



The effect of lower limb length on the energetic cost of locomotion: implications for fossil hominins

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Received 2 January 2004; accepted 4 June 2004

Abstract

The consequences of the relatively short lower limbs characteristic of AL 288-1 have been widely discussed, as have the causes and consequences of the short limbs of Neanderthals. Previous studies of the effect of limb length on the energetic cost of locomotion have reported no relationship; however, limb length could have accounted for as much as 19% of the variation in cost and gone undetected (Steudel and Beattie, 1995; Steudel, 1994, 1996). Kramer (1999) and Kramer and Eck (2000) have recently used a theoretical model to predict the effect of the shorter limbs of early hominids, concluding that the shorter limbs may actually have been energetically advantageous.

Here, we took an experimental approach. Twenty-one human subjects, of varying limb lengths, walked on a treadmill at 2.6, 2.8, 3.0 and 3.2 m.p.h., while their expired gases were analyzed. The subjects walked for 12 minutes at each speed and their rates of oxygen consumption (VO_2) over four minutes were averaged to estimate VO_2 . We also measured each subject's height, weight and lower limb length. Lean body mass and % fat were determined using dual-energy x-ray absorptiometry.

ANCOVA with total VO_2 at either speed as the dependent variable and total lean mass, % fat and lower limb length as covariates resulted in all three covariates having a significant positive effect on VO_2 at $p < 0.01$. Subjects with relatively longer lower limbs had lower locomotor costs. Thus the short lower limbs characteristic of some hominid taxa would have resulted in more costly locomotion, barring some physiological anomaly. The magnitude of this effect is substantial; Neanderthals are estimated to have had locomotor costs 30% greater than those of contemporary anatomically modern humans. By contrast the increase in lower limb length seen in *H. erectus* would have mitigated the increase in locomotor costs produced by the increase in body size.

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Keywords: limb length; cost of transport; *Australopithecus*; Neanderthal; hominids

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Introduction

Limb length is well known to differ among taxa within the hominin clade. It is established that lower limb length in *Australopithecus* (particularly AL 288-1 and Sts 14) was substantially shorter than in *Homo erectus/ergaster* and later species of *Homo* (Jungers, 1982; Jungers and Stern, 1983; McHenry and Berger, 1998; Klein, 1999). Neanderthals had shorter lower limbs, particularly the distal elements, than contemporaneous anatomically modern humans (e.g. Trinkaus, 1981, 1986; Frayer et al., 1993; Holliday and Falsetti, 1995; Holliday, 1999; Steegmann et al., 2002). What consequences would these differences in limb proportions have had for the energetic efficiency of these ancestral populations? A diversity of views can be found in the literature. Many workers (Trinkaus, 1981, 1986; Jungers, 1982; Jungers and Stern, 1983; Susman et al., 1984; Holliday and Falsetti, 1995; Steudel and Beattie, 1995) have supposed that longer limbs would result in greater energetic economy. The argument is that longer lower limbs result in fewer strides per distance traveled, resulting in lower cost. Kramer (1999) and Kramer and Eck (2000), however, have argued based on mechanical modeling of the mechanical work of locomotion, that short lower limbs would actually be energetically advantageous because shorter limbs have lower limb moments of inertia leading to a lower cost (see also Myers and Steudel, 1997).

Developing expectations about performance based purely on biomechanical arguments, however, is not always a dependable approach. For years, workers had supposed that more proximally placed limb musculature would be energetically advantageous. Yet when this was actually tested, Taylor et al. (1974) were unable to detect a difference in the energetic cost of locomotion between cheetah, goat and gazelle, three species that differ conspicuously in limb mass distribution. Thus biomechanical expectations may not always be biologically accurate (Ross et al., 2002). Further, Heglund et al. (1982) demonstrated a lack of a relationship between the mechanical work of locomotion and its energetic cost. Minetti and Alexander's (1997) model for calculating the

metabolic cost of human locomotion from a simple mechanical model also produced estimated costs that were substantially lower than actual metabolic costs. Biomechanical expectations often fail to predict energetic costs.

The effect of lower limb length on the energetic cost of locomotion is a problem that can be subjected to direct experimental testing. Previous work along these lines has failed to detect any effect of limb length on locomotor cost. Steudel and Beattie (1995) measured limb lengths in museum specimens that were similar in body mass to specimens representing 21 mammalian species on which the energetic cost of locomotion had previously been measured. Lower limb length and cost of locomotion were not significantly correlated when their mutual correlation with body mass was removed. This result obtained in spite of considerable differences in limb length among animals of similar mass. With this sample, however, lower limb length could have accounted for as much as 19% of the variation in cost and gone undetected (Steudel and Beattie, 1995). Subsequently, Steudel (1996) used data from the literature in which both cost and lower limb length were reported in walking and running human subjects. There was no evidence of a relationship between those variables. The sample size, however, was only 10 in each case, which was inadequate to detect a modest effect of lower limb length on cost. As Kramer and Eck (2000) pointed out, there has never been a series of experiments carried out designed specifically to test the effect of limb length on cost. The present study is such an attempt.

Methods

If the cost of locomotion in human walking increased linearly with speed, as it does in human running, one could appropriately compare individuals at any single comfortable speed. The cost of transport (cost per unit distance) omitting postural costs is essentially invariant in running at different speeds (Steudel, 2000). In human walking, however, there is a particular speed, or range of speeds, at which cost is at a minimum. It

seems likely that this speed(s) might be influenced by lower limb length. One possible approach to speed selection would be to have subjects walk at different speeds yielding the same Froude number (Alexander and Jayes, 1983; Alexander, 1991; Kramer, 1999), adjusted based on their lower limb length (the dynamic similarity model). In the present instance, this approach becomes very circular. One is looking for the effect of lower limb length on cost, but different locomotor tasks are assigned based on lower limb length. This approach would make it difficult to confidently compare data between subjects. Are any results more a consequence of the differences in lower limb length or of the differences in the assigned tasks? This seems particularly dubious given recent work by Donelan and Kram (1997, 2000) in which they rejected the dynamic similarity model based on their data. They conclude that their results show that “factors other than gravitational forces are the primary determinants of walking biomechanics”. Rather than compare subjects at a single variable walking speed, our subjects walked at four different speeds, 2.6, 2.8, 3.0 and 3.2 m.p.h., all near energetic optimality (Booyens and Keatinge, 1957; Bhambhani and Singh, 1985). Presumably the slower speed would be nearer the optimum for shorter limbed subjects, while the faster would be closer to the optimum for long limbed subjects. Thus we compare the performance of subjects at a series of speeds, some of which should give advantage to shorter limbed subjects and others that should benefit the longer limbed.

To be on the safe side, we retrospectively tested to see whether our experimental speeds bracketed those optimal for our various subjects. We calculated the average lower limb length of our subject population, observed the speed at which cost was minimized, and then used formula 9 in Kramer (1999) to calculate the expected optimal speeds for our longest and shortest limbed subjects. As reported in the results, this condition was met for the shortest lower limbed individual, but not for the longest limbed. Thus the data are biased against our finding that longer lower limbs are more efficient.

Twenty one human subjects, 13 female and 8 male, walked on a motor driven treadmill at the four speeds indicated above, while their rates

of oxygen consumption were monitored using a SensorMedics Vmax 29c respiratory gas analysis system. All subjects were between 18 and 35 years of age, and most were undergraduates at the University of Wisconsin. All were moderately active, but none were specialist in any particular sport. The anthropometric characteristics of the subjects can be seen in Table 1. The subjects walked for 12 minutes at each speed. Cost for each speed was determined by averaging the rate of oxygen consumption (VO_2) over a four minute period, beginning after the subject had walked at least 6 minutes. At least three separate trials for each subject at each speed were included in the data and the results averaged. We also measured each subject’s height, weight and lower limb length. Lower limb length was measured as two separate variables which were subsequently summed. Femur length was measured from the greater trochanter to the knee midpoint. Length of the lower limb segment was measured from the knee midpoint to the lateral malleolus of the fibula.

While it is well known that VO_2 is closely related to mass (e.g. Taylor et al., 1982), we

Table 1
Anthropometric characteristics of the human subjects in the study

Subject	Gender	Leg length	Percent fat	Mass (kg)	Lean mass (kg)
1	F	72.30	30.90	64.71	38.01
3	M	85.55	22.40	95.02	65.74
7	M	92.40	22.30	83.26	58.06
8	F	78.30	24.50	52.04	34.39
9	F	76.10	36.40	81.45	43.21
10	F	77.30	19.20	55.66	41.48
13	F	78.30	30.00	63.35	37.45
20	M	83.05	24.50	76.92	56.62
22	F	84.95	26.30	56.56	35.84
23	F	85.80	33.50	71.95	40.68
24	F	77.10	32.00	59.28	33.73
26	F	82.10	24.50	57.01	38.54
30	F	81.80	31.50	72.17	41.49
31	F	80.00	22.90	61.54	40.89
32	F	79.10	17.70	57.01	41.31
33	M	78.90	15.80	91.86	71.96
34	F	80.45	28.10	67.32	37.53
35	M	71.40	24.80	76.92	53.72
36	M	79.45	23.20	83.71	60.94
38	M	86.30	10.90	77.38	63.37
40	M	89.20	13.10	88.24	71.26

wondered whether the composition of that mass might be significant. Consequently lean body mass and percent fat were determined at the University of Wisconsin Clinics using dual-energy x-ray absorptiometry (DEXA). This method uses two distinct low-energy x-ray beams that penetrate body tissues to about 30 cm. Software reconstructs the bone mineral content, lean mass and fat free mass from the attenuation of the x-rays as they scan the entire body (McArdle et al., 2001). This method is rapidly becoming the gold standard in body composition analysis (Kohrt, 1995, 1998; Prior et al., 1997). In analyses we represented mass as lean mass (skeletal plus muscle mass) with percent fat as an additional variable. Lean mass and percent fat in Table 1 do not sum to total body mass because abdominal contents are not included. Analyzing data using fat mass instead of percent fat results in trivial alterations of the relevant statistics.

We focused on the relationship between limb length and the energetic cost of transport (the cost to travel a unit distance). Steudel (2000) has shown that the cost of transport is superior to other estimates of cost when used in an ecological context (see also Garland, 1983). While it is unlikely that lower limb length is adaptively significant in modern technological societies, considerable variability in lower limb length exists in modern humans (see below). What we determine here are the metabolic consequences of that variation. If limb length in modern humans has some regular mechanical influence on the cost of transport, it seems reasonable to conclude that limb length would have had a similar effect on cost in ancestral bipeds. Lower costs of transport may well have been a significant selective pressure in earlier hominins, who were likely to be subjected to greater variability of food resources.

Because both limb length and the cost of locomotion are significantly correlated with mass, the two variables will also be correlated with each other. To determine whether cost and limb length were correlated, independent of their mutual correlations with mass, we regressed each variable on lean mass and calculated the unstandardized residuals. We then regressed the residual of cost on the residual of limb length. Statistically this is completely equivalent to determining the partial

correlation between limb length and cost with mass held constant, but facilitates graphing of the relationship. The same procedure was repeated for each of the four walking speeds. We also performed multiple regression with VO_2 as the dependent variable and lean mass, limb length and percent fat as independent variables. The data were screened for outliers using Cook's distance (Cook and Weisberg, 1999).

To apply our results to fossil hominins, we collected published data from a variety of sources. We restricted our selection to fossil specimens with nearly complete, or very plausibly reconstructed, femora. Suitable fossil femora attributed to early hominins are rare, therefore, our data involved a higher percentage of more recent specimens. We collected measurements for: total femoral length, midshaft femoral circumference, estimated specimen geologic age and, where possible, body mass.

Specimen attributions and taxonomy followed that of Klein (1999) and Day (1971). Femoral data from twenty-three specimens were accumulated, divided into seven taxonomic categories, combining *H. erectus* and *H. ergaster*, as is widely done. The data are summarized in Table 2. Femur length estimates for: *KNM-ER 1481*, Tabun C1, La Chapelle 1, La Ferrassie 1 and 2, Cro-Magnon 1 and 4322, Neandertal 1, Skhul 4, 5, and 6, and Amud 1 are from Trinkaus (1993). Lengths for the specimens attributed to *Homo erectus/ergaster*, Trinil 3, OH 28, Peking I and IV, were collected from Day (1971, 1986). We used the reconstructed adult femur length for the nearly complete Nariokotome skeleton, *KNM-WT 15000*, from Walker and Leakey (1993), while Jungers (1982) was the source for the femoral estimation for the nearly complete *Australopithecus afarensis*, AL288-1. Femoral length for KNMER 1472 was taken from McHenry and Corruccini (1978); for Sts 14/Sts 34 was from Lovejoy and Heiple (1970); for OH 34 from Day and Molleson (1976). Femoral length for BOU-VP-12/1 is from Asfaw et al. (1999).

Midshaft circumferences cited from Day (1971) include those from Trinil 3, OH 28, Peking I and Peking IV. Values for KNMER 1472 and KNMER 1481 were from McHenry and Corruccini (1978). The circumference for the only

Table 2

Fossil femur age, length, midshaft circumference and estimated mass (sources of individual values are given in the text)

Taxon	Specimen	Estimated date	Femur length (cm)	Femoral midshaft circumference (mm)	Estimated body mass (kg)
<i>A. afarensis</i>	AL288-1	3100000	28.1	67	27.9
<i>A. africanus</i>	Sts 14 and 34	2500000	27.6		30.3
<i>A. garhi?</i>	BOU-VP-12/1	2500000	33.5		
<i>H. habilis?</i>	KNM-ER 1472	2000000	40.1	83	49.6
<i>H. habilis?</i>	KNM-ER 1481	2000000	39.6	83	57.0
<i>H. erectus/ergaster</i>	KNM-WT 15000	1530000	51.7	71	68.0
<i>H. erectus/ergaster?</i>	OH 34	1000000	43.2		51.0
<i>H. erectus/ergaster</i>	Trinil 3	1000000	45.5	85	
<i>H. erectus/ergaster</i>	OH 28	100000	45.6	95	54.0
<i>H. erectus/ergaster</i>	Peking I	400000	40.0	98	
<i>H. erectus/ergaster</i>	Peking IV	400000	40.7	85	
Neanderthal	Tabun C1	75000	41.0	82	*
Neanderthal	La Chapelle 1	50000	42.0	94	*
Neanderthal	La Ferrassie 1	38000	45.8	97	*
Neanderthal	La Ferrassie 2	38000	40.7	89	*
Neanderthal	Neanderthal 1	55000	44.1	94	*
Neanderthal	Amud 1	54000	48.2	102	*
Near modern	Skhul 5	100000	51.5	101	*
Near modern	Skhul 6	100000	47.5	94	*
Near modern	Qafzeh 9	100000	46.9	104	*
Near modern	Skhul 4	100000	48.8	93	*
Modern human	Cro-Magnon 1	30000	48.4	110	*
Modern human	Cro-Magnon 4322	30000	47.8	91	*

*For these taxa average values from Ruff et al. (1997) were used.

Australopithecus afarensis specimen, AL288-1, is from Hartwig-Scherer and Martin (1991). The value for KNM-WT 15000 was reported in Walker and Leakey (1993). Values for Tabun C1, La Chapelle 1, La Ferrassie 1 and 2, Cro-Magnon 1 and 4322, Neanderthal 1, Skhul 4, 5, and 6, Qafzeh 9, and Amud 1 are back calculated from Trinkaus' (1993) reporting of robusticity index.

Johanson et al. (1982) provided the estimated age of AL288-1; Johanson and Edgar (1996), the age of Sts 14 and Sts 34; Klein (1989), the age of KNM-ER-1472; and Kennedy (1983), the estimated age of KNM-ER 1481. The date for BOU-VP-12/1 is from Asfaw et al. (1999); for OH 62 from Johanson et al. (1987). For those specimens attributed to *Homo erectus/ergaster*, KNM-WT 15000, OH 28, Trinil 3, Peking I and Peking IV, and for OH 34, we used Walker and Leakey (1993), Hay (1976), and Day (1986), respectively. The estimated ages for the Neanderthal specimens, Tabun C1, La Chapelle 1, and Amud 1, were obtained from Klein (1999). The ages for the

remaining Neanderthal specimens, La Ferrassie 1, La Ferrassie 2, and Neanderthal 1, were from Day (1971). Klein (1999) was the source for the ages of the Near modern specimens, Skhul 4, 5, and 6, and Qafzeh 9. The estimations for Cro-Magnon 1 and 4322 were from Tattersall et al. (1998).

Where possible, we obtained estimates of body mass from the literature. Estimates based on the scaling of femoral head diameters in *H. sapiens* from McHenry (1992) yielded weight estimates for AL 288-1, Sts 14, KNM-ER 1472 and KNM-ER 1481. Estimates for KNM-WT 15000, OH 34 and OH 28 are from Ruff and Walker (1993). We used average body mass values for Neanderthals, early modern Homo and modern Homo from Ruff et al. (1997) and averaged the values for femur length for the samples of Neanderthal, early modern Homo and modern Homo in Table 2.

We calculated total lower limb length as femur length plus tibia length. Tibia length was estimated by applying a single estimate for crural index to all taxa to avoid error involved in the estimation of

this index. Particularly for earlier taxa, estimates of crural index are very problematic. We assumed that tibia length is 85% of femur length as reported for early anatomically modern humans (Trinkaus, 1981; Walker and Leakey, 1993). This limb segment proportionality applies well to some other hominin taxa; the equivalent value for the Nariokotome skeleton is 88% (Walker and Leakey, 1993). This method, however, undoubtedly overestimates lower limb length in Neanderthals since it is widely accepted that they were characterized by shorter distal lower limb segments (Trinkaus, 1981; Wolpoff, 1989; Frayer et al., 1993; Holliday, 1997, 1999). This method of estimating tibia length could also overestimate lower limb length in *H. habilis*, where crural indexes are not well established (e.g. Richmond et al., 2002). We used the equations given below to estimate cost of transport ($\text{ml O}_2 \text{m}^{-1}$) for the fossil taxa based on estimated total mass and lower limb length. For comparison we included cost estimates based on mass alone. We did not include separate terms for lean mass and percent fat in this analysis because there is no basis for that level of discrimination. To determine the magnitude of the error due to estimation of crural index, we recalculated cost for Neanderthals based on published estimates of crural index (Trinkaus, 1981). The resulting limb length estimate is very similar to that given as the average for male Neanderthals (Holliday, 1999).

We were also concerned about the amount of error that would result from different methods of body size estimation. We did not estimate cost for specimens representing *Australopithecus* because their estimated masses and limb lengths were far out of the range of the current sample (Fig. 3). Size estimates for earlier *H. sapiens* are fairly robust, because the appropriate reference sample (*H. sapiens*) is apparent. The problem is likely to be most trenchant with early *Homo*. To evaluate the magnitude of the problem, we chose two specimens, KNM-ER 1472 and KNM-ER 1481 for whom quite a few size estimates are available, and estimated their energetic cost of locomotion given their limb length and substituting a variety of mass estimates from the literature. (The only mass estimates we were able to find for KNM-WT

15000, OH 34 and OH 28 were the Walker and Ruff, 1993, estimates used here.)

Specifically we used mass estimates from Walker and Ruff (1993), McHenry (1988) and mass estimates calculated by Walker and Ruff (1993) based on the equations in McHenry (1991) and Jungers (1988). The McHenry (1988) results were based on shaft diameters, consequently differences between ape and human samples are minimal. Therefore, we used the average of human and interhominoid values. The estimates from Jungers (1988) are based on joint size, whose scaling differs greatly between apes and humans. Consequently we report estimates based on his entire hominoid sample (ALLHOM) and based on his non-human hominoids (NONHOM).

Results

We were able to obtain subjects showing a substantial variation in lower limb length. The most extreme subjects had lower limb lengths 9.8 cm greater and 10.5 cm lower than that predicted for their lean mass based on the equation developed for all subjects. Six of the subjects deviated more than 5 cm from their predicted lower limb length. Lower limb length and cost are both substantially related to body mass. Regression of lower limb length on lean mass resulted in $r = 0.414$. Regression of cost (VO_2) on lean mass resulted in slightly different values at the various walking speeds. Results are summarized in Table 3. To remove the mutual correlation of both variables with mass, the residuals of cost on lean mass for each speed were then regressed on the residual of lower limb length on lean mass. (As mentioned above, this is completely equivalent to doing a partial correlation analysis, except that this method allows the results to be graphed.) Finally, multiple regressions with total cost as the dependent variable and lean mass, lower limb length and percentage fat as independent variables were performed (Table 3). Percentage fat and lower limb length were added incrementally so that the effect of each on cost would be apparent. All regressions were highly significant ($p < 0.01$). Most were significant at $p < 0.001$. The effect of

Table 3

Coefficients of determination (r^2) for the effects of morphological traits on the cost of locomotion (all p values were <0.01 ; most were <0.001)

Speed (m.p.h.)	2.6	2.8	3.0	3.2
VO ₂ vs. lean mass	0.781	0.731	0.729	0.681
Residual VO ₂ vs. residual lower limb length	0.300	0.415	0.364	0.423
VO ₂ vs. lean mass and % fat	0.882	0.834	0.843	0.792
VO ₂ vs. lean mass, % fat and lower limb length	0.927	0.920	0.916	0.897

limb length on cost, with their mutual correlation to lean mass removed, is highly significant at all walking speeds. Comparison of values in the last two rows of Table 3 indicates that there is a tendency toward a larger effect of limb length at higher walking speeds. A graph of the relationship of lower limb length residual to cost residual at 2.8 m.p.h. can be seen in Figure 1. Longer limbs result in lower costs at all walking speeds. A similar analysis in ANCOVA with gender as a fixed factor indicated that gender had no significant effect on cost in an analysis in which lean mass, percent fat and limb length were included as independent variables. In the test for outliers, the highest Cook's distance score for the data points in the regression of residual cost on residual lower limb length was 0.279. A value greater than 1

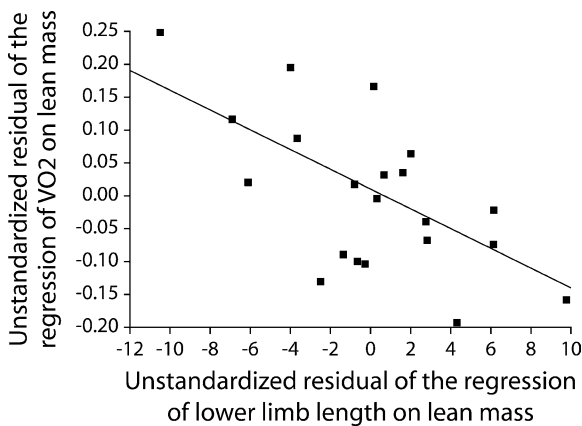


Figure 1. Unstandardized residuals of the regression of cost (VO₂) on lean mass versus the unstandardized residuals of the regression of leg length on lean mass. Longer limbs result in lower energetic costs.

indicates an outlier; some additional scrutiny is suggested for values between 0.5 and 1.0 (Cook and Weisberg, 1999). Thus none of the data points in the analysis is exerting an untoward effect on the results. Comparing the coefficients of determination for the regressions including lower limb length to those including only lean mass and percentage fat show differences close to 0.10. Thus a little under 10% of the variation in cost is accounted for by lower limb length.

Contrary to predictions based on Froude number, the effect of lower limb length on optimal walking speed was weak ($r^2 = 0.225$). Nonetheless, we used the average lower limb length in our subjects ($=77.5$ cm) and the energetically optimal walking speed for most individuals at that lower limb length ($=3.0$ m.p.h.) to calculate the optimal walking speeds for our longest and shortest limbed subjects according to the formula (modified from Kramer, 1999):

$$V_{\text{short or long}} = V_{\text{av}} \sqrt{LL_{\text{short or long}}/LL_{\text{av}}}$$

where V is optimal walking speed and LL is lower limb length. Optimal walking speed, predicted from Froude number, was 2.76 m.p.h. for our shortest limbed subject, well above our lowest experimental speed of 2.6 m.p.h. Thus our experimental speeds included those that should be optimal for our shortest limbed individuals and, as indicated above, longer limbs conferred lower costs even at those speeds. The optimal walking speed for our longest limbed subject predicted from Froude number was 3.58 m.p.h., above our highest experimental speed. Thus extension of speeds into a higher range might well show an even greater advantage to long limbs.

To estimate cost in fossil hominins, we developed equations to predict the energetic cost of transport (cost/distance). Steudel (2000) has argued that the cost of transport is the most ecologically meaningful estimate of locomotor costs. First, it excludes cost due to resting metabolism during the locomotor bout, a metabolic necessity unrelated to locomotion per se. Second, the cost of transport is essentially independent of the speed of travel, so that estimates of speed of travel become

unnecessary. While the cost of transport is not absolutely invariant in human walking, we found it to be nearly so at our test speeds, all near energetic optimality.

The equation relating the cost of transport (ml O₂/meter) to mass (kg) and lower limb length (cm) was found to be

$$\begin{aligned} \text{VO}_2(\text{ml O}_2/\text{meter}) & \\ &= 8.301 + 0.234 (\text{mass}) \\ &\quad - 0.169 (\text{lower limb length}). \quad r = 0.93. \end{aligned}$$

Equation 1

The equation relating the cost of transport (ml O₂/meter) to mass (kg) alone was

$$\begin{aligned} \text{VO}_2(\text{ml O}_2/\text{meter}) & \\ &= -3.668 + 0.209(\text{mass}). \quad r = 0.89. \end{aligned}$$

Equation 2

Application to fossil hominins

We selected 23 hominin specimens on which femur length had been measured or estimated with reasonable accuracy. The variation in lower limb length (estimated as femur length) in hominin fossils through time is shown in Figure 2. Each specimen is identified by taxon. As is well known,

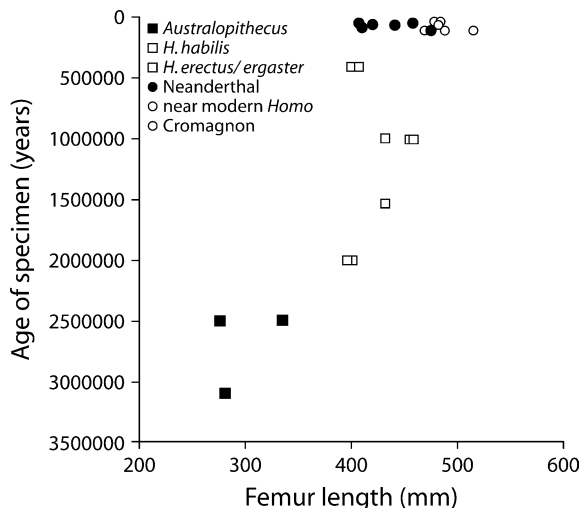


Figure 2. The increase in femur length through time in the hominin clade.

Australopithecus had shorter femora than *Homo*. These data also corroborate the widespread finding (e.g. Trinkaus, 1981, 1986; Frayer et al., 1993; Holliday and Falsetti, 1995; Holliday, 1999; Steegmann et al., 2002) that Neanderthals have short femora. ANCOVA with femur length as the dependent variable, midshaft circumference as a covariate and taxon (Neanderthal, near modern *Homo* or modern *Homo*) as a fixed factor resulted in $p = 0.044$.

Application of the above equations to specimens attributed to *Homo sapiens*, Neanderthals and *H. erectus/ergaster* was statistically appropriate because their values for mass and lower limb length were within the range of the present data (see Figure 3). As is apparent in Fig. 3, values for specimens attributed to *H. habilis* are just outside the range of the data, but close enough that cost estimates should be quite accurate. Table 4 summarizes the estimates of cost of transport based on both lower limb length and mass and cost based on mass alone for the two presumptive *H. habilis* and 3 presumptive *H. erectus/ergaster*. It also includes average values for three more recent fossil taxa, along with the estimates of mass and lower limb length on which they are based.

Cost estimates for *H. habilis* are quite modest because of their small mass. Their relatively short lower limbs, however, resulted in an approximately 10% increase in locomotor cost over what

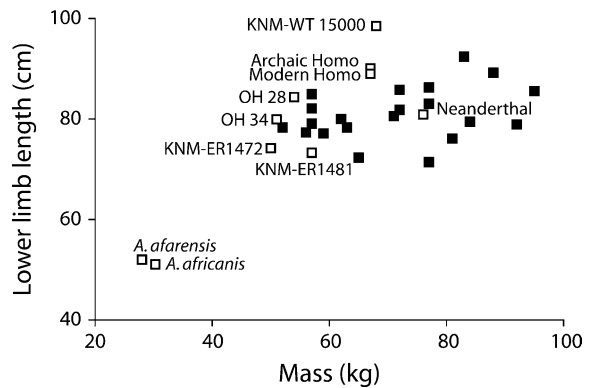


Figure 3. Limb length versus mass in the present data (closed squares) and in fossil hominin specimens (open squares). Limb length estimates are based on femur length, assuming that tibia length is 85% of femur length. See text for the effect of altering assumption about crural index.

Table 4

Estimated mass, lower limb length, cost of transport and mass-specific cost of transport for selected fossil hominins (see text for sources of fossil data)

Specimen	Mass (kg)	Lower limb length (cm)	Total cost (ml O ₂ m ⁻¹) based on mass and LL	Total cost (ml O ₂ m ⁻¹) based on mass alone
KNM-ER 1472	49.6	74.19	7.37	6.70
KNM-ER 1481	57.0	73.26	9.26	8.25
KNM-WT 15000	68	95.65	8.05	10.54
OH 34	51	79.55	6.73	6.99
OH 28	54	84.36	6.68	7.62
Neanderthal	76	81.10	12.39	12.22
Near modern Homo	66.6	90.05	8.67	10.25
Modern Homo	66.6	88.99	8.85	10.25

would have been achieved with limb proportions characteristic of modern humans (comparing values in columns 4 and 5 in Table 4). This effect may even have been greater, given that tibia length in these hominins may well have been less than 85% of femur length (though see below). Total cost of transport in KNM- WT 15000 would have been similar to that of *H. habilis* in spite of the substantially increased mass (we used the adult mass estimate from Ruff and Walker, 1993), as a consequence of the substantially longer lower limbs. Cost drops in the more recent OH 28 and OH 34, largely due to the much smaller estimated mass. Comparing the last two columns shows that OH 28, in particular, reaped substantial energetic advantage from its long lower limbs. Naturally, one can never be sure how well these available specimens reflect actual limb lengths and body masses characteristic of the population from which they were drawn.

To assess the effects of different techniques for mass estimation, we calculated the energetic cost of locomotion based on limb length and a variety of sources for mass. The results can be seen in Table 5. The results are surprisingly consistent between those used here, Walker and Ruff (1993) and McHenry (1988, 1991). Relatively small differences in mass estimates result in relatively small differences in cost estimates. It is only when femoral head size is used to estimate mass based on a reference sample including substantial numbers of non-human hominoids (Jungers, 1988) that the mass estimates, and consequently the cost estimates, show substantial deviation from the others. This is a consequence of the substantial differences between humans and apes in the scaling of femoral head size relative to mass. McHenry (1991) bases his estimates on femoral head size in humans only, resulting in estimates similar to those using shaft variables.

Neanderthals had much higher costs of locomotion than did modern and near modern *Homo* and were also less efficient due to their shorter lower limbs. The difference (using tibia length = 85% femur length) was a remarkable 30%! Estimating lower limb length using the value for crural index actually observed in Neanderthal (Trinkaus, 1981) resulted in an increase of 32%. Happily, therefore, variation in crural index does not seem to have a particularly substantial effect on the results. The 10 kg difference in mass between Neanderthal and modern *Homo* would have resulted in an approximately 16% increase in cost. Lower limb length accounts for the rest. To evaluate the reasonability of this difference, we compared actual cost in two subjects whose differences in mass and lower limb length were similar to those between Neanderthals and modern *Homo*. The observed difference in cost was 32%, nearly identical to that predicted.

Table 5

Energetic cost of locomotion (ml O₂/meter) based on limb length and body mass using a variety of mass estimates from the literature

Specimen	Present study (see text for source)	Walker and Ruff, 1993	McHenry, 1988	McHenry, 1991	Jungers, 1988 (ALLHOM)	Jungers, 1988 (NONHOM)
KNM-ER 1472	7.37	6.76	7.78	7.37	11.61	14.67
KNM-ER 1481	9.25	6.68	7.50	9.59	16.25	20.84

Because of the small mass and very short femora of AL288-1, Sts 14/34, and BOU-VP-12/1, these specimens fall substantially outside the range of data on which equations 1 and 2 are based (see Figure 3). Consequently it is inappropriate to make numerical cost estimates for these specimens. It is safe to say, however, that total cost will have been relatively low due to the smaller body mass (Steudel, 1996). The much shorter lower limbs, however, will have resulted in a very substantial increase in cost. The exact magnitude of the effect is, however, difficult to estimate.

Discussion

Thus lower limb length has a demonstrable effect on the energetic cost of locomotion with longer limbs resulting in lower costs at all speeds tested. The relatively short lower limbs characteristic of various fossil hominins would have resulted in their having higher energetic costs of locomotion than similarly sized modern *Homo*. Body mass, however, has an even more significant effect on cost (Steudel, 1994, 1996). The energetic cost of transport has a correlation with total mass of 0.95 across endotherms (Taylor et al., 1982). In the present study, with much smaller variation in mass, correlations between VO_2 and total mass remain near 0.90. As can be seen in Table 3, lean mass accounts for between 68% and 78% of the variation of cost with speed. Percent fat accounts for approximately another 10%, with the final approximately 10% due to lower limb length. Previous attempts to establish an effect of lower limb length on cost could not have detected an effect unless greater than 19% of the cost variation was attributable to lower limb length (Steudel and Beattie, 1995; Steudel, 1996). Thus the approximately 10% effect reported here was not detectable in earlier attempts.

Implications for locomotor energetics in A. afarensis

Previous work on locomotor economy in early hominids has focused primarily on the effects of body mass (Steudel, 1994, 1996; Leonard and

Robertson, 1997; Steudel-Numbers, 2003) and gait (Lovejoy, 1973, 1988; Stern and Susman, 1983; Wolpoff, 1983; Susman et al., 1985; Crompton et al., 1998; Stern, 1999). Steudel (1996) estimated cost for AL 288-1 to have been around 60% that of modern *Homo*, based on her estimated mass, with male *A. afarensis* having a cost about 30% greater than that of AL 288-1 due to their larger body size (Steudel, 1994). While the smaller size of *afarensis* results in greater locomotor economy, it also results in lower efficiency; it costs more for them to travel a given distance for each kg of body mass moved (Steudel, 1994, 1996). This distinction is important because the size of the digestive tract is highly correlated with mass (e.g. Calder, 1984), making the organism's ability to process food size dependent. Other aspects of an animal's energy balance are also size dependent (e.g. Peters, 1983; Calder, 1984).

The present study demonstrates that the shorter lower limbs characteristic of *A. afarensis* and *A. africanus* would have resulted in much higher locomotor costs reducing both efficiency and economy. Because both body mass and lower limb length in these species are so far outside the range of the present data, the formula (Eq. 1) given above to calculate the effect of lower limb length on cost cannot be applied. Extrapolating, however, from the effect of the somewhat shortened lower limbs of Neanderthals on their locomotor cost suggests that the effect on cost of lower limbs as short as those of these specimens would have been very substantial.

It is interesting that the short lower limbs characteristic of our earliest ancestors were retained for at least a half a million years, and likely longer. Ward (2002) suggests that "the basic pattern of postcranial anatomy exhibited by *A. afarensis* appears to persist for over 3 million years, suggesting that its locomotor adaptation was stable". During this phase of human evolution, it seems certain that hominins were commonly subjected to periods of reduced food availability and consequent caloric stress. In such a situation, selection for greater energetic efficiency, including a lower cost of transport, would be unavoidable and yet short lower limbs were retained for hundreds of thousands of years or more. This strongly suggests that there must have

been some considerable countervailing selection for short lower limbs. We see two possibilities.

First, some investigators argue that mechanisms of lateral balance control during locomotion were underdeveloped in AL 288-1 and even in Sts 14 (Stern and Susman, 1983; Susman et al., 1985; but see Robinson, 1972; Lovejoy, 1973). Evidence in favor of this view is particularly trenchant for AL-288-1 if one accepts the pelvic reconstruction of Stern and Susman (1983) showing the iliac blades oriented in the coronal plane. Reconstruction by Lovejoy (1973) produces quite a different picture. Robinson (1972) argued, for Sts 14, that the “weak degree of medialward bending in *A. africanus* is compensated for by the greater protuberance of the anterior part of the ilium”, resulting in perfectly adequate lateral balance control. Thus there is no consensus on how different lateral balance control was in AL 288-1, or whether AL 288-1 and Sts 14 differed in this respect. If, however, lateral balance was a problem, the shorter lower limbs may act to moderate the lateral motion of the center of mass, making balancing on two lower limbs easier. A given angular deviation of the center of mass will result in a smaller absolute deviation in a shorter limbed individual.

Second, it is widely supposed (Cartmill, 1974; Jungers, 1978; Susman et al., 1984, 1985; Stern, 2000) that short lower limbs would confer an advantage in climbing, either to maintain an effective intermembral index (Cartmill, 1974; Jungers, 1978; Susman et al., 1984, 1985) or because of the greater ability to generate the power needed to raise the center of mass against gravity (e.g. Smith and Savage, 1955). If australopiths were spending a considerable amount of time in the trees, selection for the short lower limbs useful for climbing might have mitigated selection for the longer lower limbs that would increase locomotor efficiency on the ground. Thus the retention of short limbs for so long in *Australopithecus*, in spite of the obvious disadvantage conferred in the efficiency of terrestrial locomotion, strongly suggests the retention of substantial arboreal activity.

Of course, if *Australopithecus* walked with a bent knee bent hip gait as some workers (Susman

et al., 1984; Preuschoft and Witte, 1991; Stern, 1999) think, or with a slightly elevated pelvis on the swing side (Ruff, 1998), this would cause an additional cost increment. Either gait would increase the mechanical work of locomotion, which would almost certainly result in some increase in cost.

Implications for locomotor costs within Homo

H. habilis was relatively economical (though less efficient) compared to modern humans because of their small body size. The elongation of their limbs in comparison to those of similarly sized *Australopithecus* would have given them an energetic advantage. Because total lower limb length was estimated using a value for tibia length of 85% femur length, a value that may not be appropriate for *H. habilis*, the precise amount of this energetic advantage is not clear. Substantial increase in lower limb length results in estimated cost of transport for the Nariokotome specimen being very similar to that of presumed *H. habilis*, in spite of the larger mass. The somewhat later OH 28 and OH 34, continuing the trend toward longer lower limbs, would have had particularly economical locomotion because of their long lower limbs and low mass. The extent to which this is a real trend or simply an artifact of small sample size is not entirely clear. Aiello and Key (2002) and Aiello and Wells (2002) have recently discussed the energetic consequences of the increased body size of *H. erectus* females. The substantial increase in lower limb length in (particularly the African) members of this species may result in locomotor costs lower than those of *Australopithecus*. The present estimates for the cost of locomotion for the *Homo erectus/ergaster* females OH 28 and OH 34 are 6.68 and 6.73 ml O₂ m⁻¹ respectively (Table 4). Steudel (1996) estimated the cost of locomotion for the *afarensis* female, AL 288-1 as 6.53 ml O₂ m⁻¹, using the Taylor et al., 1982 equation for endotherms based on mass alone. As discussed above, the short lower limbs of AL 288-1 would have resulted in a substantial elevation of that value. Thus the cost of locomotion in *H. erectus* females is likely to have been lower than that of *A. afarensis* females in spite of the increased

mass of the former. Thus the longer lower limbs characteristic of *H. erectus* will have, to some extent, mitigated the energetic consequences of increased body mass. How significant this would be for the overall energetic economy of the *erectus* females will, of course, depend on how much locomotion contributes to the daily energy expenditure.

That Neanderthal limbs, particularly their distal elements, are short compared to that of anatomically modern humans is widely accepted (e.g. Trinkaus, 1981, 1986; Frayer et al., 1993; Holliday and Falsetti, 1995; Holliday, 1999; Steegmann et al., 2002). Most investigators attribute the short limbs of Neanderthals to cold adaptation (e.g. Trinkaus, 1981, 1986; Holliday, 1997), an example of Allen's Rule, and see the longer lower limbs of contemporaneous near modern and modern humans as indicating a heat adapted strategy (Trinkaus, 1981, 1986; Holliday, 1997, 1999). Holliday and Falsetti (1995), however, point out that the energetic consequences of lower limb length could be an additional selective force. The present data demonstrate that the differences in lower limb length characteristic of Neanderthals and anatomically modern *Homo*, that may have been selected primarily for their thermal consequences, would have had consequences for energetic efficiency. Long limbed, anatomically modern humans would have been able to cover long distances more economically than would the larger, shorter limbed Neanderthals. The magnitude of this effect can be seen in Table 4. The cost to travel a given distance would have been around 30% greater for Neanderthals than for anatomically more modern humans.

Given this substantial energetic benefit, it is not surprising that modern humans retained their (presumably) heat adapted long lower limbs after their appearance in more northerly climates. What seems particularly interesting is that Neanderthals retained their relatively short limbs. Two alternative explanations seem likely: 1. Neanderthals possessed less sophisticated sartorial capabilities. Perhaps their ability to insulate their bodies with clothing was not sufficient to mitigate selection to reduce heat loss through the extremities. 2. The Neanderthal life style involved activities in which

the greater power conferred by their shorter lower limbs (Smith and Savage, 1955) was of more importance than energetic efficiency. There is evidence (Schmitt et al., 2003) that Neanderthals hunted with thrusting spears, engaging their prey directly. Powerful lower limbs could prove very useful in such a context.

The gradually increasing lower limb lengths seen in the hominin fossil record (Fig. 2) would have resulted in an increasing locomotor efficiency through time. Can we conclude that the increase in lower limb length apparent in the evolution of *Homo* from *Australopithecus* resulted from selection for energetic efficiency? Certainly the present study demonstrates that longer lower limbs result in lower energetic costs and that the effect can be substantial. It is difficult to believe that our ancestors lived in a setting in which caloric availability was never, or even rarely, limiting. The substantial savings in locomotor costs resulting from longer limbs could be used to enhance growth and/or reproduction, and, consequently, seem very likely to be selected. Other advantages, however, may also have accrued to longer limbs, such as increased speed and, perhaps, increased height.

These results, actually observed in living humans, are the opposite of that predicted by Kramer (1999) and Kramer and Eck (2000). This demonstrates again that mechanical models may not reflect metabolic reality. Because of the impossibility of actually measuring locomotor costs in fossil forms and the difficulty of measuring cost in many large extant mammals, there is widespread interest in developing mechanical models that allow predictions of cost based on morphology and presumed gait. The difficulty is that, to date, the relationship between mechanical work and actual metabolic cost has yet to be established. In addition to the discrepancy in the present instance, Heglund et al. (1982) demonstrated a lack of a relationship between the mechanical work of locomotion and its energetic cost. Minetti and Alexander's (1997) model for calculating the metabolic cost of human locomotion from a simple mechanical model also produced estimated costs that were substantially lower than actual metabolic costs. Biomechanical

expectations often fail to predict energetic costs. More work needs to be done using metabolic data to calibrate mechanical models.

Acknowledgements

The authors wish to thank Tim Weaver and Patricia Kramer for many useful comments on the manuscript as well as interesting general discussions. We also thank our undergraduate lab assistant, Sara Murphy, and our many subjects who so graciously donated their time. Randy Clark at the University of Wisconsin Clinics Fitness center kindly performed the DEXA scans, and Bill Feeny drew the figures. Financial support was provided by the L.S.B. Leakey Foundation.

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