

Energetics in *Homo erectus* and other early hominins: The consequences of increased lower-limb length

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Abstract

Previous studies of daily energy expenditure (DEE) in hominin fossils have estimated locomotor costs using a formula that was based on six species, all 18 kg or less in mass, including no primates, and that has a number of other problems when applied in an ecological context. It is well established that the energetic cost of human walking is lower than that of representative mammals, particularly for individuals with long lower limbs. The current study reevaluates the daily energy expenditures of a variety of hominin species using more appropriate approaches to estimating locomotor costs. To estimate DEE for primates, I relied on published data on body mass, day range, and the percentage of time spent in various activities. Based on those data, I calculated a value for nonlocomotor DEE. I then used a variant of a method that I have suggested elsewhere to calculate the daily cost due to locomotion (DEEL) and summed the two to calculate total DEE. The more up-to-date methods for calculating the cost of travel result in lower estimates of this aspect of the energy budget than seen in previous studies. Values obtained here for DEE in various representatives of *Australopithecus* are lower than reported previously by around 200 kcal/day. Taking into account the greater economy of human walking, particularly the effect of the longer lower limbs found in many later *Homo* species, also results in lowered estimates of DEE. Elongation of the lower limbs in *H. erectus* reduced relative travel costs nearly 50% in comparison to A.L. 288-1 (*A. afarensis*). The present method for calculating DEE indicates that female *H. erectus* DEE was 84% greater than that of female *Australopithecus*; this disparity is even larger than that suggested by previous workers.

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Keywords: *Homo erectus*; Energetics; Leg length; Human evolution; Locomotion

Introduction

Previous studies of primate daily energy expenditure (DEE) (Leonard and Robertson, 1997; Key and Ross, 1999) have obtained their estimates of the cost of locomotion from an equation in Taylor et al. (1970). That study included data from only six species, all nonprimates, with the largest specimen weighing 18 kg. Thus, the sample was limited and is particularly problematic when extrapolating to primates the size of *Homo*. Subsequent work by several investigators collected data on locomotor costs from a wide variety of additional species. Taylor et al. (1982) summarized data from a total of 62

species representing a much wider range of size. This sample included data from 10 primates, whose locomotor costs are consistent with that of the general sample (Heglund, 1985; Steudel-Numbers, 2003). Another potential source of error in previous efforts to estimate DEE has been that investigators calculated the cost of locomotion based both on the daily movement distance (DMD) and on the amount of time spent moving from place to place. Because the cost of locomotion (per unit time) is heavily speed-dependent (Taylor et al., 1970, 1982), estimates of cost that are based on time require data on travel speed. Unfortunately, rate of locomotion is not measured in the relevant field studies. Leonard and Robertson (1997) and Key and Ross (1999) adjusted for this factor by assuming a constant travel speed of 4.5 km/hr. While this speed seems reasonable for a variety of primates, DMD calculated under this assumption is not similar to observed values (see

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below), creating inconsistencies in applying the formula. Additional assumptions involved in estimating DEE are described in the Methods (below).

Steudel (2000) pointed out that the cost to travel a given distance is essentially invariant with speed when the “postural cost” of locomotion is omitted. Here, I use a variation on that approach, which is discussed further below. It seems worthwhile to reevaluate the scaling of DEE in primates using both more recent estimates of the scaling of locomotor cost and a relatively speed-invariant method of estimating travel costs. This issue becomes particularly important in extrapolations to the hominin fossil record. If, as many investigators believe, DMDs in *H. erectus* were similar to those of modern human hunter-gatherers, locomotor costs may have been a substantial component of DEE in this species. Earlier hominins may also have increased their DMD above that seen in modern apes (e.g., Kramer and Eck, 2000).

Steudel-Numbers and Tilkens (2004) demonstrated that longer lower limbs result in a lower cost for human walking. While *Australopithecus* retained relatively short lower limbs (Ward, 2002), it is widely recognized that an increase in lower-limb length occurred in the genus *Homo* (Ruff and Walker, 1993; Klein, 1999; Aiello and Wells, 2002; Richmond et al., 2002; Ward, 2002; Bramble and Lieberman, 2004; Steudel-Numbers and Tilkens, 2004). *Homo erectus* appears to have attained essentially human body proportions, characterized by substantial lower-limb elongation. Would the changes in lower-limb length seen in the fossil record have significantly influenced the locomotor capacities of these hominins and their DEE? The present study evaluates the magnitude of these effects. I will follow the conventional view and consider *H. erectus* and *H. ergaster* as a single taxon, referred to as *H. erectus* (Ruff and Walker, 1993; Leonard and Robertson, 1997; Wrangham et al., 1999; Aiello and Key, 2002; Aiello and Wells, 2002; O’Connell et al., 2002; Bramble and Lieberman, 2004; Steudel-Numbers and Tilkens, 2004).

The first objective of this research was to evaluate the effect on estimates of primate DEE of (1) substituting more recent estimates of locomotor costs than those of Taylor et al. (1970) and (2) using estimates of the cost of transport (per unit distance) based on Taylor et al. (1982) rather than cost of locomotion (per unit time). Once these new estimates of the primate DEE were calculated, I used them to extrapolate to the hominin fossil record. Thus, the second objective was to evaluate the effect on hominin daily energy budgets of the increased lower-limb length of *H. erectus*, and to make comparisons with samples of *Australopithecus* and early *Homo* sp.

Methods

The scaling of DEE in primates

A number of studies have estimated daily energy expenditure for various groups of primates (see summaries in Leonard and Robertson, 1997; Key and Ross, 1999). These estimates were based on estimates of the metabolic cost of various

activities coupled with estimates of the time spent in each activity from field studies. These estimates are rough. Estimates of the costs of various activities were obtained by proportional scaling of the cost of the same activity measured in humans (Coelho et al., 1976; Coelho, 1986). These human values for cost were based on a number of early studies (Passmore and Durnin, 1955; McDonald, 1961; Durnin and Passmore, 1967) cited by the World Health Organization (FAO/WHO/UNU, 1985). Often, the methodologies of these studies are not sufficiently clearly described to make one confident in the accuracy of the results. Nonetheless, I am inclined to agree with Passmore and Durnin (1955), who argued that there is probably greater error in the estimates of the time spent in various activities than in the cost of the activity itself. Another source of potential error is that time spent sleeping is assumed to be at basal or resting metabolic rate (Leonard and Robertson, 1997; Key and Ross, 1999). Given the unlikelihood of actually measuring the cost of sleeping in wild primates, this assumption seems unavoidable. On the other hand, if nighttime temperatures drop below those at which the animals are thermally neutral, they may elevate their metabolic rates above the basal level to generate heat. Passmore and Durnin (1955) thought that estimated values for daily energy expenditure (DEE) were accurate to within 10 percent. I believe that this value is a minimum for the error term. Given the current availability of data, however, no alternative strategy suggests itself. Certainly, the available data should provide reasonable general approximations.

To estimate DEE for primates, I followed the method of Leonard and Robertson (1997) and Key and Ross (1999), using data on body mass, day range, and the percentage of time spent in various activities from the electronic appendix to Key and Ross (1999). Their sample comprised 19 species, representing Cebidae, Cercopithecidae, Hylobatidae, and Hominiidae. The strategy used here and in both previous efforts involved calculating

$$DEE = \sum_{i=1}^n A_i,$$

where A_i is the energetic cost in kcal of each category of activity i and

$$A_i = (D_i \times BMR \times T_i) \times 100,$$

where T_i is the percentage of each day spent in each activity category and D_i is the “energy constant” for each activity, adapted by Leonard and Robertson (1997) from the data in Coelho et al. (1976). Specifically $D_{sleep} = 1.00$, $D_{rest} = 1.25$, $D_{feed} = 1.38$, and $D_{social} = 2.35$ (Leonard and Robertson, 1997). Daily energy expenditure was calculated in kcal per day. Basal metabolic rate (BMR) was calculated from the Kleiber (1932) equation for the interspecific relationship between BMR and mass.

Based on those data, I calculated a value for nonlocomotor DEE. Next, I calculated the cost due to locomotion (DEEL). I have argued elsewhere (Steudel, 2000) that the

cost of transport (CT, cost per unit distance) is superior to the cost of locomotion (cost per unit time) in estimating cost in an ecological context. Specifically, I advocated using what I will call the net cost of transport (NCT, the total cost per unit distance minus what has been called the “postural” cost). The NCT is thus CT subtracting the cost of other general metabolic activities during the travel period and is essentially speed-invariant (Steudel, 2000), representing the direct cost of traveling from point A to point B. During the time spent in locomotion, however, the body continues the metabolic activities of other organ systems, which is included in the calculation of CT and must be included in any estimation of total DEE. Since “postural” costs come from many activities not involving posture, I will here refer to such cost as general metabolism (GM).

It is thought that this GM cost is about 1.7 times that of BMR (Taylor, 1977). This is similar to the increase in BMR produced by light activities. James and Schofield (1990) have shown that light exercise, such as playing darts, playing the piano, carpet weaving, or cooking produce similar multiples of BMR. The multiples of BMR used for the general daily activities of primates are also similar: 1.38 for feeding and 2.35 for socializing (Leonard and Robertson, 1997; Key and Ross, 1999). Given that primates would be unlikely to drop back to BMR were they not locomoting, it seems appropriate to estimate the additional metabolic expenditure during the time spent locomoting at 1.7 times BMR. (The average of the increase in BMR due to feeding and socializing is 1.86.) Consequently, I estimated locomotor cost (per unit time) based on Taylor et al. (1982) and then calculated the time to travel the movement distance reported in Key and Ross (1999) at 4.5 km/hr, the velocity assumed by Leonard and Robertson (1997) and Key and Ross (1999). This method gives an estimate of both the cost (per unit distance) of the locomotion itself and that of the nonlocomotor metabolism occurring during the travel period.

To demonstrate the relationships of CT, NCT, and GM with speed, I regressed the three cost variables on speed. Locomotor costs were calculated from the Taylor et al. (1982) equation based on mass and velocity. This shows that the NCT is very nearly speed-invariant and that the decrease in CT with increasing speed is due to including a smaller amount of GM in the fraction of DEE assigned to locomotion.

Calculations of DEEL for estimates of primate DEE were made assuming a travel speed of 4.5 km/hr, which was converted to kcal assuming that 1 ml O₂ is the equivalent of 0.0048 kcal, given a mixed diet (R.Q. = 0.82) (McArdle et al., 2001). Nonlocomotor DEE and DEEL were then summed to calculate total DEE. The scaling of total DEE with body mass was then determined using least-squares regression. I also determined the scaling of nonlocomotor DEE with body mass, which was used to estimate the nonlocomotor portion of DEE in fossil hominins, as described below. For both equations, both the correlation coefficient and the standard error of the estimate (the standard deviation of the error term, which is the square root of the mean square residual) are reported.

Estimation of DEEL and DEE for fossil hominins

In estimating DEE and DEEL in the hominin fossil record based on both body mass and lower-limb length, one is limited to specimens for which both variables can be estimated with reasonable accuracy. The only specimens for which this is the case are *Australopithecus afarensis* (A.L. 288-1), *Homo* sp. (KNM-ER 1472 and KNM-ER 1481), and presumed *H. erectus* (OH 28, OH 34, KNM-ER 736, KNM-ER 737, KNM-ER 1808, and KNM-ER 15000). Unfortunately, the small body mass and extremely short lower limb of A.L. 288-1 put this specimen well out of the range of data that were used to develop the equation for calculating the cost of transport based on body mass and leg length. Consequently, one cannot validly estimate cost based on both mass and lower-limb length for that specimen. The remaining specimens, however, are within the range of data on which the equations are based (see Fig. 3 in Steudel-Numbers and Tilkens, 2004).

Estimates of DEE for fossil specimens were obtained in a number of ways. For *Australopithecus*, DEE was calculated from the primate regression equation determined here. Estimated body masses for male and female *A. afarensis*, *A. africanus*, *A. robustus*, and *A. boisei* were taken from Aiello and Key (2002), following McHenry (1994). This method assumes travel distances similar to those in modern apes. Kramer and Eck (2000) estimated the daily range of A.L. 288-1 to have been 20–40% smaller than that of modern *Homo*. If correct, then DEE in *Australopithecus* may have been 100 kcal or so greater than estimated.

The only two specimens attributed to early *Homo* “that do not need a considerable amount of estimation for determination of their length” are KNM-ER 1481 and KNM-ER 1472 (Haeusler and McHenry, 2004: 450). The taxonomic status of both fossils is uncertain. Geological context suggests that these fossils were older than those attributed to *H. erectus* (see summary of fossil femora and attributed dates in Steudel-Numbers and Tilkens, 2004; see also McHenry and Corruccini, 1978; Haeusler and McHenry, 2004). In addition, KNM-ER 1472 and 1481 are somewhat shorter than specimens with similar estimated mass attributed to *H. erectus* (Steudel-Numbers and Tilkens, 2004). I used these specimens here to give some idea of how the lower-limb lengths and body masses of these specimens would have influenced their DEE. Body mass estimates for both specimens are from McHenry (1992), who used least-squares regression estimates from data on *H. sapiens*. Femur length estimates were taken from Ruff and Walker (1993). Total limb length was calculated assuming a crural index of 81.1 (Jungers and Stern, 1983). Steudel-Numbers and Tilkens (2004) showed that modest variation in estimates of crural index does not have a substantial effect on estimates of cost. The DMD of early *Homo* is unknown. In estimating the daily cost of locomotion for these specimens, I attempted to bracket the actual value by using two estimates of DMD, one characteristic of modern *Pan troglodytes* (Key and Ross, 1999) and the other the average of the values given for modern foragers by Leonard and Robertson (1997) and Binford (2001).

Many workers interpret the postcranial proportions of *H. erectus* as suggestive of an adaptation to travel over considerable distances, similar to that in modern foragers (Issac, 1984; Leonard and Robertson, 1997; Foley and Elton, 1998; Wrangham et al., 1999; Binford, 2001; Aiello and Wells, 2002; O'Connell et al., 2002; Bramble and Lieberman, 2004). Here, I have followed that model. Body-mass and femur-length estimates for the fossil specimens attributed to *H. erectus* were taken from Ruff and Walker (1993). I used Ruff and Walker's (1993) adult estimates for femur length and body mass in KNM-WT 15000. Specimen KNM-WT 15000 was taken as the exemplar male *H. erectus*. I also assumed that the larger of the other *H. erectus* specimens (KNM-ER 736 and KNM-ER 1808) represent males, and accordingly, I used DMDs from modern male hunter-gatherers (see below) for estimating locomotor costs. The smaller KNM-ER 737, OH 28, and OH 34 were assumed to represent *H. erectus* females, so that DMDs were estimated based on modern female foragers (see below). Values for male and female *H. erectus* body mass obtained in this way are identical to those given in Leonard and Robertson (1997) and Aiello and Key (2002). Limb length for *H. erectus* was calculated assuming a crural index of 85 (Trinkaus, 1981; Ruff and Walker, 1993). The DMD for *H. erectus* was taken from two sources: values for !Kung and Ache societies used by Leonard and Robertson (1997) and data on a wider array of hunter-gatherers from Table 7.13 of Binford (2001).

Because human walking is energetically cheaper than that of many quadrupeds (Steudel, 1996), it would not be appropriate to use the Taylor et al. (1982) equation to estimate locomotor costs for fossil hominins. Consequently, to estimate total DEE for fossil *Homo*, I calculated the portion of DEE due to metabolic activities other than locomotion based on the data in Key and Ross (1999) and then added estimates of DEEL from the equation predicting the cost of transport based on mass and lower-limb length in Steudel-Numbers and Tilkens (2004). This allowed for the assessment of the magnitude of the energetic effect of the increased lower-limb length characteristic of *Homo*. Since that equation was based on human walking only, the results assume that distances were traveled primarily using that gait. On the other hand, if Carrier (1984) and Bramble and Lieberman (2004) are correct in supposing that running was also important in distance travel, these values would have to be modified.

To evaluate the consequences of the substantial lengthening of the lower limb that has taken place in *Homo*, I calculated the lower-limb length in the various specimens of *Homo* that would be predicted by increasing A.L. 288-1 to the size of the *Homo* specimens assuming geometric similarity. Specifically, I calculated the ratio in A.L. 288-1 of femoral length divided by the cube root of body mass, assuming a length of 28.1 cm (Jungers, 1982) and a body mass of 27.9 kg (McHenry, 1992). I then multiplied that value by the cube root of the mass estimates for each *H. erectus* specimen. To determine the robusticity of the method, the process was repeated using a mass estimate for A.L. 288-1 of 30 kg. Tibial length was calculated assuming a crural index of 81.1 (Jungers and Stern, 1983), as A.L. 288-1 did not have the elongated distal limb segments characteristic of later *Homo*.

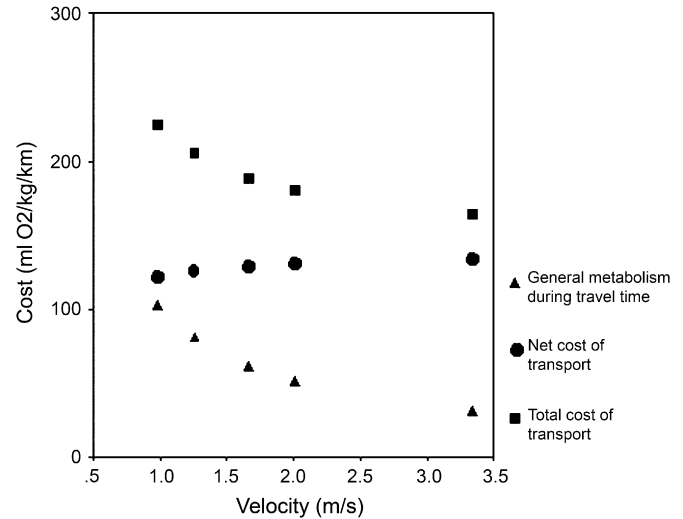


Fig. 1. Variation in the metabolic cost to travel a given distance with speed. Both cost to transport (CT) and general metabolism (GM) decline with increasing speed because travel times become shorter and, consequently, less GM is included in estimates of locomotor cost. Subtracting GM from CT gives the cost of the locomotion itself (NCT), which varies little with velocity. See text for more details.

Results

Velocity effects on the cost of transport

Figure 1 shows the relationships of CT, NCT, and GM to velocity. In all cases, the correlations with velocity are high ($r = 0.927$, $p = 0.023$ for all three equations). This result is a consequence of the fact that velocity is an important term in the equations on which the values for each cost variable are based. As is apparent, both CT and GM decline sharply with increasing velocity ($CT = 235 - 23.3 \times \text{velocity}$; $GM = 115.6 - 28.0 \times \text{velocity}$). With higher velocity comes decreased travel time, leading to less of the general metabolic cost being included in the estimate of locomotor cost. Notice that the values for slopes in the two equations are quite similar. The 95% confidence limits overlap considerably (-40 to -6 for CT compared to -48 to -7 for GM). The decrease in CT is driven by the smaller fraction of GM included at higher velocities. On the other hand, NCT increases very marginally with velocity ($NCT = 120 + 4.6 \times \text{velocity}$). In calculating DEEL, CT was the variable used, combining the actual cost of traveling from point A to point B (NCT), which is nearly speed-invariant, with an estimate of GM for the time spent traveling.

The scaling of DEE in primates

The reassessment of the scaling of DEE in primates substituting more appropriate estimates of locomotor costs resulted in the following equation:

$$\text{Log}_{10} \text{DEE} = 1.887 + 0.769(\text{log}_{10} \text{Mass});$$

$$r = 0.996, \text{ S.E.E.} = 0.034.$$

The y-intercept reported here is significantly different from that of Key and Ross (1999) at $\alpha = 0.05$ level, but the slopes are not significantly different. The equivalent equation for nonlocomotor DEE is:

$$\text{Log}_{10} \text{DEE}_{\text{partial}} = 1.864 + 0.762(\text{log}_{10} \text{Mass});$$

$$r = 0.996, \text{S.E.E.} = 0.037.$$

DEE in fossil hominins

Table 1 shows the daily energy expenditure for locomotor activities (DEEL) for specimens attributed to *H. erectus* under a variety of assumptions about limb proportions and daily movement distances. Both male and female *H. erectus* individuals had substantially lower DEEL with their actual limb proportions compared to the value of DEEL estimated under the assumption of *A. afarensis*-like proportions. Estimates of DEEL under the two different assumptions of body mass in A.L. 288-1 differ little. Using the average of the two estimates, locomotor costs increase by more than 50% in male individuals and by more than 40% in females when leg length is made proportional to that of A.L. 288-1. The !Kung and Ache DMDs for males given in Leonard and Robertson (1997) are very similar to those reported by Binford (2001), and thus there is little difference between the two DMD estimates for males. On the other hand, the two sources show somewhat greater differences between female values. Consequently, under that model, there are substantial differences in the estimates of the amount of energy that must be allocated to locomotion in females. Nonetheless both male and female *H. erectus* individuals had substantially lower DEEL values with their actual limb proportions compared to what DEEL would have been under the assumption of *A. afarensis*-like limb proportions. In the two specimens representing early *Homo* sp., the lower limbs have lengthened considerably over those of *Australopithecus*, but not to the extent seen in specimens attributed to African *H. erectus* (see Table 2 in Steudel-Numbers and Tilkens, 2004). Consequently, the effects of A.L. 288-1 limb proportions on DEEL are much less apparent (see Table 2). Nonetheless, actual limb proportions in early *Homo* sp. (as represented here by KNM-ER 1472 and 1481) would have resulted in approximately 20% savings in locomotor costs (see Table 2) over that of A.L. 288-1.

Table 3 shows the consequences for total DEE of the various assumptions about DMD and limb proportions in *H. erectus*. Again, variation in both DMD and limb proportions have conspicuous effects on total daily energy consumption. In male *H. erectus*, the total DEE would have increased more than 13% given the limb proportions of A.L. 288-1. In females, the effect was similar (7–12%). Based on the specimens included here, the lower limbs of early *Homo* sp. appear to have lengthened compared to *Australopithecus*, but not to the extent seen in *H. erectus* (Steudel-Numbers and Tilkens, 2004). This suggests some selection for energetic efficiency, but perhaps not to the extent seen in later *Homo*. Consequently, I bracketed DMDs assuming modern hunter-gatherer travel distances and those for chimpanzees (Table 4). The effect of lengthening the lower limb to the extent seen in early *Homo* would have had only a 1–2% effect on DEE under the chimpanzee foraging pattern. Under the modern hunter-gatherer model the effect would have been around 5%.

Data in Tables 3 and 4 allow comparisons of DEE in early *Homo* to that of *H. erectus*. Estimates of DEE in early *Homo* are, of course, heavily influenced by whether one assumes a chimpanzee-like foraging pattern or one characteristic of modern hunter-gatherers, as well as by the small sample of early *Homo* specimens used here. Assuming similar DMD and observed lower-limb proportions, DEE is similar in *H. erectus* and early *Homo*, in spite of the increased body size in *H. erectus*. The DEEs for female and male *Australopithecus* are estimated at around 1000 and 1400 kcal/day, respectively, assuming chimpanzee DMDs. If Kramer and Eck (2000) are correct in positing that the daily range of A.L. 288-1 would have been 20–40% smaller than that of modern *Homo*, then DEE in *Australopithecus* may have been 100 kcal or so greater than the above estimates.

Table 5 summarizes estimates of DEE in various fossil hominins based on the present study and two earlier efforts. The values given here for early *Homo* assume modern human foraging distances (values for various travel distances can be seen in Table 4). The selected values from Leonard and Robertson (1997) used the same assumptions about DMD that I used: values for *Homo* species assumed DMDs of modern foragers and values for *Australopithecus* relied on the general primate equation developed above. Again, estimates for *Homo* are based on human walking. If running was an

Table 1

Daily energy expenditure for locomotion alone (DEEL) in *H. erectus* under different assumptions regarding daily movement distance (DMD) and limb length

Specimen	Mass (kg)	Nonlocomotor DEE	DMD from Leonard and Robertson (1997)			DMD from Binford (2001)		
			Actual proportions	Proportions of A.L. 288-1 (30 kg)	Proportions of A.L. 288-1 (27.9 kg)	Actual proportions	Proportions of A.L. 288-1 (30 kg)	Proportions of A.L. 288-1 (27.9 kg)
KNM-ER 15000	68	1821.3	658.8	1057.9	1034.9	672.3	1079.6	1056.2
KNM-ER 736	62	1697.5	587.4	970.9	946.6	599.5	990.9	966.0
OH 28	54	1527.9	301.7	460.4	448.0	478.1	729.7	709.9
OH 34	51	1462.7	298.3	438.3	426.0	472.8	694.5	675.1
KNM-ER 1808	59	1634.5	311.9	498.1	485.2	494.2	789.3	768.9
KNM-ER 737	52	1484.5	294.9	445.6	433.3	467.3	706.2	686.6

Table 2
Daily energy expenditure for locomotion alone (DEEL) for early *Homo* under different assumptions regarding daily movement distance (DMD) and limb length

Specimen	Mass (kg)	Nonlocomotor DEE	Modern human DMD ¹			Chimpanzee DMD		
			Actual proportions	Proportions of A.L. 288-1 (30 kg)	Proportions of A.L. 288-1 (27.9 kg)	Actual proportions	Proportions of A.L. 288-1 (30 kg)	Proportions of A.L. 288-1 (27.9 kg)
KNM-ER 1481	57	1452.1	786.3	917.6	896.1	160.0	186.7	182.3
KNM-ER 1472	49.6	1308.3	432.7	558.0	544.0	99.0	127.7	124.5

¹ DMD = the average of those reported by Leonard and Robertson (1997) and Binford (2001).

important component of distance travel (Carrier, 1984; Bramble and Lieberman, 2004), estimates of DEEL may increase (Steudel, 1996).

These estimates of DEE are based on a number of previous estimations. Smith (1996) argued that some idea of the effect of multiple estimations on confidence intervals should be provided. None of the previous work on DEE (Leonard and Robertson, 1997; Key and Ross, 1999; Aiello and Key, 2002) has involved any formal estimation of error, except for the effect of lactation in Key and Ross (1999). Table 6 gives an idea of the error variance in the present study resulting from these multiple estimates. Estimates of DEE for *Australopithecus* are relatively simple as compared to those for *Homo*. They are based on two variables: estimated mass of fossil taxa from McHenry (1992) and the equation developed here for DEE in primates. *Australopithecus* was assumed to have DMDs typical for a primate of their body size. “Mass” gives the average mass for each taxon (McHenry, 1992), along with the 95% confidence intervals (McHenry, 1994). As is apparent, these size estimates have enormous error variance, in some cases fivefold or more, so that this large error is passed along to the estimation of any other variable based on estimated mass. “Upper DEE” and “Lower DEE” give a sense of the additional error added from the equation for primate DEE. Estimates for *Homo* will have even greater error variance because, in addition to separate estimation of DEEL, there will be error based on what assumptions are made about DMD. A sense of the magnitude of that effect can be obtained from Tables 1–4. I attempted to bracket DMD for early *Homo* by using estimates from modern foragers and from chimpanzees. As one might expect, the estimates of DEE and DEEL show considerable differences between the two assumptions. Results for *H. erectus* are much more consistent, but again, this assumes that their DMDs were similar to that of modern

foragers. Thus, while the present study results in lower estimates for both DEE and DEEL as compared to previous studies (Leonard and Robertson, 1997; Key and Ross, 1999), the error in the estimation of mass alone removes any possibility that the differences among these studies would be statistically significant.

Discussion

The scaling of DEE in primates

As indicated above, the equation developed here for the scaling of primate DEE is significantly different than that of Key and Ross (1999) in y-intercept, but not in slope. This result is due solely to different estimates of locomotor costs. The problem with using the Taylor et al. (1970) equation for estimating DEEL, and assuming a constant travel speed of 4.5 km/hr (Leonard and Robertson, 1997; Key and Ross, 1999), is that it requires estimates of both time spent traveling and distance traveled. Key and Ross (1999) provided tables (in the electronic appendix to their paper) specifying the values that they used for both of these variables. If one calculates the distance that a primate would travel at 4.5 km/hr given the percent of the day spent moving, one comes up with values that are much higher than reported DMDs, suggesting that many primate species were traveling at speeds substantially less than 4.5 km/hr. Figure 2 shows the relationship between reported DMD and DMD calculated from reported move times and assuming a travel speed of 4.5 km/hr (Leonard and Robertson, 1997; Key and Ross, 1999). The substantially elevated values of the latter are readily apparent. Thus, application of the Taylor et al. (1970) equation to these primate data, assuming a constant travel speed, results in internal inconsistencies that vitiate its applicability. It is also evident that the discrepancy

Table 3
Total daily energy expenditure (DEE) for *H. erectus* under different assumptions about daily movement distance (DMD) and limb length

Specimen	Mass (kg)	Nonlocomotor DEE	DMD from Leonard and Robertson (1997)			DMD from Binford (2001)		
			Actual proportions	Proportions of A.L. 288-1 (30 kg)	Proportions of A.L. 288-1 (27.9 kg)	Actual proportions	Proportions of A.L. 288-1 (30 kg)	Proportions of A.L. 288-1 (27.9 kg)
KNM-ER 15000	68	1821.3	2480.1	2879.2	2856.2	2493.6	2900.9	2877.4
KNM-ER 736	62	1697.5	2284.9	2668.4	2644.0	2297.0	2688.3	2663.5
OH 28	54	1527.9	1829.6	1988.3	1975.8	2006.0	2257.5	2237.7
OH 34	51	1462.7	1761.1	1901.0	1888.8	1935.5	2157.3	2137.9
KNM-ER 1808	59	1634.5	1946.4	2132.6	2119.8	2128.8	2423.9	2403.5
KNM-ER 737	52	1484.5	1779.4	1930.2	1917.8	1951.8	2190.7	2171.2

Table 4

Total daily energy expenditure (DEE) for early *Homo* under different assumptions regarding daily movement distance (DMD) and limb length

Specimen	Mass (kg)	Nonlocomotor DEE	Modern human DMD ¹			Chimpanzee DMD		
			Actual proportions	Proportions of A.L. 288-1 (30 kg)	Proportions of A.L. 288-1 (27.9 kg)	Actual proportions	Proportions of A.L. 288-1 (30 kg)	Proportions of A.L. 288-1 (27.9 kg)
KNM-ER 1481	57	1452.1	2378.4	2509.7	2488.2	1752.1	1778.8	1774.5
KNM-ER 1472	49.6	1308.3	1864.8	1990.1	1976.0	1531.11	1559.7	1556.5

¹ DMD = the average of those reported by Leonard and Robertson (1997) and Binford (2001).

between the two values increases substantially as DMDs increase, as would be expected. Thus, extrapolation of equations based on Taylor et al. (1970) to hominins, which are assumed to have substantially increased DMDs compared to nonhuman primates will substantially overestimate both DEEL and DEE.

DEE in fossil hominins

Estimates of DEE for *Australopithecus* using the present equation differ from similar estimates based on the Key and Ross (1999) equation by substantial amounts, often by more than 200 kcal per day. This difference represents nearly 15% of DEE, with values based on the present study consistently lower than those previously reported (Leonard and Robertson, 1997; Aiello and Key, 2002). The DEE estimates reported here for *H. erectus* were somewhat higher than those in Aiello and Key (2002), a consequence of differences in our estimates of DMD. Aiello and Key (2002) estimated DEE for all fossil hominins in their study based on the general primate equation developed by Key and Ross (1999), assuming typical primate DMDs. The present study assumed that DMDs in *H. erectus* were similar to those of modern hunter-gatherers. Values obtained here for *H. erectus* females are similar to those reported by Leonard and Robertson (1997), but values for *H. erectus* males are much lower, in spite of our using identical mass values. Furthermore, Leonard and Robertson's

(1997) estimates assumed DMDs characteristic of modern hunter-gatherers, similar to the assumptions made here. The difference between our estimates of DEE is a consequence of the difficulties in applying the Taylor et al. (1970) equation for DEEL in the present context, as discussed above. Because of the relatively larger travel distances assumed for male *H. erectus*, the discrepancy becomes particularly pronounced. Also, my values for DEEL take into account the relative efficiency of modern human walking, as well as the energetic benefit of the long lower limbs characteristic of this species.

Aiello and Key (2002) argued that DEE in female *H. erectus* increased substantially over that of *Australopithecus*, resulting in shifts in reproductive strategies and in the way they obtained and used energy. The results obtained here suggest that the increase in the DEE of female *H. erectus* was 84% greater than that of the average of the four female *Australopithecus*, even larger than that suggested by previous workers (Aiello and Key, 2002; Aiello and Wells, 2002). This difference stems primarily from the reduction in estimates of DEEL in *Australopithecus* that results from estimating the cost of transport using the Taylor et al. (1982) equation rather than the Taylor et al. (1970) equation. It is interesting that the estimates of DEE for *H. erectus* presented here are so similar to those suggested by Aiello and Key (2002). This appears to be a consequence of two opposing effects. Aiello and Key (2002) and Aiello and Wells (2002) assumed that general

Table 5

Estimated body mass and daily energy expenditures (DEE) for various hominin species¹

Species	Sex	Mass	DEE (present study)	DEE (Leonard and Robertson, 1997)	DEE (Aiello and Key, 2002)
<i>A. afarensis</i>	M	44.6	1430.0	1741.0	1610.6
	F	29.3	1035.2	1248.0	1175.3
<i>A. africanus</i>	M	40.8	1335.4	1622.0	1506.6
	F	30.2	1059.6	1278.0	1202.3
<i>A. robustus</i>	M	40.2	1320.2	1603.0	1489.9
	F	31.9	1105.1	1335.0	1252.1
<i>A. boisei</i>	M	48.6	1527.6	1863.0	1717.8
	F	34.0	1160.7	1404.0	1314.0
Early <i>Homo</i> ²					
KNM-ER 1481	?	57.0	2378.4	Not estimated	Not estimated
KNM-ER 1472	?	49.6	1864.8	Not estimated	Not estimated
<i>H. erectus</i>	M	63	2271.8	3165.0	2086.9
	F	52.3	1909.5	2087.0	1807.2

¹ See text for information on the assumptions made about DMD in the three studies.

² Note that the discrepancy between values from the present study and those from Leonard and Robertson (1997) for early *Homo* result in part from the fact that my estimates are specifically for particular specimens, while theirs were gender specific averages, with lower body mass averages than for the specimens used here.

Table 6
The effect of multiple estimations on DEE¹

Species	Size estimate	Mass	DEE	Upper DEE	Lower DEE
<i>A. afarensis</i>					
Male					
	Average	44.6	1430.008	1686.780	1212.323
	Upper	63.1	1867.336	2202.635	1583.079
	Lower	26.1	947.102	1117.163	802.928
Female					
	Average	29.3	1035.193	1221.072	877.609
	Upper	45.0	1439.861	1698.402	1220.676
	Lower	13.6	573.709	676.724	486.375
<i>A. africanus</i>					
Male					
	Average	40.8	1335.358	1575.135	1132.081
	Upper	58.1	1752.473	2067.147	1485.701
	Lower	23.5	873.678	1030.555	740.681
Female					
	Average	30.2	1059.559	1249.814	898.267
	Upper	49.7	1554.168	1833.235	1317.583
	Lower	10.7	477.085	562.751	404.461
<i>A. robustus</i>					
Male					
	Average	40.2	1320.231	1557.291	1119.257
	Upper	56.0	1703.557	2009.447	1444.231
	Lower	24.4	899.296	1060.774	762.400
Female					
	Average	31.9	1105.134	1303.572	936.904
	Upper	53.4	1642.401	1937.310	1392.385
	Lower	10.4	466.765	550.578	395.712
<i>A. boisei</i>					
Male					
	Average	48.6	1527.648	1801.952	1295.100
	Upper	83.2	2309.802	2724.550	1958.190
	Lower	14.0	586.641	691.978	497.339
Female					
	Average	34.0	1160.666	1369.075	983.982
	Upper	47.7	1505.846	1776.236	1276.617
	Lower	20.3	780.664	920.841	661.827

¹ Average body masses for each species are from McHenry (1992) with the upper and lower limit based on 95% confidence intervals (McHenry, 1994). Upper and lower bounds for the 95% confidence intervals about estimates of DEE from the present study are also given.

primate DMDs obtained in all hominins. Here the same assumption was made for *Australopithecus*, but DMDs similar to modern foragers were assumed for *H. erectus*. This difference elevated the present estimates of DEEL in the latter. On the other hand, the present study assumed locomotor energetics similar to those of modern humans and included a term that adjusted for the energetic benefits of human bipedalism and of the longer lower limbs of this species. Thus, the longer limbs appear to have nearly compensated for the substantial increase in DMD assumed here.

Based on the two specimens included here, no significant increase was observed in DEE in *H. erectus* as compared to early *Homo* because longer limbs in *H. erectus* mitigated the consequences of larger mass. The significance of this result is difficult to evaluate. Many estimates of average body size

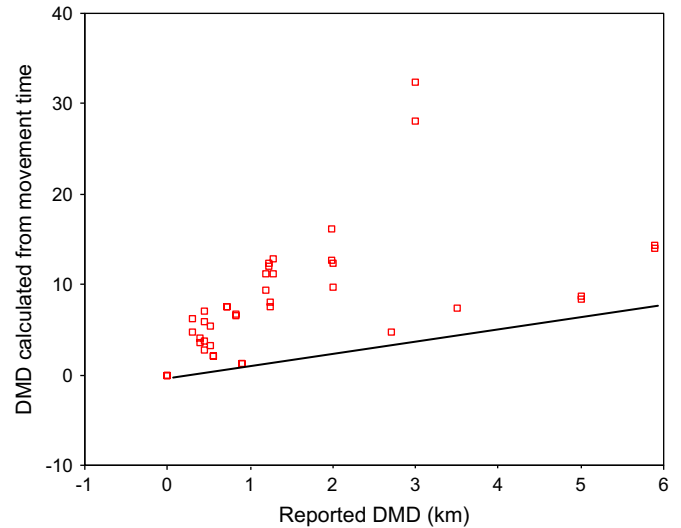


Fig. 2. A comparison of daily movement distances (DMDs) reported in the literature with DMDs calculated from reports of movement times, assuming a movement speed of 4.5 km/hr, as done by Leonard and Robertson (1997) and Key and Ross (1999). The line that would indicate equivalence of the two methods of estimating DMD is included. Note that the discrepancy between the reported DMDs and the DMDs calculated from movement time diverge as DMD increases, suggesting that many primate species were traveling at speeds substantially less than 4.5 km/hr. Thus, extrapolation of equations based on Taylor et al. (1970) to hominins, which are assumed to have substantially increased DMDs compared to nonhuman primates, will substantially overestimate DMD and, consequently, both DEEL and DEE.

in early *Homo* are lower than those estimated for the two specimens used here (e.g., McHenry, 1992). Smaller individuals would see a decrease in DEE. Furthermore, the values for early *Homo* in Table 5 assume DMDs similar to those of modern foragers, an interpretation that is certainly open to question. As can be seen in Table 4, assumptions about DMD have a substantial effect on estimates of DEE. Nonetheless, it appears that the longer limbs in *H. erectus* may have offset increases in locomotor costs due to increased mass.

Aiello and Wells (2002) suggested that there were three major changes in energy requirements in *Homo*, particularly *H. erectus*: (1) an increase in DEE due to greater body size, (2) a shift in allocation of DEE to brain metabolism, and (3) a slower rate of childhood growth. The results reported here suggest that there was a fourth major change in the energetics of *H. erectus*—namely, a reduced cost of transport due to the increased lower-limb length found in this species. This effect is so substantial that it very nearly balances the increase in DEE that would occur under the assumption of an adaptive strategy that required the adoption of DMDs similar to those of modern hunter-gatherers.

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