.5 m s^{-1}), where stride frequencies greatly exceed the estimated natural frequency of the leg. For quadrupeds, estimated leg-swing costs were lower, accounting for
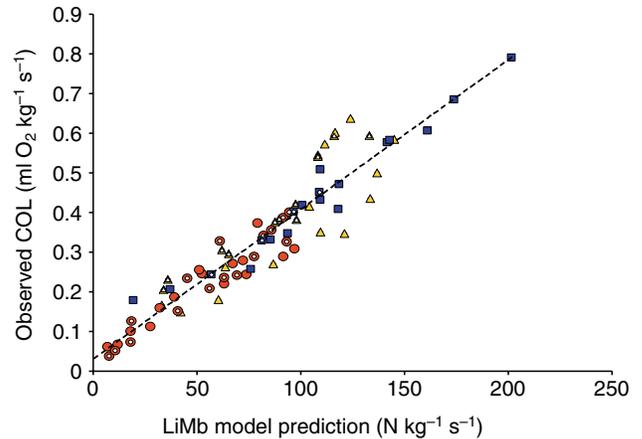
approximately 15% of COL during walking and 10% during running (Fig. 7). Unfortunately, no direct measures of leg-swing cost comparable to those in humans and guinea fowl are available for quadrupeds. Finally, horizontal forces accounted for roughly 20–25% of total predicted force production for all species both walking and running (Fig. 7). These estimates appear to be in line with previous GRF studies (Winter, 1990; Breit and Whalen, 1997; Lee et al., 2004), and are similar to those reported for human running (~40%) (Chang and Kram, 1999) but less than those reported for human walking (~50%) (Gottschall and Kram, 2003).

Discussion
Energetics and kinematics: what determines cost?

The LiMb model reliably predicted COL and COT for quadrupeds and bipeds during both walking and running gaits over a range of speeds and body sizes. Moreover, the LiMb model consistently outperformed other predictors of cost including contact time (Fig. 5). The agreement between the estimated rate of force production and the observed rate of energy expenditure over a range of species, gaits and speeds lends further support to the Force Production Hypothesis (Kram and Taylor, 1990; Taylor, 1994). Further, the performance of the LiMb model relative to contact time supports recent work (Chang and Kram, 1999; Gottschall and Kram, 2003; Marsh et al., 2004; Doke et al., 2005; Modica and Kram, 2005; Gottschall and Kram, 2005), suggesting that horizontal and leg-swing forces are important components of locomotor cost.

While the LiMb model was developed in the context of 'pendular' walking mechanics and 'mass-spring' running mechanics (Pontzer, 2005), it is not inconsistent with recent work suggesting collisional mechanics dictate locomotor
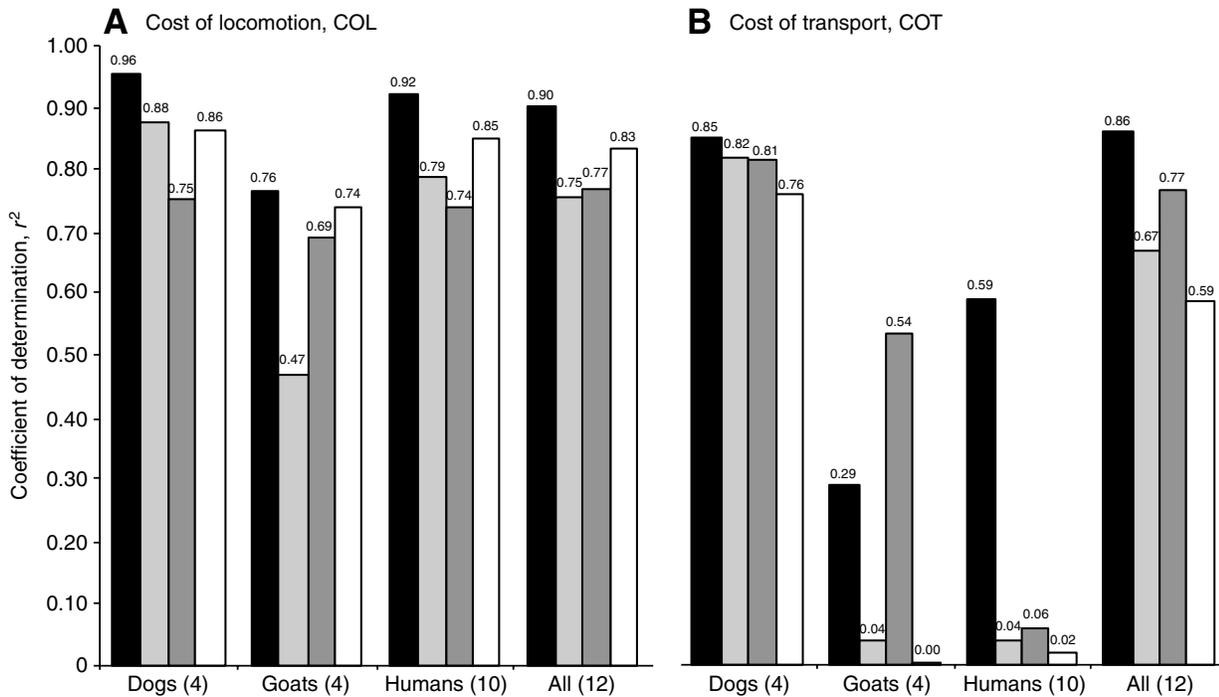
Fig. 5. The performance of the LiMb model compared to other predictors of locomotor cost. (A) r^2 values (coefficients of determination) for the LiMb model (black bars), contact time (t_c^{-1}) (light grey bars), Froude number ($U^2L^{-1}g^{-1}$) (dark grey bars) and hindlimb length (UL^{-1}) (white bars), calculated *via* LSR with observed COL (ml O_2 kg^{-1} s^{-1}). r^2 values are given above each bar. Numbers in parentheses indicate sample size (number of subjects). Interspecific comparison ('All') is calculated for dogs ($N=4$), goats ($N=4$) and a subset of humans ($N=4$), as shown in Fig. 4. (B) r^2 values for the LiMb model (black bars) contact time ($t_c^{-1}U^{-1}$) (light grey bars), hindlimb length (L^{-1}) (dark grey bars) and body mass (white bars), calculated *via* LSR with observed COT (ml O_2 kg^{-1} m^{-1}).

kinematics (Bertram et al., 1999; Donelan et al., 2002; Collins et al., 2005; Ruina et al., 2005). For example, while fast locomotion in gibbons approximates collision-free ricochetal brachiation (Bertram et al., 1999), even optimal trajectories with no collisional losses require muscle-generated centripetal forces while the animal swings in an upward arc beneath its support. Similarly, whether limbs behave elastically or pseudo-elastically during running (Ruina et al., 2005), muscle force is necessary to prevent the limb from collapsing entirely. Whatever energy-saving mechanical paradigm prevails (pendular, mass-spring or collisional), substantial muscle forces are required for the limb to act as an effective strut while supporting body weight. For real-world animals with collapsible limbs, terrestrial locomotion can be cheap, but never free.

The LiMb model calculates the rate of force production as (mean force per step)×(step frequency) (see Figs 1, 2). This approach is consistent with physiological studies suggesting the volume of muscle activated per step, rather than the rate of cross-bridge cycling, determines locomotor cost. For example, differences in the muscle volume activated to produce a given ground force predict differences in energy use between bipeds and quadrupeds (Roberts et al., 1998b) and between walking and running in humans (Biewener et al., 2004). Further, studies of leg swing in humans (Doke et al., 2005; Kuo, 2001) suggest the volume of muscle activated per step cycle determines

energy consumption, a hypothesis initially proposed by Biewener (Biewener, 1989; Biewener, 1990). Indeed, the effectiveness of the LiMb model in predicting cost for a range of speeds in animals from 5.6–94.8 kg suggests the volume of muscle activated per step and step frequency are sufficient for predicting changes in COL with speed, gait and body size. Thus, while faster speeds and shorter contact times may require faster, more energetically expensive muscle fibers (Kram and Taylor, 1990; Taylor et al., 1994; Ellerby et al., 2005), this mechanism might not be necessary to explain the increase in COL with speed or with decreased body size. Instead, the volume of muscle activated per step and step frequency may explain most of the variation in cost.

This view may be more consistent with the scaling of locomotor cost with body size. Across a large range of body size, COT has been shown to scale as $M_b^{-0.32}$ (Taylor et al., 1982). In contrast, the rate of cross-bridge cycling in locomotor muscles of terrestrial animals, measured indirectly as maximum shortening velocity *in vitro*, has been shown to scale as $M_b^{-0.12}$ (Rome et al., 1990; Medler, 2002). However, the rate of force production as predicted by the LiMb model (mean force per step×step frequency) is expected to scale as L^{-1}, because over a large range of body size variation in limb length will outpace changes in k, ϕ or C_{limb} (Eqn 1) (see Pontzer, 2005). Since limb length scales isometrically (Alexander et al.,
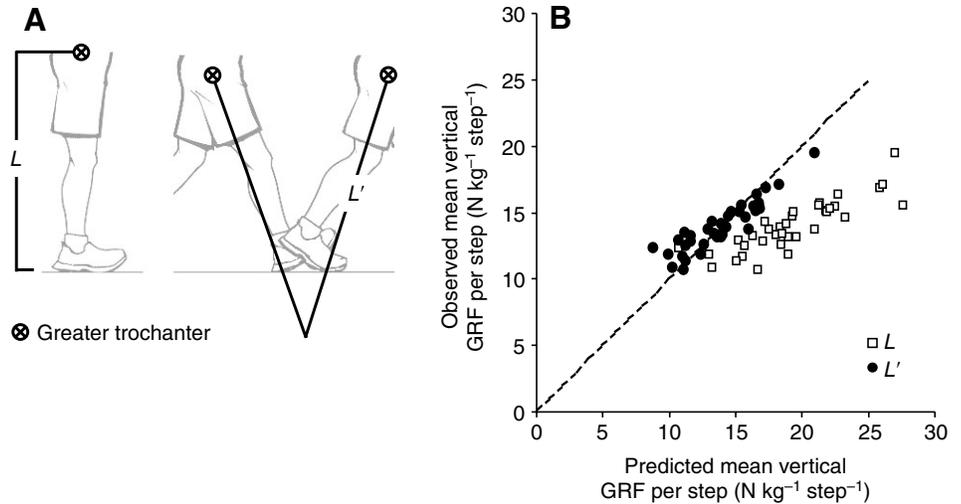
Fig. 6. Predicted *versus* observed mean vertical GRF. (A) Because the point of foot–ground contact shifts forward between heel-strike and toe-off, standing hip height, *L*, underestimates the effective length of the hindlimb, *L'*. (Adapted from Gottschall and Kram, 2005.) (B) Using *L* to predict vertical GRF *via* the LiMb model consistently overestimates vertical GRF (open squares), while *L'* provides a reasonably good fit (closed circles). Broken line indicates *y*=*x*.

1979), the LiMb model thus predicts COT to scale as $M_b^{-0.33}$, which is similar to the scaling relationship reported in Taylor et al. (Taylor et al., 1982).

If the mean force per step and step frequency do dictate cost, this may suggest that muscle activation costs play a large role in determining locomotor cost. Indeed, activation costs are substantial during short isometric contractions, typically much larger than the metabolic cost of maintaining tension after activation (Bergstrom and Hultmann, 1988; Hogan et al., 1998; Russ et al., 2001; Verburg et al., 2001). Since terrestrial locomotion is characterized by such short-duration contractions, activation costs might largely dictate locomotor cost. If so, this suggests that the well-characterized differences in metabolic cost associated with cross-bridge cycling frequency in different muscle types (Crow and Kushmerick, 1982) play a lesser role in determining cost. Instead, the volume of muscle activated per step and activation frequency (i.e. step frequency) may largely determine locomotor cost. Further work, focusing on changes in the rate of cross-bridge cycling and activation costs within muscle *in vivo* across a range of species and speeds, may clarify the relative importance of cross-bridge cycling frequency and active muscle volume in dictating locomotor cost.

Predicting GRF and leg-swing forces

While the LiMb model reliably predicted mean vertical GRF, the marked effect of foot length on GRF was unexpected. Foot length increases the effective length of the hindlimb, and therefore should lower locomotor costs by decreasing the magnitude of vertical GRF for plantigrade species. In this study, this effect of foot length may explain why the cost coefficient, *k*, for humans was similar to *k* for goats and dogs, when previous studies (Roberts et al., 1998a; Roberts et al., 1998b) have reported higher values for *k* in bipeds (including humans) *versus* quadrupeds. The use of hip height for *L* will consistently underestimate effective hindlimb length in humans and other plantigrade species, resulting in higher estimates of force production (Fig. 6) and therefore in lower estimates of *k*.

Vertical and horizontal forces accounted for the majority of estimated COL, but leg-swing costs were also considerable, especially in humans (Fig. 7). Thus, while vertical forces may be useful for predicting large-scale patterns of locomotor cost
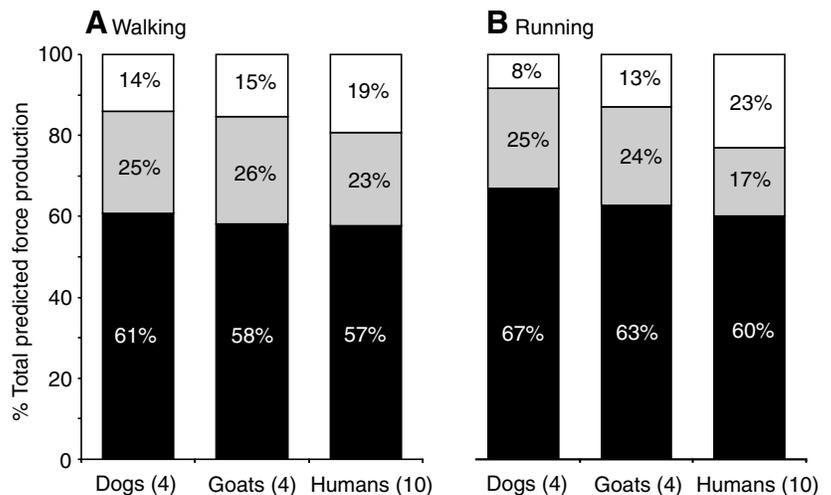

Fig. 7. The relative contributions of vertical (black), horizontal (gray), and leg-swing (white) forces to total force production predicted by the LiMb model for (A) walking and (B) running. Sample sizes (subjects) are given in parentheses. For humans, walking values are for speeds near subjects' preferred speed (1.5 m s⁻¹).

(e.g. Kram and Taylor, 1990), incorporating leg-swing costs may be critical for more in-depth comparisons of locomotor energetics. Because locomotor anatomy and kinematics differ markedly between humans and avian bipeds (Gatesy and Biewener, 1991), the high predicted cost of leg swing seen here for humans may not be representative of all bipeds. However, if bipeds do have consistently higher leg-swing costs than quadrupeds as suggested here, this will affect comparisons of quadrupedal and bipedal energetics. For example, although it has been reported that bipeds are relatively uneconomical in producing ground forces during locomotion (Roberts et al., 1998a; Roberts et al., 1998b), this may be due in part to greater leg swing costs in bipeds. If leg swing accounts for a substantial portion of COL, then dividing oxygen consumption by contact time (a measure of vertical ground force) to determine the cost coefficient (ml O_2 N^{-1}), as is often done (Kram and Taylor, 1990; Roberts et al., 1998a; Roberts et al., 1998b; Biewener et al., 2004), will produce higher estimates of k than if horizontal and leg-swing forces are included.

The agreement between predicted and observed vertical GRF validates the LiMb model approach for estimating vertical forces. Similarly, a recent study investigating the cost of leg swing in humans (Doke et al., 2005) found that the force required, and energy expended, to swing the limb could be predicted accurately by treating the limb as a driven pendulum. This supports the similar approach to model leg-swing forces used by the LiMb model. Finally, while LiMb model predictions for horizontal forces appear reasonable given the relative magnitude of vertical and horizontal GRF (Winter, 1990; Breit and Whalen, 1997; Lee et al., 2004), these estimates are less than those reported for human walking and running (Chang and Kram, 1999; Gottschall and Kram, 2003). Further work comparing horizontal GRF to those estimated by the LiMb model may determine whether the LiMb model must be modified to account for larger horizontal forces.

Predicting COL and COT

In this study, the LiMb model was the most effective predictor of COL and COT both within and between species (Fig. 5). Since the LiMb model predicts the COL *via* (mean force per step×step frequency), it would be interesting to test the model during galloping, in which step frequencies change little with increasing speed (Heglund and Taylor, 1988). If the LiMb model is valid, and if the economy of generating ground force does not change substantially with speed in galloping animals, then mean ground force per step (Fig. 1) ought to increase with speed in these quadrupeds, such that the increase in (mean force per step×step frequency) corresponds with any increase any COL. Similarly, the independence of COL and speed in hopping wallabies (Baudinette et al., 1992) suggests ground forces and hopping frequency might be moderated to maintain a constant rate of force production, and thus a constant rate of oxygen consumption. Alternatively, the economy of generating ground force may increase with speed for these animals, resulting in a constant COL even as the rate of force production increases with speed.

Not surprisingly, all models were more effective in predicting COL than COT (Fig. 5). Speed is a covariate of COL and its predictors, which improves the correlation between predicted and observed cost; there is no equivalent shared component for predicted and observed COT. As with other predictors of cost, the utility of the LiMb model was dependent upon the scale of comparison. All predictors performed well over a large range of body size (e.g. dogs, combined-species sample), but were less effective when body size and limb length were similar (e.g. goats, humans). In particular, when variation in body size or proportion is low, as in the goat sample, individual differences in k, the economy of ground force generation, may affect model performance significantly. Methods for estimating k *a priori* (e.g. Roberts et al., 1998b; Biewener et al., 2004) may therefore improve model performance.

When direct measurements of locomotor cost are not feasible, such as in large-scale comparisons of locomotor morphology or ecological studies measuring ranging costs in the field, the availability of anatomical and kinematic variables will dictate the method used to estimate COL and COT. If the kinematic data required by the LiMb model are not available, L can be used to estimate COL (COL=$0.09685UL^{-1}$–0.0135, r^2=0.84, LSR; Fig. 3A) and COT (COT=$0.09063L^{-1}$+0.0003, r^2=0.78, LSR; Fig. 5B). These estimates were typically more effective than contact time in predicting cost in this dataset (Fig. 5), and may be easier to calculate in the field. Body mass should be used only when other predictors are unavailable, since mass is a relatively poor predictor (Fig. 5).

The results of this study support the hypothesis that limb length drives the scaling of locomotor cost for legged, terrestrial animals (Kram and Taylor, 1990; Pontzer, 2005). This link between anatomy and performance may aid investigations of form–function relationships in living and extinct taxa. Moreover, by placing limb length in the context of other determinants of locomotor cost, the LiMb model may provide a useful tool for comparing locomotor morphology and performance in terrestrial animals.

List of symbols and abbreviations

C_{limb}	metabolic cost of swinging limb
CI	confidence interval
COL	mass-specific cost of locomotion (ml O_2 kg^{-1} s^{-1})
COL_{run}	COL during running or trotting
COL_{walk}	COL during walking
COT	mass-specific cost of transport (mlO_2 kg^{-1} m^{-1})
D	radius of gyration of the limb (m)
f	stride frequency (Hz)
g	gravitational acceleration (9.8 m s^{-2})
GRF	ground reaction force (N)
k	cost coefficient (ml O_2 N^{-1})
L	limb length (cm)
L'	effective limb length, accounting for foot length (cm)
LSR	least squares minimum
M_b	body mass (kg)

M_L	limb mass/body mass
T	stride period (s)
T_0	estimated natural period of the limb (s)
t_c	contact time (s), i.e. stance duration
U	speed of travel (m s^{-1})
ϕ	excursion angle

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