

The mass-specific energy cost of human walking is set by stature

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SUMMARY

The metabolic and mechanical requirements of walking are considered to be of fundamental importance to the health, physiological function and even the evolution of modern humans. Although walking energy expenditure and gait mechanics are clearly linked, a direct quantitative relationship has not emerged in more than a century of formal investigation. Here, on the basis of previous observations that children and smaller adult walkers expend more energy on a per kilogram basis than larger ones do, and the theory of dynamic similarity, we hypothesized that body length (or stature, L_b) explains the apparent body-size dependency of human walking economy. We measured metabolic rates and gait mechanics at six speeds from 0.4 to 1.9 m s⁻¹ in 48 human subjects who varied by a factor of 1.5 in stature and approximately six in both age and body mass. In accordance with theoretical expectation, we found the most economical walking speeds measured (J kg⁻¹ m⁻¹) to be dynamically equivalent (i.e. similar U , where $U = \text{velocity}^2 / \text{gravity} \cdot \text{leg length}$) among smaller and larger individuals. At these speeds, stride lengths were directly proportional to stature whereas the metabolic cost per stride was largely invariant (2.74 ± 0.12 J kg⁻¹ stride⁻¹). The tight coupling of stature, gait mechanics and metabolic energy expenditure resulted in an inverse relationship between mass-specific transport costs and stature ($E_{\text{trans}}/M_b \propto L_b^{-0.95}$, J kg⁻¹ m⁻¹). We conclude that humans spanning a broad range of ages, statures and masses incur the same mass-specific metabolic cost to walk a horizontal distance equal to their stature.

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INTRODUCTION

The metabolic and mechanical requirements of human walking influence a broad array of structural, functional and health relationships. This global functional importance has stimulated a body of scientific literature that now spans more than a century and encompasses a variety of experimental objectives. These range from basic biological inquiry to applied efforts to predict speed, energy expenditure and other variables in laboratory and field settings. However, in spite of the extensive scientific consideration that human walking has received, some aspects of basic understanding remain limited.

A primary example of incomplete contemporary understanding is the body size dependency long observed for the metabolic requirements of this gait. As would be expected, larger individuals do expend more energy than smaller ones when the metabolic energy expended is expressed in absolute terms. However, the differences observed are not directly proportional to body mass. When expressed on a per kilogram basis, the energy expended to walk a fixed distance or at a given speed can be as much as two to three times greater for smaller *versus* larger individuals. At present, a quantitative explanation for the relationship between body size and the energy cost of human walking has not been established.

The greater mass-specific metabolic rates consistently observed for smaller *versus* larger human walkers have been considered from several perspectives. Ontogenetic approaches have appropriately considered both maturation (DeJaeger et al., 2001; Morgan et al., 2002) and body size (McCann and Adams, 2002) but have not resolved their quantitative importance. Mechanical approaches have estimated that the mass-specific mechanical work that small children

and adults perform during walking differs only marginally (Cavagna et al., 1983; Bastien et al., 2003; Schepens et al., 2004) and therefore does not account (Schepens et al., 2004) for the much larger differences observed in metabolic cost. The current lack of quantitative understanding is reflected in the use of different generalized equations to estimate the energy expended by adult (ACSM, 2006; Pandolf et al., 1971) and child populations (Morgan et al., 2002). In both cases, population-specific equations predict the same mass-specific metabolic rates for individuals who differ in height and mass.

A potential explanation for the apparent body-size dependency of the metabolic cost of human walking is a corresponding rate dependency in executing the mechanics of each walking stride (Alexander, 1976; Heglund and Taylor, 1988). Clearly, the shorter statures of smaller *versus* larger walkers require more, and more frequent, strides in order to travel any fixed distance or at any given speed. If the mechanical components of each walking stride were to require the same expenditure of metabolic energy per kilogram of body mass, shorter walkers might have greater mass-specific metabolic rates simply because they take more frequent strides. This possibility seems most plausible if shorter and taller individuals were to walk in dynamically similar ways, i.e. with both stride lengths and times related to the body's length (L_b) by some constant proportion. Although widely embraced (DeJaeger et al., 2001; McCann and Adams, 2002; Cavagna et al., 1983), the validity of the dynamic similarity assumption is not strictly known. Thus, the simple possibility that the energy cost per stride at equivalent speeds may be the same for short and tall individuals has not been evaluated.

Here, we tested the idea that the mass-specific energy cost of human walking is determined by stature. Our expectations of approximate geometric similarity in bodily proportions and dynamic similarity in gait among shorter and taller individuals led us to evaluate this idea in two ways. First, we hypothesized that the mass-specific metabolic energy expended per stride would not vary between short and tall individuals. Second, we hypothesized that mass-specific energy expended per unit distance walked would be inversely related to stature ($\propto L_b^{-1.0}$). Both hypotheses were tested at equivalent walking speeds.

MATERIALS AND METHODS

Experimental design

We employed several design strategies to maximize the rigor of the two tests of our stature hypothesis. First, we recruited subjects who spanned relatively broad ranges of age, stature and body mass. Second, we divided the 48 recruited subjects into four discrete groups on the basis of stature to minimize the influence of individual variability in walking economy that is not related to stature on our analyses. Third, we considerably increased the robustness of our scaling analysis by using the published literature to expand the number of stature groups included from our original four groups to a total of 29. Fourth, we took considerable care to address two issues that could potentially confound both hypothesis tests: (1) making metabolic comparisons only at those walking speeds that are equivalent for subjects of different statures and (2) correctly partitioning basal *versus* walking metabolism.

Equivalent walking speeds

Because walking transport costs vary with speed and do so in a stature-dependent fashion (DeJaeger et al., 2001; McCann and Adams, 2002), identifying equivalently economical speeds for individuals of different body sizes was a crucial prerequisite for valid analysis. Intuition and previous results (DeJaeger et al., 2001; McCann and Adams, 2002; Alexander, 1976) both indicated that any given absolute speed would be relatively slower for shorter individuals and relatively faster for taller ones. Accordingly, the speeds of our subjects were not likely to be either equivalent (Alexander, 1976) or equivalently economical (Heglund and Taylor, 1988) at any given absolute speed. We adopted an empirical solution to this challenge, identifying equivalent speeds for shorter and taller individuals as that speed at which a minimum transport cost ($E_{\text{trans-min}}$, $\text{J kg}^{-1} \text{m}^{-1}$) was measured for each. These empirically determined minimums were subsequently used to compare the energy cost per walking stride and to identify the exponential relationship of best fit between metabolic transport costs and stature.

Given the crucial importance of making stature-based comparisons at walking speeds that are equivalent, and equivalently economical, for smaller and larger individuals, we adopted two *post hoc* criteria to evaluate whether the most economical walking speeds were mechanically equivalent: the duty factor, or ratio of foot ground-contact time to total stride time (t_c/t_{str}), and the Froude number derived from the principle of dynamic similarity [i.e. similar U , where $U=V^2/(gL_{\text{leg}})$, V is speed, g is gravity and L_{leg} is leg length]. In the event that the most economical speeds measured for the different stature groups were not equivalent, these two well-established mechanical indices would quantify the lack of equivalence present. Alternatively, the expected equivalence would result in the most economical speeds observed increasing as a predictable function of body length (speed at $E_{\text{trans-min}} \propto L_b^{0.50}$) but occurring at the same duty factor and Froude number in all four stature groups.

Basal *versus* walking metabolism

Correctly quantifying the metabolic energy incurred by walking necessitated subtracting out that portion of the body's total metabolic rate not devoted to walking, i.e. basal metabolism. Although some investigators have subtracted the metabolic rate measured during quiet standing for this purpose, we subtracted basal rather than standing metabolic rates. We did so because standing rates include muscular support costs (Joseph and Nightingale, 1952; Loram et al., 2007; Weyand et al., 2009) that are also incurred during walking (Biewener et al., 2004; DeJaeger et al., 2001; Grabowski et al., 2005; Griffin et al., 2003; McCann and Adams, 2002; Weyand et al., 2009). The basal rates subtracted from both our original data and qualifying literature data were calculated from the age, gender, mass and stature of each subject using the generalized equations of Schofield et al. (Schofield et al., 1985) (hereafter 'Schofield equations'). Using estimates rather than direct measures was necessary in order to: (1) include the 25 qualifying group means from the literature in our scaling analysis and (2) treat both original and literature data points in the same quantitative manner. Directly measuring the basal metabolic rates of the subjects in the qualifying literature populations was clearly not possible. Accordingly, to also evaluate the predictive accuracy of the Schofield equation estimates, we measured post-absorptive resting metabolic rates in six adult subjects (three male and three female) who were available for testing.

The error introduced into our analyses of group data as a result of necessarily using estimated rather than measured basal metabolic rates was considered using both original measures and previously reported results. The Schofield age, height, mass and gender equations have been extensively validated and are the most extensively used equations for this purpose. The error that results from using these equations to predict the mean basal metabolic rates of either children or adult groups was established in the original work as ± 2.2 – 3.4% for groups of 10 subjects (Schofield et al., 1985). Similar accuracy for predicting group means has been subsequently reported by a number of other investigators (De Lorenzo et al., 2001; Piers et al., 1997; Johnstone et al., 2006; Rodriguez et al., 2000; van der Ploeg et al., 2001).

Subjects

Forty-eight healthy individuals, 24 males and 24 females, between the ages of five and 32 years of age were included in the study. The 32 subjects who were 18 years of age or younger were tested at the Children's Nutrition Research Center of the Baylor College of Medicine and the 16 subjects who were over the age of 18 were tested at the Locomotion Laboratory of Rice University. Written informed assent and consent was obtained in accordance with the Institutional Review Boards of the Baylor College of Medicine and Rice University. For the purpose of analysis and without regard to age, subjects were divided into four groups on the basis of stature (A, B, C and D). The age, gender, body mass (M_b), stature (L_b) and leg length (L_{leg}) means of the four stature groups appear in Table 1.

Treadmill testing protocol

Walking trials were administered on a level treadmill at constant speeds of 0.4, 0.7, 1.0, 1.3, 1.6 and 1.9 m s^{-1} . The protocol began at 0.7 m s^{-1} and was administered continuously in a staggered speed fashion until all the speeds at which the subjects could maintain a walking gait were completed. After a first completion of the protocol, subjects were allowed a 5- to 10-min break before repeating each walking speed a second time. The initial trial of each

Table 1. Physical and descriptive characteristics of the four stature groups

Group	N (male, female)	Age (years)	M _b (kg)	L _b (m)	L _{leg} (m)
A	7 (2,5)	5.4±0.3 ^{†,‡}	21.3±2.7 ^{*,†,‡}	1.14±0.02 ^{*,†,‡}	0.58±0.02 ^{*,†,‡}
B	10 (5,5)	10.5±0.6 ^{†,‡}	44.1±4.0 ^{†,‡}	1.42±0.02 ^{†,‡}	0.77±0.02 ^{†,‡}
C	18 (9,9)	17.2±1.3 [‡]	56.6±2.3 [‡]	1.62±0.01 [‡]	0.86±0.01 [‡]
D	13 (8,5)	22.2±1.5	75.9±2.2	1.77±0.01	0.94±0.01

All values are means ± s.e.m.
M_b, body mass; L_b, stature; L_{leg}, leg length.
*, significantly different from group B; †, significantly different from group C; ‡, significantly different from group D.

protocol lasted 4 to 6 min. Subsequent trials lasted until a minimum 2-min steady-state period with respect to the rate of oxygen uptake was observed in real time. All of the adult subjects tested walked steadily and provided reproducible rates of oxygen uptake at each speed. Four of a total of 36 children tested did not maintain a consistent position on the treadmill and had rates of oxygen uptake that differed by more than 5% across the different trials completed at common speeds. The data from these four children were not included in the analysis.

All subjects were instructed to walk and not run during the testing. The shortest subjects, those in group A, were able to walk at the four speeds through 1.3 ms⁻¹ successfully, but could not attain speeds of 1.6 and 1.9 ms⁻¹ without running. The subjects in group B were able to walk at the five speeds through 1.6 ms⁻¹ successfully, but could not do so at 1.9 ms⁻¹. All but three of the subjects in group C and all the subjects in group D were able to walk at all six speeds, including 1.9 ms⁻¹.

Metabolic measures

Indirect calorimetry was used to determine rates of metabolic energy expenditure from measurements of expired gases during steady-state treadmill walking using a computerized metabolic system (Parvo Medics TrueOne 2400, Sandy, UT, USA) per our previous description (Weyand et al., 2006). Expired gases were directed *via* a one-way breathing valve and corrugated tubing through a pneumotach into a mixing chamber. Aliquots were drawn from the mixing chamber and analyzed for O₂ and CO₂ fractions using paramagnetic and infrared gas analyzers, respectively. Rates of oxygen uptake at each treadmill walking speed were averaged over a 2-min steady-state period to obtain values for each trial. Measures from the two trials completed at each speed were averaged for subsequent analysis. Mean rates of oxygen uptake were divided by body mass and converted to rates of energy expenditure ($\dot{E}_{\text{metab}}$, W kg⁻¹) using an energetic equivalent of 20.1 J ml⁻¹ O₂. The same Parvo Medics TrueOne metabolic system was used in both laboratory locations. The system was calibrated using a three-liter syringe to introduce volume flow rates that spanned the range of ventilation rates present during testing. The O₂ and CO₂ analyzers were calibrated using a two-point calibration procedure using room air and known concentrations in the physiological range for expired gases. Validations of the TrueOne system were performed using precision blended N₂-CO₂ mixtures infused at rates to simulate rates of oxygen uptake ranging from 0.3 to 1.0 l min⁻¹ in accordance with the technique described by Moon et al. (Moon et al., 1995). The agreement between precision-simulated rates of oxygen uptake and those measured by the TrueOne metabolic system across 15 infusion trials spanning the aforementioned range was 2.8±2.0%.

Gross mass-specific metabolic rates (W kg⁻¹) were converted to net mass-specific metabolic rates ($\dot{E}_{\text{metab-net}}$, W kg⁻¹) by subtracting rates of basal metabolism in accordance with the original suggestion

of Schmidt-Nielsen (Schmidt-Nielsen, 1972). The basal rates subtracted for individual subjects were estimated from the generalized Schofield equations using age, height, mass and gender. Resting metabolic rates were also measured in six adult subjects who lay quietly in a supine position for a minimum of 60 min after reporting to the laboratory in a post-absorptive state in the early morning. Resting metabolic rate was determined from the lowest consecutive 10-min mean over the last 30 min of testing. The mean value from this group of six subjects was compared with that predicted by Schofield et al. (Schofield et al., 1985) per our previous description (Weyand et al., 2009) in order to directly assess the predictive accuracy of the Schofield equations on a portion of our original data.

Metabolic or walking transport costs, i.e. the mass-specific metabolic energy expended to walk a unit distance (E_{trans} , J kg⁻¹ m⁻¹) were determined by dividing net mass-specific metabolic rates by the speed of the walking trial. Additionally, walking transport costs were standardized to body length by multiplying net mass-specific transport costs by stature to obtain the net mass-specific metabolic energy expended to travel a distance equal to the height of the body (J kg⁻¹).

Walking kinematics

The durations of each stride and foot ground-contact period were determined from 30 Hz video (Sony model DCR-TRV19, 30 Hz) by counting the frames during slow playback over 25 consecutive contact periods of the same foot. Stride time (t_{str}) was defined as the time elapsing between consecutive foot strikes of the same foot. Stride length (L_{str}) was determined by multiplying stride time by belt speed. Foot ground-contact time (t_c) was determined from the number of frames a single foot was in contact with the treadmill belt. The duty factor was determined by dividing foot ground-contact time by stride time. An index of equivalent speed (U) was determined from walking speed leg length and gravity using the Froude number: $U=V^2/(gL_{\text{leg}})$. Leg lengths were measured by palpating the hip joint axis of rotation during standing and slow swinging of the limb in the sagittal plane. One subject ($L_b=1.77$ m) in group D was not available for leg length measurements after completing the metabolic testing.

The scaling of walking transport costs with body size

Best-fit exponential relationships between the minimum measured metabolic cost of transport ($E_{\text{trans-min}}$) and both stature and body mass were conducted on both our original stature group means and on these original data plus qualifying group means taken from the literature. Literature values were included only from those studies that provided the information necessary to conduct the same analysis as that performed on our original data: stature, body mass and steady-state gross metabolic rates during level walking across a sufficient number of speeds to exhibit a minimum. A data point was considered a valid minimum only when greater values from both faster and

Table 2. Literature values for net transport costs during level walking in humans

Subjects	N	Age (years)	Height (m)	Mass (kg)	$E_{\text{trans-min}}$ (J kg ⁻¹ m ⁻¹)	Source
Adults	10	23.7	1.76	66.6	2.59	Bastien et al., 2005
Obese adult males	10	25.6	1.76	104.7	2.09	Browning et al., 2006
Obese adult females	9	25.3	1.67	94.8	2.20	Browning et al., 2006
Non-obese adult males	10	20.6	1.82	74.7	1.88	Browning et al., 2006
Non-obese adult females	10	26.6	1.68	58.7	2.08	Browning et al., 2006
Adult males	11	19.4	1.726	61.54	2.41	Cotes and Meade, 1960
Children; ages 3–4	6	4.07	1.03	18.03	3.83	DeJaeger et al., 2001
Children; ages 5–6	6	6.22	1.17	21.27	3.08	DeJaeger et al., 2001
Children; ages 7–8	6	7.64	1.27	25.18	3.08	DeJaeger et al., 2001
Children; ages 9–10	6	9.85	1.40	34.03	2.60	DeJaeger et al., 2001
Children; ages 11–12	6	11.56	1.52	39.62	2.46	DeJaeger et al., 2001
Adults	6	24.28	1.77	64.87	2.45	DeJaeger et al., 2001
Male children	4	7.5	1.291	25.8	4.37	Freedson et al., 1981*
Obese children	23	9.3	1.378	46.2	3.73	Maffei et al., 1993
Non-obese children	17	9.2	1.367	30.3	3.47	Maffei et al., 1993
Young active adults	15	21.3	1.691	63.2	2.23	Martin et al., 1992*
Young sedentary adults	15	20.6	1.649	62.4	2.32	Martin et al., 1992*
Adolescents	40	15.5	1.67	62.0	2.48	McCann and Adams, 2002*
Adults	42	40.7	1.68	71.6	2.54	McCann and Adams, 2002*
Adult males	12	26.6	1.762	78.0	2.34	Mian et al., 2006*
Children; age 6	23	6.22	1.186	22.5	2.77	Morgan et al., 2002
Children; age 7	23	7.24	1.259	25.9	2.69	Morgan et al., 2002
Children; age 8	23	8.23	1.322	29.7	2.68	Morgan et al., 2002
Children; age 9	23	9.25	1.388	34.1	2.70	Morgan et al., 2002
Children; age 10	23	10.28	1.453	39.4	2.44	Morgan et al., 2002

$E_{\text{trans-min}}$, the minimum measured metabolic cost of transport, determined by subtracting basal metabolic rate values (Schofield et al., 1985) from gross metabolic rates and then dividing by velocity.

*Means from one or more subject groups were excluded because they did not meet the inclusion criteria.

slower speeds were also reported. Our literature search of more than 115 original potentially qualifying studies dating from the early 1900s onwards yielded 25 group means that satisfied these criteria. We did not include data points from subjects ≥ 65 years of age because they may not walk in a dynamically similar manner to individuals who are less than 65 years old (Ortega and Farley, 2007). Qualifying literature data and sources are reported in Table 2.

In addition to predicting a stature scaling exponent of -1.0 for human walking economy, our theoretical framework can also be used to predict a scaling exponent for body mass. Among geometrically similar subjects, body mass increases with stature to the third power ($M_b \propto L_b^{3.0}$). Therefore, given the approximate geometric similarity that we assumed *a priori* for our test subjects, our stature hypothesis ($E_{\text{trans-min}} \propto L_b^{-1.0}$) predicts that the mass-specific energy cost of human walking should scale with body mass to the negative one-third power ($E_{\text{trans-min}} \propto M_b^{-0.33}$).

Statistics

Group means for physical characteristics (body mass, stature and leg length), the metabolic energy expended per stride (J_{stride}^{-1}) and mechanical data (stride length, duty factor and Froude number) at the most economical walking speed were assessed using a one-way ANOVA with a Tukey's test of *post hoc* means. Gender differences in net metabolic rates were assessed using unpaired *t*-tests within each of the height groups in order to control for the effect of stature. Percentage error was determined as: [(predicted – actual)/actual] $\times 100$.

RESULTS

Walking energy expenditure

The gross mass-specific metabolic rates measured at six walking speeds from 0.4 to 1.9 m s^{-1} conformed to patterns expected on the

basis of stature. These rates increased with walking speed in a curvilinear fashion for all four stature groups (Fig. 1A), roughly doubling from the slowest to the fastest walking speed within each group. Group means ranged from an overall minimum of $2.56 \pm 0.06 \text{ W kg}^{-1}$ to a maximum of $6.80 \pm 0.14 \text{ W kg}^{-1}$. At each of the six speeds and for all 28 of the possible between-group comparisons, gross mass-specific metabolic rates varied in an inverse manner with stature, differing by a factor of 1.5 – 2 between the shortest and tallest groups.

For all four stature groups, walking transport cost–speed relationships conformed to the same general pattern, exhibiting minimums at intermediate walking speeds and greater values at both slower and faster speeds (Fig. 1B). As with gross metabolic rates, net walking transport costs were inversely related to stature, with the minimums of the four stature groups varying by a factor of just less than 1.5 between the shortest and tallest group (group A, $3.07 \pm 0.14 \text{ J kg}^{-1} \text{ m}^{-1}$ and group D, $2.12 \pm 0.17 \text{ J kg}^{-1} \text{ m}^{-1}$, respectively). Within stature groups, walking transport costs were not related to gender.

Walking transport costs standardized to stature, which represent the net mass-specific metabolic cost of transporting 1 kg a horizontal distance equal to the body's stature, are shown in Fig. 1C. This expression largely eliminated the between-stature group differences that were present prior to standardization for stature. At the four intermediate and most economical speeds, i.e. from 0.7 to 1.6 m s^{-1} , the overall mean value for the net metabolic energy required to travel a forward distance equal to the body's stature was 3.93 J kg^{-1} (0.94 calories kg^{-1}).

The mass-specific metabolic energy expended per stride at the most economical walking speeds did not differ among the four stature groups (Table 3) and varied by an average of only 4.4% for the six possible between-group comparisons.

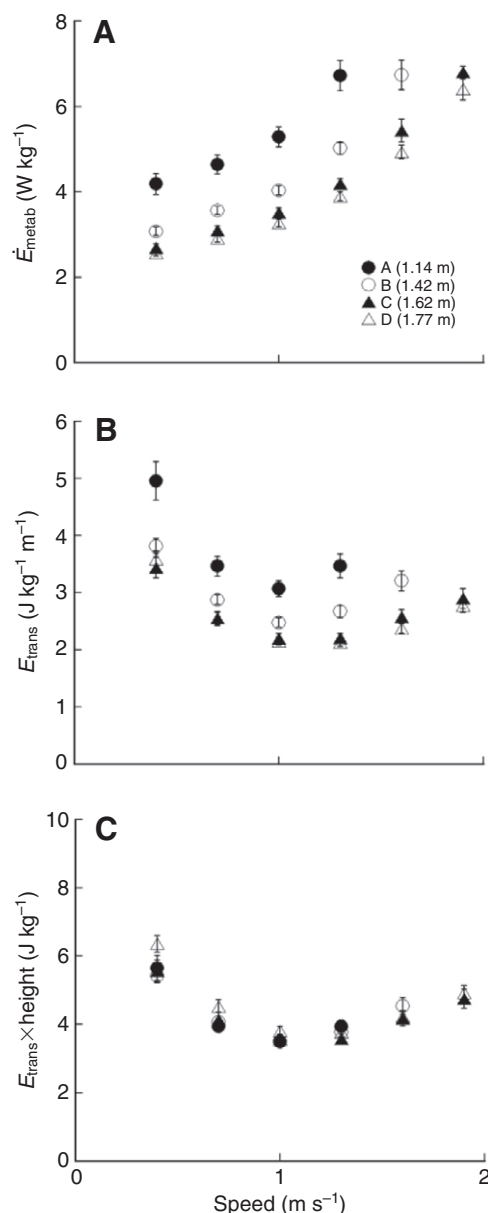


Fig. 1. (A) Mass-specific gross metabolic rates ($\dot{E}_{\text{metab}}$), (B) net metabolic transport costs (E_{trans}) and (C) the net metabolic transport costs to walk a forward distance equal to the body's stature in relation to walking speed for groups differing in stature (mean stature for each group is given in parentheses in A).

Basal energy expenditure

The mean basal metabolic rates for stature groups A, B, C and D, as calculated from the Schofield equations, were: 2.18 ± 0.12 , 1.55 ± 0.06 , 1.31 ± 0.0 , and 1.13 ± 0.03 W kg⁻¹, respectively. These values comprised 43.0, 38.0, 34.8 and 30.9% of the gross metabolic rates measured for the respective groups at their most economical walking speeds. The mean basal metabolic rate values calculated using the Schofield equations for all 25 literature group values included in the scaling analysis and their fractional contributions to the total metabolic rates reported during walking appear in supplementary material Table S1.

The average percentage difference between the mean metabolic rates predicted by the Schofield equations and the actual post-absorptive resting rates measured in the six original adult subjects

tested was $+3.2 \pm 1.4\%$ (1.11 ± 0.02 vs 1.08 ± 0.02 W kg⁻¹, respectively).

Scaling of the energy cost of human walking

The exponents providing the best fit between walking transport cost minimums and stature ($E_{\text{trans}} \propto L_b^{-0.90}$) and mass ($E_{\text{trans}} \propto M_b^{-0.32}$) among our original four stature groups were in good agreement with our theoretical predictions ($E_{\text{trans}} \propto L_b^{-1.0}$ and $M_b^{-0.33}$, respectively; Fig. 2A,B). When literature values with the necessary information – stature, body mass and gross metabolic rates across a sufficient number of speeds to exhibit a clear minimum – were added to the analysis, the exponential scaling factors for stature ($E_{\text{trans}} \propto L_b^{-0.95}$) and body mass ($E_{\text{trans}} \propto M_b^{-0.29}$) were both within 0.05 or less of the values predicted.

The relationship that best described the stature to mass relationship for our four stature groups conformed reasonably to our expectation of geometric similarity: $M_b = 15.2 L_b^{2.83}$.

Mechanical equivalency of the most economical walking speeds

The stature group means for the most economical walking speed, stride length to body length ratios (L_{str}/L_b), duty factors and Froude numbers appear in Table 3. The most economical walking speeds of the respective groups increased with the linear dimensions of the body as expected (speed at $E_{\text{trans-min}} \propto L_b^{0.52}$), and stride length to body length ratios, duty factors and the Froude number were all but identical across the four different stature groups at their respective most economical walking speeds.

DISCUSSION

We set out to evaluate the straightforward hypothesis that the mass-specific energy cost of human walking is set by stature. Under the equivalent conditions necessary for valid comparisons, both of the empirical tests we conducted supported the validity of this basic idea. In accordance with our first hypothesis, we found that the mass-specific energy expended per walking stride was nearly invariant among subjects who varied by a factor of more than 1.5 in stature and roughly six in both age and body mass. This direct coupling of the stride cycle to the metabolic energy expended provides a single, simple explanation for the height, weight and age trends previously observed for the economy of human walking. Next, because the stride lengths of these subjects were directly proportional to their heights, we found that the mass-specific energy expended per unit distance traveled was inversely related to stature. In the latter case, the exponents that best described the walking-transport-cost–stature relationship in our original (0.90), and original plus literature data (0.95) agreed well with the theoretical projection of our second hypothesis ($E_{\text{trans-min}} \propto L_b^{-1.0}$). Accordingly, we conclude that humans spanning a broad range of ages, statures and masses incur the same mass-specific metabolic cost to walk a horizontal distance equal to their stature.

Equivalent speeds and energy expenditure in walking gaits

A first issue of significant concern from the outset of the study was identifying speeds that were truly equivalent for individuals who spanned the broad range of body sizes examined. From the design stage forward, we recognized that the speed-specific nature of walking metabolic rates and transport costs, and the systematic variation of this speed-specificity in relation to stature, would confound metabolic comparisons made at the same absolute speeds. We addressed this issue experimentally by making comparisons only at the most economical speeds measured for each of our respective

Table 3. Walking speed, gait mechanics and per stride energy expenditure at $E_{\text{trans-min}}$ for the four stature groups

Group	Speed (m s ⁻¹)	L_{str}/L_b	Duty factor (t_c/t_{str})	Froude number	$\dot{E}_{\text{metab-net}}/f_{\text{str}}$ (J kg ⁻¹ stride ⁻¹)
A	0.96±0.04*	0.76±0.03	0.685±0.005	0.16±0.01	2.65±0.11
B	1.03±0.03*	0.76±0.02	0.684±0.004	0.14±0.01	2.71±0.11
C	1.13±0.04	0.78±0.02	0.676±0.003	0.15±0.01	2.72±0.14
D	1.21±0.04	0.76±0.02	0.680±0.003	0.16±0.01	2.88±0.12

All values are means ± s.e.m.

See Table 1 for stature group details.

$E_{\text{trans-min}}$, the minimum measured metabolic cost of transport; L_{str} , stride length; L_b , body length; $\dot{E}_{\text{metab-net}}$, net walking metabolic rate (gross metabolic rate – basal metabolic rate); f_{str} , stride frequency.

*, significantly different from group D.

stature groups. However, we could not know *a priori* exactly how accurately this experimental approach would ultimately identify the equivalent speeds desired.

Our *post hoc* evaluations indicate that our empirical technique fully met the intended objective. First, as expected from both intuition and mechanical principles, the walking speeds that were most economical became progressively faster from the shortest to the tallest stature group. This stature-induced variability is well illustrated by the transport cost data of each of our four stature groups (see Fig. 1B). The agreement between the increases in speed predicted from mechanical principles in relation to body and leg lengths (speed at $E_{\text{trans-min}} \propto L^{0.50}$) with the empirical values observed ($\propto L_b^{0.52}$; $\propto L_{\text{leg}}^{0.46}$) was nearly exact. In addition to supporting the efficacy of the empirical approach taken, this result also supports the general validity of our original assumptions regarding dynamic similarity in gait and approximate geometric similarity in bodily proportions among the subjects tested. Additional and equally robust empirical support for mechanical equivalence was provided by the two indices specifically used for this purpose: the duty factor and the Froude number. As can be seen in Table 3, the duty factors and Froude numbers at the most economical speeds measured were all but identical across the four stature groups. Mean values of the ratio of stride length to body length were also virtually constant. The nearly exact agreement between theoretical mechanical predictions and empirical results provides compelling evidence that the body's linear dimensions set both the gait and mass-specific metabolic cost patterns observed across individuals who differ in body size.

The second design concern was correctly subtracting the basal contributions to gross walking metabolic rates for our analysis. We used predictive equations rather than direct measurements for this purpose because doing so was necessary for the inclusion and consistent treatment of the 25 qualifying literature data points

used in our scaling analysis. The literature amply supports the ability of the population equations used to predict group means (De Loreonzo et al., 2001; Piers et al., 1997; Johnstone et al., 2006; Rodriguez et al., 2000; Schofield et al., 1985; van der Ploeg et al., 2001; Weyand et al., 2009), indicating an approximate accuracy of 3% for the group sizes assessed here. Indeed, for the six adult subjects on whom we took direct measurements, this was the accuracy observed; the mean predicted value was 3.2% greater than the measured value. In specific application, the presence of a +3.2% error in the basal metabolic rate estimates of groups A, B, C and D would underestimate the net metabolic rates quantified for walking by only 1.4 to 2.2%. These error values incorporate basal contributions to gross metabolic rates that averaged just over one-third for these four groups (mean=36.7%; see Results and supplementary material Table S1). Thus, for our purpose of analyzing group data across a range of body sizes, empirical observations indicate that the technique utilized introduced negligible error while allowing for a consistent and considerably more comprehensive scaling analysis.

Hypothesis test I: does the mass-specific energy cost per stride vary with stature?

Our first evaluation of a basic mechanistic link between stature and metabolic energy cost was a comparison of the net metabolic energy expended per stride at the most economical speeds for different-sized individuals. As can be seen in Table 3, the mass-specific metabolic energy expended on a per stride basis was essentially invariant across our four stature groups whereas stride lengths were directly proportional to stature. Because shorter and taller subjects do indeed walk in a dynamically similar fashion (Table 3), these data support the original idea that the metabolic energy expended to execute each walking stride at equivalent speeds is the same

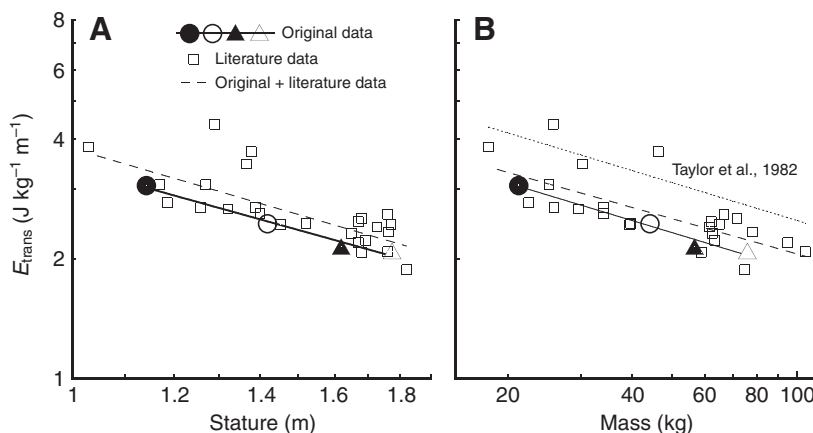


Fig. 2. Mass-specific net metabolic transport costs (E_{trans}) in relation to (A) stature (L_b) and (B) body mass (M_b) at the most economical walking speeds illustrated on logarithmic coordinates for the original data presented (open and closed circles and triangles) and qualifying literature values (open squares). Exponential relationships of best fit are provided for the original data and the original data plus literature data points. Stature: original data, $E_{\text{trans}}/M_b = 3.41 L_b^{-0.90}$, $R^2 = 0.98$; original + literature data, $E_{\text{trans}}/M_b = 3.80 L_b^{-0.95}$, $R^2 = 0.52$. Mass: original data, $E_{\text{trans}}/M_b = 7.98 M_b^{-0.31}$, $R^2 = 0.98$; original + literature data, $E_{\text{trans}}/M_b = 7.98 M_b^{-0.29}$, $R^2 = 0.50$; Taylor et al., 1982, $E_{\text{trans}}/M_b = 10.71 M_b^{-0.32}$ (dotted line).

regardless of the stature of the individual. The direct coupling of stride and metabolic rates identifies the rates at which the movements of each stride are completed as a crucial determinant of mass-specific metabolic rates. By contrast, existing literature amply indicates that the size-dependent economy of human walking is not explained by existing measures of the rates at which mechanical work is performed (Cavagna et al., 1983; Bastien et al., 2003; Schepens et al., 2004; Donelan et al., 2002; Kuo et al., 2005).

In the interest of providing a simple, quantitative expression of the direct link between walking mechanics and energy expenditure, we averaged the mass-specific energy expended per standardized unit distance at, and slightly beyond, the most economical walking speeds used for both of our hypothesis tests. For this additional purpose, we used the four speeds from our protocol that fall within the range of speeds that humans typically select during overground walking (Cavagna et al., 1983; Bornstein and Bornstein, 1976). At the four qualifying speeds from 0.7 to 1.6 ms⁻¹, the mean energy expended by all four stature groups to travel a forward distance equal to their stature was 0.94 cal kg⁻¹. For simple application and more convenient cost estimation for individual walkers, we rounded this mean to the more practical value of 1.0 cal kg⁻¹ and found that it provides a reasonable approximation (mean % error=9.3%, *n*=183 trials from 48 subjects) of the net mass-specific metabolic cost of human walking on firm, level surfaces.

Hypothesis test II: are mass-specific transport costs inversely related to stature?

The results of our second hypothesis test – the scaling analysis conducted on our original four stature groups – also supported the basic validity of our original stature idea. The exponents providing the best fit between walking transport cost minimums and both stature ($E_{\text{trans-min}} \propto L_b^{-0.90}$) and mass ($E_{\text{trans-min}} \propto M_b^{-0.32}$) were in good agreement with our theoretical predictions ($E_{\text{trans-min}} \propto L_b^{-1.0}$ and $M_b^{-0.33}$, respectively; Fig. 2A,B). In the latter case, the mass exponent derived agreed with the classical value of Taylor et al. for adult birds and mammals to the second decimal place (Taylor et al., 1981). When we tested the relationship more robustly, by adding literature values with the necessary information – stature, body mass and gross metabolic rates across a sufficient number of speeds to exhibit a clear minimum – the exponents obtained agreed as well, or perhaps slightly better, with our original predictions. As can be seen in Fig. 2A,B, adding qualifying literature data (Table 2) to our original data yielded exponential scaling factors for stature ($E_{\text{trans}} \propto L_b^{-0.95}$) and body mass ($E_{\text{trans}} \propto M_b^{-0.29}$) that were both within 0.05 or less of the values predicted by our stature hypothesis.

General implications of both hypothesis tests

In addition to providing basic support for our stature hypothesis, the human data presented here and elsewhere can also be used to better evaluate the possibility that body mass (Nudds et al., 2009) rather than stature provides a more direct explanation for the scaling of locomotor economy with body size. Several independent literature observations on humans support the opposite conclusion: that mass-specific transport costs are set by the length of the body and are minimally affected by variation in body mass at any given stature. First, obese and non-obese subjects of the same stature walk with similar mechanics (Browning and Kram, 2005; Browning and Kram, 2006) and have the same or very similar mass-specific metabolic costs (Browning and Kram, 2005; Browning and Kram, 2006; Ayub and Bar-Or, 2003). Second, subjects who lose weight have the same mass-specific walking metabolic rates when body mass changes and stature does not

(Hunter et al., 2008). Finally, a mechanistic basis for a causal link between mass-specific metabolic transport costs and body mass is difficult to envision, whereas stature has a direct and highly predictable influence on the mechanics of walking (Table 3) that determine the muscular activity and costs incurred.

An additional conclusion that can be drawn from the direct relationship we have identified between stature and human walking economy is that ontogeny has no measurable effect on the metabolic cost of human walking that is independent of body size. Certainly inferior skill, coordination or perhaps mismatches between periods of muscular force development and muscle fiber speeds could all conceivably compromise the locomotor economy of children. Yet, when we expressed metabolic costs on a per stride basis at equivalent speeds, we found no difference in the mass-specific cost per stride incurred by 5- to 7-year-old subjects in our shortest group *versus* the 20- to 32-year-old subjects in the tallest group (Table 3). The absence of an age effect is similarly supported by the close agreement between the mass scaling exponents presented for human children plus adults and that established for adult vertebrates spanning a much greater body mass range (Taylor et al., 1981). A more recent but less comprehensive walking-specific vertebrate scaling value (Rubenson et al., 2007) similarly supports the conclusion that children walk at least as economically as adults when the effect of body size is taken into account. These observations suggest that humans establish mature walking patterns sometime before they reach 6 years of age.

Concluding remarks

Although formulated for the basic purpose of relating stature and mass to the metabolic cost of human walking, the quantitative relationships we have identified have immediate potential application. Walking is the primary form of physical activity for a large proportion of the world's population and occurs in nearly all human habitats. Accordingly, dozens of predictive equations have been developed for use in clinical, military, recreational and other settings. By incorporating the fundamental effect of body size, the following expressions allow the metabolic energy expended during human walking to be estimated from the distance covered and either stature and mass combined or mass alone:

$$E_{\text{trans}}/M_b = 3.80L_b^{-0.95}, \quad (1)$$

$$E_{\text{trans}}/M_b = 7.98M_b^{-0.29}, \quad (2)$$

where E_{trans} is given in J m⁻¹, M_b is in kg and L_b is in m. Because humans walk at or near the speeds that minimize the metabolic cost of walking the majority of the time (Cavagna et al., 1983; Bornstein and Bornstein, 1976), these relationships allow the metabolic energy expended while walking on firm level surfaces to be estimated with a minimum of information.

Finally, we note that the new scaling relationships we introduce for the walking transport costs of humans also have general biological implications and applications. In the former case, our finding that the transport costs of walking humans are substantially lower than the norms for terrestrial vertebrates (Taylor et al., 1981) by a virtually constant margin of one-third across the broad range of body masses examined here (Fig. 2B) can inform comparative and evolutionary arguments (Rubenson et al., 2007; Alexander, 2004; Carrier, 1984; Rodman and McHenry, 1980; Pontzer et al., 2009) that depend on quantitative estimates of the relative locomotor economy of humans. In the latter case, the new scaling relationships could provide more specific estimates of the locomotor costs of early hominids from fossil-based estimates of stature and mass.

LIST OF ABBREVIATIONS

$\dot{E}_{\text{metab}}$	energy expenditure
$\dot{E}_{\text{metab-net}}$	net energy expenditure
E_{trans}	walking transport cost
$E_{\text{trans-min}}$	minimum transport cost
f_{str}	stride frequency
g	gravity
L_b	body length (stature)
L_{leg}	leg length
L_{str}	stride length
M_b	body mass
t_c	foot ground-contact time
t_c/t_{str}	duty factor (ratio of foot ground-contact time to total stride time)
t_{str}	total stride time
U	index of equivalent speed
V	walking speed

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