



The metabolic cost of walking in humans, chimpanzees, and early hominins

Herman Pontzer^{a,*}, David A. Raichlen^b, Michael D. Sockol^c

^a Washington University, Department of Anthropology, St. Louis MO 63130, USA

^b University of Arizona, Department of Anthropology, Tucson AZ 85721, USA

^c University of California at Davis, Department of Anthropology, Davis CA 95616, USA

ARTICLE INFO

Article history:

Received 3 October 2007

Accepted 28 July 2008

Keywords:

Locomotion

Energetics

Hominin evolution

Biomechanics

ABSTRACT

Bipedalism is a defining feature of the hominin lineage, but the nature and efficiency of early hominin walking remains the focus of much debate. Here, we investigate walking cost in early hominins using experimental data from humans and chimpanzees. We use gait and energetics data from humans, and from chimpanzees walking bipedally and quadrupedally, to test a new model linking locomotor anatomy and posture to walking cost. We then use this model to reconstruct locomotor cost for early, ape-like hominins and for the A.L. 288 *Australopithecus afarensis* specimen. Results of the model indicate that hind limb length, posture (effective mechanical advantage), and muscle fascicle length contribute nearly equally to differences in walking cost between humans and chimpanzees. Further, relatively small changes in these variables would decrease the cost of bipedalism in an early chimpanzee-like biped below that of quadrupedal apes. Estimates of walking cost in A.L. 288, over a range of hypothetical postures from crouched to fully extended, are below those of quadrupedal apes, but above those of modern humans. These results indicate that walking cost in early hominins was likely similar to or below that of their quadrupedal ape-like forebears, and that by the mid-Pliocene, hominin walking was less costly than that of other apes. This supports the hypothesis that locomotor energy economy was an important evolutionary pressure on hominin bipedalism.

© 2008 Elsevier Ltd. All rights reserved.

Introduction

The adoption of habitual terrestrial bipedalism is evident in the earliest fossil hominins (White et al., 1994; Ward et al., 2001; Galik et al., 2004; Zollikofer et al., 2005) and has long been considered the distinctive evolutionary event marking our divergence from the other African apes (Darwin, 1871; Dart, 1925; Washburn, 1967; Richmond et al., 2001; Ward, 2002). This critical transition has received nearly continuous attention for well over a century (see Richmond et al., 2001), and yet, robust debate regarding the origin of our bipedalism persists. Since energy efficiency is often thought to be an important evolutionary pressure, and since human walking is efficient when compared to other species (Rubenson et al., 2007), several studies over the past four decades have focused on the energetic cost of walking in early hominins and the longstanding hypothesis that selection for increased locomotor efficiency drove the adoption and persistence of hominin bipedalism (e.g., Rodman and McHenry, 1980; Stern and Susman, 1983; Susman et al., 1984; Leonard and Robertson, 1997; Sockol et al., 2007).

In this paper, we examine locomotor energetics in early hominins by applying new biomechanical and energetic data from

chimpanzees and humans to several competing hypotheses for early hominin anatomy and gait. We use chimpanzees as a model for the last common ancestor (LCA) of humans and chimpanzees, primarily as a matter of parsimony. Our place within the African ape clade as a sister-taxon to the panines (chimpanzees and bonobos; Ruvolo, 1997), and the postcranial and locomotor similarities shared by gorillas, bonobos, and chimpanzees, suggest that quadrupedal knucklewalking was the ancestral condition for the hominin lineage (Washburn, 1967; Pilbeam, 1996). Further, morphological evidence supports the hypothesis that hominins evolved from knucklewalking apes (Richmond and Strait, 2000; Richmond et al., 2001). However, while a chimpanzee-like knucklewalking ape is our working model for the human-chimpanzee LCA, the methods developed here can be extended to alternative reconstructions, such as recent work suggesting that the extended bipedal gait used by orangutans in the canopy may be the ancestral hominin condition (Thorpe et al., 2007).

Reconstructing hominin locomotor costs

Comparative approaches

Previous efforts to reconstruct locomotor energetics in early hominins have ranged from comparative allometric approaches to

* Corresponding author.

E-mail address: hpontzer@artsci.wustl.edu (H. Pontzer).

sophisticated computer modeling. In an early study investigating energetics and the origin of hominin bipedalism, Rodman and McHenry (1980), using a comparative allometric approach, presented data indicating that human walking was less costly and chimpanzee walking more costly, than expected for a quadruped of similar body mass. Noting that previous work on chimpanzees and capuchins indicated that bipedalism was no more costly than quadrupedalism for these quadrupedally-adapted primates (Taylor and Rowntree, 1973), Rodman and McHenry (1980) went on to suggest that the bipedalism of early hominins likely provided an energetic advantage over their quadrupedal forebears, since any adaptations for habitual bipedalism would likely have improved locomotor efficiency. A similar approach was taken by Leonard and Robertson (1997), who argued that the energetic advantage of early hominin bipedalism was likely even greater for females. Such comparative approaches have the advantage of being straightforward and drawing on robust data sets, but present challenges in incorporating details of early hominin locomotor anatomy other than body mass and do not consider differences in posture.

Other reconstructions of hominin locomotor performance have focused on morphology preserved in fossil material. Much of this work has centered on *Australopithecus afarensis* (Stern and Susman, 1983; Susman et al., 1984; Latimer, 1991; Stern, 2000; Ward, 2002), since postcrania from earlier hominins are poorly known (Ward, 2002). These analyses have resulted in competing reconstructions of early hominin locomotor performance, with some (Stern and Susman, 1983; Susman et al., 1984; Stern, 2000) suggesting that the hind limb anatomy of *A. afarensis* indicates an inefficient, “bent-hip, bent-knee” (BHBK) gait for this species and others (Latimer, 1991), arguing that walking in *A. afarensis* was similar in gait and efficiency to that of modern humans (see Ward, 2002 for a review of this debate). While these morphological analyses present a detailed assessment of locomotor form and function in early hominins, distinguishing between their competing conclusions is hampered by a lack of experimental studies linking the implicated aspects of morphology, such as pelvic architecture (see Stern, 2000), directly to walking kinematics or cost.

Modeling approaches

Various modeling approaches have also been used to assess locomotor performance in early hominins, and have the advantage of examining gaits and anatomy not present in extant taxa. For example, Crompton et al. (1998), using an inverse dynamics approach, suggested that a BHBK gait is implausible for *A. afarensis* due to high muscle power requirements and associated heat load (but see Stern, 1999). Recent inverse (Wang et al., 2004) and forward (Nagano et al., 2005; Sellers et al., 2005) dynamics models have indicated that, even using a human-like upright gait, *A. afarensis* would have used more energy per kilogram of body mass than do modern humans. This result is consistent with a recent numerical model (Pontzer, 2005, 2007a,b) indicating that walking costs are greater for individuals and species with shorter hind limbs, a condition present in early bipeds (Jungers, 1982). In contrast, Kramer (1999; Kramer and Eck, 2000) using an inverse dynamics model, has argued that walking in *A. afarensis* was more efficient than in modern humans due to reduced mechanical work associated with swinging shorter hind limbs.

These mathematical simulations provide useful, quantitative comparisons for different hypotheses regarding early hominin gait and posture, but like any model are constrained by the assumptions and data used to construct and validate them. Inverse dynamics models (Crompton et al., 1998; Kramer, 1999; Kramer and Eck, 2000; Wang et al., 2004) require movement patterns and limb segment properties as inputs, details typically derived from humans. Forward dynamics approaches, in which locomotion for

a given species is modeled through iterative computer simulation (Sellers et al., 2003, 2005; Nagano et al., 2005), generate movement profiles de novo and are flexible enough to incorporate a range of anatomical designs and optimization criteria. Previous forward dynamics studies of fossil hominin gait have used human-like muscle lengths and limb segment inertias as inputs (Nagano et al., 2005; Sellers et al., 2005), and a narrow range of optimization criteria (maximizing energetic efficiency: Sellers et al., 2005; maintaining a human-like posture: Nagano et al., 2005). While this powerful approach can be validated against experimental data (e.g., Sellers et al., 2003, 2005), the lack of experimental data on locomotor cost in non-human apes has prevented the validation of forward dynamics models for these species, important points of comparison for early hominins.

Experimental approaches

Experimental approaches to reconstructing early hominin walking cost have been limited by the inherent difficulties of measuring oxygen consumption during locomotion in captive primates. Until recently (Sockol et al., 2007), the only study of locomotor energy cost in apes examined two juvenile chimpanzees (Taylor and Rowntree, 1973) and notably found no difference in cost between bipedal and quadrupedal running. While this study has been central to the debate regarding early hominin energetics (e.g., Rodman and McHenry, 1980), the use of juveniles and the lack of biomechanical analyses makes it difficult to assess the reliability of the metabolic data in this study (see Steudel-Numbers, 2003), or to link the high cost of locomotion reported for chimpanzees to any aspect of anatomy or gait. Sockol and colleagues (2007) addressed these issues by examining energetics and mechanics in a sample of adult chimpanzees. Results of this study supported previous work indicating that chimpanzee locomotion is energetically costly relative to humans and other mammals (Taylor and Rowntree, 1973; Taylor et al., 1982). However, the relative costs of bipedalism and quadrupedalism in chimpanzees varied, with three of five chimpanzees using more energy to walk bipedally, and two having equivalent or even lower bipedal costs (Sockol et al., 2007). Notably, differences in cost corresponded to differences in the volume of muscle activated to support bodyweight at each step, indicating a strong causal link between locomotor anatomy, posture, and cost (Sockol et al., 2007).

Other experimental studies have used modern humans or highly trained macaques as models for investigating walking costs in early hominins. Carey and Crompton (2005), in a study of humans, found BHBK walking to be approximately 50% more expensive than upright walking, consistent with earlier modeling work (Crompton et al., 1998). A comparison of quadrupedal and bipedal walking in trained macaques (Nakatsukasa et al., 2004, 2006) indicated that bipedalism was approximately 25% more expensive, in contrast to the earlier data from chimpanzees and capuchins (Taylor and Rowntree, 1973). The use of tractable model species provides a greater degree of experimental control and depth of analysis for these studies, but as with computer models, anatomical and kinematic differences between early hominins and these species constrain their application.

An integrated experimental-numerical approach

In this study, we investigate early hominin walking cost using an integrated approach that combines experimental measures of cost and kinematics in chimpanzees and humans with a numerical model linking locomotor anatomy and gait to cost. Previous work has indicated a predictable, causal relationship between locomotor anatomy and gait, and the metabolic cost of locomotion in terrestrial animals (Kram and Taylor, 1990; Roberts et al., 1998a,b;

Pontzer, 2007a,b). We apply this framework here, using recent kinetic, kinematic, and metabolic data from chimpanzees and humans (Sockol et al., 2007), as well as published data for a range of other species to construct and test a predictive numerical model for locomotor cost based on work by Roberts and colleagues (1998a,b). Our model reliably predicts the mass-specific cost of transport ($\text{VO}_2 \text{ kg}^{-1} \text{ m}^{-1}$) using three parameters, each closely tied to anatomy or gait: 1) effective mechanical advantage, which is a function of posture and muscle moment arm length (Biewener, 1989), 2) step length, which is a function of limb length (Kram and Taylor, 1990; Hoyt et al., 2000; Pontzer, 2007a,b), and 3) muscle fascicle length. These links between anatomy, gait, and cost allow us to estimate the walking costs of early hominins for a range of hypothetical limb lengths, postures, and muscle lengths, using bipedal chimpanzees and modern humans as boundary conditions for anatomy and gait.

We then use the validated model to examine the hypothesis that locomotor efficiency was a critical selective pressure for the origin of hominin bipedalism. Comparing estimates of walking cost from the model against observed quadrupedal walking costs in chimpanzees, we test the prediction that bipedalism in early hominins was less costly than the quadrupedalism of their ape-like forebears. Specifically, we investigate the degree to which limb length, muscle length, and posture would need to change in order for early ape-like hominins to reap an energetic benefit from adopting a bipedal gait. Further, we compare the independent effects of limb length, muscle length, and posture on locomotor cost. Finally, we reexamine previous reconstructions of *A. afarensis* within the framework of the present model in order to establish a range of plausible locomotor costs for this species.

Methods

Modeling locomotor cost

While it is generally accepted that walking and running cost derive from the muscle activity required to support and propel the body and move the limbs (Biewener, 2003), several approaches have been used for predicting locomotor cost. Some workers have used multivariate statistics to link locomotor cost to anatomical variables (e.g., Steudel-Numbers and Tilkens, 2004). This inductive approach is useful for explicating the statistical relationship between anatomy and cost, but is inherently sample-specific and is therefore difficult to apply to broader comparative contexts. Others have focused on the mechanical work done to move the center of mass and limbs (Cavagna and Kaneko, 1977; Heglund et al., 1982; Willems et al., 1995; Minetti et al., 1999), or more recently, to redirect the center of mass during the heel-strike collision (Donelan et al., 2002; Collins et al., 2005). However, while the mechanical work performed must be reflected in the metabolic energy consumed during locomotion, mechanical work has proven to be a relatively poor predictor of metabolic cost in empirical studies because the apparent efficiency with which work is performed changes with speed and between species (Cavagna and Kaneko, 1977; Heglund et al., 1982; Willems et al., 1995; Minetti et al., 1999). An alternative approach is to estimate locomotor cost from the rate at which muscle force is generated to support bodyweight (Kram and Taylor, 1990; Taylor, 1994; Roberts et al., 1998a,b; Pontzer, 2005, 2007a). This force-production approach is related to analyses of work, since greater displacements of the center of mass will generally require higher forces. However, the approaches are mathematically distinct (see Kram and Taylor, 1990; Pontzer, 2005) and by focusing on muscle force rather than muscle work, the force-production approach better incorporates isometric contractions, which constitute a large portion of muscle activity during terrestrial locomotion (e.g., Roberts et al., 1997), but which perform no mechanical work because they produce no displacement.

Finally, some forward-dynamics approaches (e.g., Sellers et al., 2003, 2005) have used complex, empirically validated muscle models (e.g., Umberger et al., 2003) to convert muscle activation patterns to metabolic cost. This method shares similarities with both force-production and work approaches, since increases in work and muscle force will increase predicted cost. We use the force-production approach here, because it does not require muscle activation patterns and because it has proven reliable in predicting locomotor energy cost (Kram and Taylor, 1990; Taylor, 1994; Roberts et al., 1998a,b; Pontzer, 2005, 2007a).

During walking and running on level ground the body's center of mass rises and falls with each step. Gravity accelerates the body downward, while muscles act to accelerate the body upward. When averaged over a stride cycle, these accelerations must be equal in magnitude, effectively canceling each other. However, while the magnitude of gravity is constant, the magnitude of upward acceleration, measured as the vertical ground force exerted by the limbs, changes over the course of the stride cycle. This is most apparent during running: vertical ground force is zero during the aerial portion of the stride and two- to three-times bodyweight during stance phase. As contact time (i.e., stance phase duration) decreases, the magnitude of ground forces must increase so that the mean vertical ground force magnitude, averaged over the entire stride, is equal to bodyweight (Kram and Taylor, 1990; Biewener, 2003; Pontzer, 2005).

Previous experimental work, using the force-production approach for explaining locomotor cost (Kram and Taylor, 1990; Taylor, 1994), has indicated that the metabolic cost of locomotion is a product of the volume of muscle activated each step to produce these ground forces (Taylor et al., 1980; Kram and Taylor, 1990; Taylor, 1994; Roberts et al., 1998a,b; Pontzer, 2005, 2007a). This relationship explains both the increase in energy use with speed and the scaling of transport cost, two consistent trends in studies of running energetics. First, since contact time decreases as an animal runs faster, ground force impulses increase with speed, so that the rate of energy use ($\text{VO}_2 \text{ s}^{-1}$) increases with speed (Kram and Taylor, 1990). Second, animals with shorter legs take shorter, more frequent steps, and therefore, must generate greater ground forces at higher rates than longer-legged animals running at the same speed. Consequently, the mass-specific cost per meter ($\text{VO}_2 \text{ kg}^{-1} \text{ m}^{-1}$) is primarily a function of effective limb length, or hip height, with longer-legged animals using less energy per meter (Kram and Taylor, 1990; Pontzer, 2007a, b)¹. While walking mechanics differ markedly from running mechanics, these relationships between contact time, limb length, and cost hold; with shorter contact times leading to larger, more frequent ground forces, and thus, higher metabolic costs (Pontzer, 2005, 2007a).

Calculating the volume of muscle activated during walking or running in order to estimate metabolic cost requires information on the magnitude of the ground force impulse, the length of the muscle fascicles (l_{fasc}), and the ratio of the anatomical moment arm of the muscles (r) to the load arm of the ground force vector (R). The product of the force generated by the limb muscles and their anatomical moment arm ($F_{\text{muscle}} \times r$) must balance the torque generated by the ground force ($F_{\text{ground}} \times R$). This relationship can be rearranged as $F_{\text{muscle}} = F_{\text{ground}}/EMA$, where EMA is the effective mechanical advantage of the limb (r/R ; Biewener, 1989). Since the tension generated by a muscle is a product of the cross-sectional area of active muscle, and the magnitude and frequency of ground

¹ In contrast, the work needed to swing the limbs should theoretically increase with limb length. However, the proportion of total locomotor cost spent on leg swing is relatively small (~20%; Marsh et al., 2004; Pontzer, 2007a) and does not appear to scale strongly with body mass (Hildebrand, 1985; Pontzer, 2007a). Thus, we make the simplifying assumption of ignoring swing cost here.

force impulses is inversely proportional to contact time (t_c ; Kram and Taylor, 1990; Pontzer, 2005, 2007a), the mass-specific volume of muscle activated per second (\dot{V}_{musc}) at a given joint, or for a simplified idealized one-joint limb, can be calculated as:

$$\dot{V}_{\text{musc}} = g \times \frac{1}{\sigma} \times \frac{l_{\text{fasc}}}{\text{EMA}} \times \frac{1}{t_c} \quad (1)$$

where g is gravitational acceleration and σ is a constant relating tension to muscle cross-sectional area (usually 20 N/cm²; Biewener et al., 2004). Note that in this generalized equation, l_{fasc} and EMA are mean values for the entire limb, weighted by muscle physiological cross-sectional area (PCSA; see Roberts et al., 1998b; Biewener et al., 2004). Also, note that the volume of muscle calculated by Equation 1 is inherently mass-specific (i.e., the cm³ of muscle per kg of body mass), because the term $1/t_c$ gives the mass-specific rate of ground force production (Kram and Taylor, 1990; Pontzer, 2005, 2007a).

Because both l_{fasc} and EMA scale as (body mass)^{0.26} (Biewener, 1989; Kram and Taylor, 1990), these variables generally cancel in interspecific comparisons, leaving only $1/t_c$ as the critical variable determining the rate of muscle activation. This was the key insight of the Kram and Taylor (1990) study demonstrating that muscle activation, and thus locomotor cost, was a function of $1/t_c$ for terrestrial animals. Subsequent work demonstrated the importance of considering l_{fasc} and EMA for species that do not conform to mammalian scaling patterns (Roberts et al., 1998a,b). Given the variation in l_{fasc} and EMA among the species in our data set, particularly the long muscle fibers and crouched posture of chimpanzees compared to humans, we calculated muscle volume for all species following Equation 1 as:

$$\dot{V}_{\text{musc}} = \frac{1}{\sigma} \times \left(\frac{l_{\text{fasc},a}}{\text{EMA}_a} + \frac{l_{\text{fasc},b}}{\text{EMA}_b} + \dots + \frac{l_{\text{fasc},i}}{\text{EMA}_i} \right) \times \frac{g}{t_c} \quad (2)$$

where $l_{\text{fasc}}/\text{EMA}$ is calculated for each limb joint (a, b, ...i) and summed, and this sum multiplied by $1/t_c$. For each joint, l_{fasc} and r are calculated as the mean fascicle length and anatomical moment arm for all muscles that extend the joint, weighted by each muscle's PCSA (see Roberts et al., 1998b; Biewener et al., 2004). Equation 2 gives the rate of muscle activation (cm³ kg⁻¹ s⁻¹) to calculate the mass-specific volume of muscle activated per distance traveled (cm³ kg⁻¹ m⁻¹); Equation 2 is divided by walking or running speed to give:

$$V_{\text{musc}}/m = \frac{1}{\sigma} \times \left(\frac{l_{\text{fasc},a}}{\text{EMA}_a} + \frac{l_{\text{fasc},b}}{\text{EMA}_b} + \dots + \frac{l_{\text{fasc},i}}{\text{EMA}_i} \right) \times \frac{g}{L_{\text{step}}} \quad (3)$$

where L_{step} is step length, the horizontal distance covered by the center of mass during stance phase. This was the equation used to predict the metabolic cost per distance traveled.

Testing the model

To test the locomotor cost model, we assembled data on metabolic cost, kinematics, and kinetics during walking and running for a broad comparative sample of birds and mammals, including humans and chimpanzees (Table 1). Data for l_{fasc} , EMA, and L_{step} were taken or calculated from the literature (Roberts et al., 1998b; Thorpe et al., 1999; Biewener et al., 2004; Sockol et al., 2007). Due to the limited number of species for which published force-plate data is available, the ratio of $l_{\text{fasc}}/\text{EMA}$ for turkeys was used for guinea fowl, bobwhite quail, rhea, and emu (Roberts et al., 1998b). This approach implicitly assumes that the ratio of $l_{\text{fasc}}/\text{EMA}$ is similar for these birds, which is consistent with previous work on the metabolic cost of running in these species (Roberts et al., 1998a). Metabolic cost data, specifically, the mass-specific net cost

of transport (COT; ml O₂ kg⁻¹ m⁻¹), for dogs and all bird species; were taken from studies combining metabolic and force-production measurements (Roberts et al., 1998a, b). Cost data for chimpanzees were taken from Sockol et al. (2007) for the three chimpanzees (see Sockol et al., 2007, subjects C1–3 in their Table 1) for whom force-plate and cost data were both collected.

COT data for humans were collected separately for this study, using six healthy human subjects (2♀, 4♂; mean body mass = 69.0 kg, mean hip height = 89.6 cm) with no apparent gait abnormalities, size-matched to the samples used in force-plate studies of human walking (Sockol et al., 2007) and running (Biewener et al., 2004). Washington University approval for human data collection was obtained prior to the study and subjects gave informed consent prior to their participation; institutional guidelines were followed throughout. Walking and running costs were measured while walking and running on a treadmill (Sole Fitness F85) at a range of speeds, using standard open-flow methods described previously (Fedak et al., 1981; Pontzer, 2007a). Briefly, subjects wore a loose mask and air was drawn past their face, through the mask, at a high rate (mass-flow rate: 200–300 lpm) in order to capture all expired air. Collected air was continuously sampled and monitored for oxygen concentration (Sable Systems PA-1B) after having water vapor and CO₂ removed; oxygen concentration was recorded at a rate of 10 Hz using AxoScope data acquisition software (Molecular Devices®). Mean oxygen concentration was calculated for the last minute of each trial, after a minimum of three minutes of steady walking. Only trials in which oxygen consumption visibly plateaued, indicating steady-state aerobic energy use, were included. Note that while early energetics studies often used much longer trials (ca. 20 minutes, see for example Taylor and Rowntree, 1973; Taylor et al., 1982), the continuous monitoring of oxygen concentration afforded by improved equipment has enabled shorter trial lengths to be used (e.g., Roberts et al., 1998a; Wickler et al., 2000; Griffin et al., 2004; Pontzer, 2007a). For example, recent energetics work in horses (Wickler et al., 2000; Griffin et al., 2004) has used three-minute trials, since these shorter exercise bouts produced equivalent results to much longer (~15 minute) trials (Wickler et al., 2000) and are less taxing for the subjects.

To calculate the net rate of oxygen consumption (i.e., with resting oxygen use subtracted), we used the intercept-subtraction method as in Taylor and Rowntree (1973) and many other locomotor studies (see Taylor et al., 1982; Rubenson et al., 2007): for each subject, we fit a trendline to a plot of oxygen consumption per second versus speed and subtracted the intercept value (i.e., the expected value at 0 ms⁻¹; see Rubenson et al., 2007). This approach was used for the chimpanzee sample (Sockol et al., 2007), and is employed here for humans to maintain similar methods. Note that mean intercept cost for chimpanzees (4.63 ml O₂ s⁻¹), which was not reported in Sockol et al. (2007), was near the predicted value for their body mass (4.53; see Taylor et al., 1982), while the human intercept cost for the sample in this study (6.56) was marginally higher than expected for their mass (5.73). The net rate of oxygen consumption was divided by body mass, and the mass-specific rate of oxygen consumption was calculated for speeds matched to the walking and running force-plate studies (Table 1). This rate of oxygen consumption was then divided by speed to give the mass-specific COT (ml O₂ kg⁻¹ m⁻¹), the cost to travel a meter.

Estimating l_{fasc} and EMA

Mean fascicle length for each joint (l_{fasc}) and EMA for all species in this data set were calculated using similar methods (Roberts et al., 1998b; Biewener et al., 2004; Sockol et al., 2007). First, fascicle length for each muscle in a given muscle group (plantar flexors, knee extensors, hip extensors, shoulder extensors, elbow extensors,

Table 1
Anatomical and biomechanical variables and locomotor cost for humans and chimpanzees

Group	Mass (kg)	Hip height (cm)	Speed ^b (m s ⁻¹)	COT (V O ₂ kg ⁻¹ m ⁻¹)	L _{step} (m)	Mean muscle fascicle length and moment arms (cm)															V _{muscle} /m ^c	Source ^d							
						Hip			Knee			Ankle			Shoulder			Elbow					Wrist						
						l _{fasc}	r	R	l _{fasc}	r	R	l _{fasc}	r	R	l _{fasc}	r	R	l _{fasc}	r	R			l _{fasc}	r	R				
Quadrupedal chimpanzees ^a	49.8	49.5	1.0	0.17	0.90	15.1	5.2	26.3	7.9	2.5	1.3	7.1	3.7	10.6	10.6	1.7	1.7	6.2	2.1	5.8	8.0	2.0	1.7	43.7	1				
Bipedal chimpanzees ^a	49.8	49.5	1.0	0.25	0.64	15.1	5.2	18.3	7.9	2.5	3.7	7.1	3.7	6.0												58.2	1		
Human walk	69.3	92.3	1.3	0.08	0.83	6.5	5.3	3.0	10.0	1.4	0.7	3.9	3.9	10.6													11.4	1,2	
Human run	69.0	89.6	2.5	0.18	0.82	6.5	5.3	3.0	10.0	1.4	5.6	3.9	3.9	10.6													32.3	2,3	
Dog	4.5	22.6	2.0	0.33	0.27																							69.9	4
Turkey	5.3	35.8	2.0	0.31	0.55																							86.0	4
Emu	40.1	81.5	–	0.18	0.93																							51.2	5
Rhea	19.9	82.0	–	0.21	0.76																							62.3	5
Guinea fowl	1.3	20.3	–	0.42	0.38																							125.3	5
Bobwhite quail	0.13	10.0	–	1.05	0.11																							416.5	5

^a Subjects C1, C2, and C3 in Table 1 of Sockol et al. (2007).
^b Mean speed from force-plate trials.
^c Calculated using Eq. (3).
^d Sources: 1) Sockol et al., 2007, 2) new metabolic data, 3) Biewener et al., 2004, 4) Roberts et al., 1998b, 5) Roberts et al., 1998a.
^e Mean for all joints.
^f Estimated from ratio for turkeys.

and wrist flexors; see Roberts et al., 1998b; Thorpe et al., 1999; and Biewener et al., 2004 for group definitions) was weighted by that muscle's PCSA to determine mean l_{fasc} for that group, following Roberts et al. (1998a,b). Thus, l_{fasc} for an extensor group consisting of a set of muscles (d, e, ...i) was calculated as:

$$l_{fasc} = \frac{(l_{fasc,d} \times PCSA_d) + (l_{fasc,e} \times PCSA_e) + \dots + (l_{fasc,i} \times PCSA_i)}{\sum_d PCSA} \quad (4)$$

These cadaver-based values for the l_{fasc} of each extensor group were then scaled to each subject, assuming the relevant cadaver-based ratio of l_{fasc} to limb segment length (e.g., knee extensor l_{fasc}:thigh length) was similar for all subjects within a species. Weighted mean values of l_{fasc} for each joint for humans and chimpanzees are given in Table 1.

Mean anatomical moment arm (r) for each muscle group (Table 1) was taken from published values for humans (Biewener et al., 2004, their Table 2) or chimpanzees (Thorpe et al., 1999; their Tables 9 and 15). Shoulder values for chimpanzees were estimated from the plot of coracobrachialis and biceps moment arms about the shoulder in Thorpe et al. (1999), since the forelimb ground reaction force (GRF) vector generally passes posterior to the shoulder during stance (see Sockol et al., 2007). These mean values of r were then scaled to each subject assuming r scales geometrically, as (body mass)^{0.33}. Using a point-estimate for r is a simplification, since in fact r changes with joint angle (Thorpe et al., 1999). However, since these estimates are for mid-stance, when GRF magnitude is greatest, and since using a point-estimate of r greatly simplifies calculation of V_{MUSC}, we considered this approach appropriate for our model.

The moment arm of the ground reaction force vector (R) was calculated from kinematic and force-plate data. In the simplest case, R could be calculated solely as the perpendicular distance from the GRF vector to the center of joint rotation (e.g., Biewener, 1989; Roberts et al., 1998b; Hutchinson, 2004; Fig. 1). Here, we used a modified approach in which the GRF vector, limb segment accelerations, and the flexor moments generated by two-joint muscles were combined to calculate net joint moments, following Winter (2005) and Biewener and colleagues (2004). First, kinematic data were smoothed using a fourth-order zero-lag Butterworth filter with a 12 Hz low-pass filter, following Biewener and

colleagues (2004), and segment accelerations were calculated using the finite differences method (Winter, 2005). Net inertial, gravitational, and GRF moments (M) were then calculated for each kinematic frame at each joint using the free-body method described in Winter (2005: p.91)². Extensor muscle forces (F_{ankle}, F_{knee}, ... F_{shoulder}) needed to generate these moments were then calculated by solving the system of equations given in Biewener and colleagues (2004: Eqs. 1–3):

Hind limb system:

$$M_{ankle} = F_{ankle}r_{ankle} \quad (5)$$

$$M_{knee} = F_{knee}r_{knee} - F_{G,knee}r_{G,knee} - F_{H,knee}r_{H,knee} \quad (6)$$

$$M_{hip} = F_{hip}r_{hip} - F_{RF,hip}r_{RF,hip} \quad (7)$$

Forelimb system:

$$M_{wrist} = F_{wrist}r_{wrist} \quad (8)$$

$$M_{elbow} = F_{elbow}r_{elbow} - F_{WF,elbow}r_{WF,elbow} \quad (9)$$

$$M_{shoulder} = F_{shoulder}r_{shoulder} - F_{T,shoulder}r_{T,hip} \quad (10)$$

Flexor moments generated by two-joint muscles (G: gastrocnemius, H: hamstrings, RF: rectus femoris, WF: wrist flexors, T: triceps, long head) were calculated assuming the force produced by each muscle in an extensor group is proportional to its PCSA (Biewener et al., 2004) and using scaled anatomical moment arms for these muscles (r) as described above. For each system of equations (5–7 for the hind limb and 8–10 for the forelimb of quadrupedal chimpanzees), the muscle force at the most distal joint was calculated first (i.e., Eqs. 5 and 8) and the other two equations for each limb were then solved simultaneously.

Using a Matlab[®] routine, extensor muscle force at each joint was calculated for each video frame of a step and mean net moment was calculated for the step, disregarding any frames for which the joint

² Segment inertial properties were calculated from segment lengths following Winter (2005) for humans or from segment lengths and circumferences following Raichlen (2004) for the chimpanzees.

Table 2
Predicted dimensions for 30 kg hominoids

Model	Mass (kg)	Hip height (cm)	L_{step} (m)	Hip			Knee			Ankle			Shoulder			Elbow			Wrist			$V_{\text{muscle}}/\text{m}^3$	Estimated COT ^b
				l_{fasc}	r	R	l_{fasc}	r	R	l_{fasc}	r	R	l_{fasc}	r	R	l_{fasc}	r	R	l_{fasc}	r	R		
Quadrupedal chimpanzee	30	41.8	0.78	12.8	4.4	22.2	6.6	2.1	1.1	6.0	3.1	9.0	9.0	1.4	1.5	5.3	1.8	4.9	6.8	1.7	1.4	42.6	0.18
Bipedal chimpanzee	30	41.8	0.55	12.8	4.4	15.5	6.6	2.1	3.1	6.0	3.1	5.1										57.9	0.23
Human	30	70.0	0.64	4.9	4.0	2.3	7.6	1.1	0.5	3.0	3.0	8.0										10.9	0.09

^a Volume of muscle activated per meter traveled (cm^3/m), calculated following Equation 3.

^b Calculated from V_{muscle} using the OLS regression equation given in Fig. 2d.

moment was <25% the maximum for that step, following Biewener and colleagues (2004). Mean extensor moment (Fr) was then divided by mean GRF magnitude to calculate R. This was performed for 2 to 5 successful force plate strides per subject and the mean R for these strides used for analysis; values are given in Table 1. Calculating R in this manner is analogous to calculating R from $F_{\text{ground}} R = F_{\text{muscle}} r$, but essentially modifies F_{muscle} to account for segment inertia and gravity as well as the action of two-joint muscles. This approach is computationally more intensive, but has the advantage of providing a more accurate measure of V_{muscle} . By comparison, R calculated from the GRF vector and joint centers as in Fig. 1, neglecting limb segment inertia and two-joint muscles, provides similar measures. For the four humans and three chimpanzees for whom kinetic measurements were taken, the difference in R calculated using these two approaches did not achieve statistical significance ($p = 0.07$, student's two-tailed paired t -test), although a larger sample would likely reveal statistically significant differences. We discuss the merits and effects of these different approaches below.



Fig. 1. Schematic of parameters used to estimate active muscle volume adapted from a video frame of a bipedal chimpanzee force plate trial. F_{ground} = the ground force trajectory (indicated by block arrow); r = muscle moment arm; R = ground force moment arm; l_{fasc} = muscle fascicle length; L_{step} = step length. Circles (\otimes) indicate centers of rotation for the hip, knee, and ankle. EMA is shown here for the hip; l_{fasc} is shown for the ankle extensors.

Muscle volume versus locomotor cost

Muscle volume activated per meter was calculated following Equation 3, using values given in Table 1, assuming $\sigma = 20 \text{ N}/\text{cm}^2$. For bipedal chimpanzees, humans, and birds, $l_{\text{fasc}}/\text{EMA}$ was summed for the ankle, knee, and hip joints. EMA for running humans was adapted from walking values, keeping EMA the same at the hip and ankle, but decreasing EMA at the knee by 75%, following Biewener et al., (2004). For quadrupedal walking in chimpanzees and trotting in dogs, $l_{\text{fasc}}/\text{EMA}$ was summed for the ankle, knee, hip, wrist, elbow, and shoulder, and these values were weighted by the proportion of bodyweight supported by the forelimb or hind limb. Values of $l_{\text{fasc}}/\text{EMA}$ for the wrist, elbow, and shoulder were multiplied by 30.5%, the percentage of bodyweight borne by the forelimb, while $l_{\text{fasc}}/\text{EMA}$ values for hind limb joints were multiplied by 69.5%. Separate joint values of $l_{\text{fasc}}/\text{EMA}$ for dogs are not given in Roberts et al. (1998b), and thus, the mean value of $l_{\text{fasc}}/\text{EMA}$ was used for all joints, with forelimb and hind limb values weighted evenly (i.e., each multiplied by 50%).

The mass-specific active muscle volume per meter (Eq. 3) was plotted against COT for each species to determine the reliability of this approach for predicting locomotor cost. Ordinary least squares (OLS) was used to determine the relationship between muscle activation and cost. Other commonly used predictors of COT, including step length, body mass, and limb length, were also plotted against COT to determine the performance of these predictors relative to active muscle volume.

Modeling walking cost in early hominins

Upon validating our approach for predicting locomotor cost (see below), we used our model to estimate walking cost for early hominins. Following Equation 3, we estimated active muscle volumes for a range of morphologies and postures, manipulating l_{fasc} , EMA, and L_{step} independently. We then calculated a predicted locomotor cost using the OLS equation from the validation study.

Boundary values for l_{fasc} , EMA, and L_{step} were adapted from means for bipedal chimpanzees and humans, assuming that plausible values for early hominins fall between these extremes. In order to control for differences in morphology due purely to differences in body size, values of l_{fasc} , EMA, and L_{step} were calculated for a 30 kg human and 30 kg chimpanzee, assuming geometric similarity within species. Species means for l_{fasc} , r , and R were calculated for each species and estimated for a 30 kg individual of that species assuming that these lengths scale with (body mass)^{0.33}. To estimate a scaled value of L_{step} , the ratio of L_{step} to hip height was first calculated, since step length is a function of hip height (Kram and Taylor, 1990; Hoyt et al., 2000; Pontzer, 2007a, b). Hip height was calculated for a 30 kg human and chimpanzee assuming that this length scales with (body mass)^{0.33}. L_{step} was then calculated from hip height, using the ratio of $L_{\text{step}}/(\text{hip height})$ for chimpanzees or humans. For purposes of comparison, these values and an estimated COT were also calculated for a 30 kg

quadrupedal chimpanzee. Values of l_{fasc} , EMA, L_{step} , and COT for 30 kg chimpanzees and humans are given in Table 2.

We then estimated walking cost for a 30 kg early hominin over a range of hypothetical morphologies and gaits, varying l_{fasc} , EMA, and L_{step} independently between the chimpanzee-like and human-like conditions. These costs were compared to those for a 30 kg quadrupedal chimpanzee to determine what degree of change in l_{fasc} , EMA, or L_{step} would lower walking costs for early hominins below those of quadrupedal apes. Parameter values were calculated by the general formula:

$$\text{Parameter} = (\% \text{Chimpanzee} \times \text{ChimpanzeeValue}) + (\% \text{Human} \times \text{HumanValue}) \quad (11)$$

where %Chimpanzee and %Human are the degrees to which the parameter is chimpanzee-like or human-like, respectively, and Chimpanzee and Human Values are those estimated for a 30 kg chimpanzee or human, given in Table 2. Values were assumed to fall along a continuum between boundary conditions such that %Chimpanzee = 100 – %Human. Thus, 100%Chimpanzee is the chimpanzee-like boundary condition for a parameter, 100%Human is the human-like boundary condition (Table 2). Hip height, R, r, and l_{fasc} were calculated directly using Equation 11. For L_{step} , the ratio of $L_{step}/(\text{hip height})$ was calculated using Equation 11 assuming that the %Chimpanzee for this ratio was equal to the %Chimpanzee for EMA. This ratio and estimated hip height were then used to calculate L_{step} ; thus, L_{step} values change both as a function of hip height and EMA. Varying L_{step} in this way acknowledges its dependence on posture, as well as hip height, with more crouched postures and greater limb excursions resulting in longer L_{step} relative to hip height (see Schmitt, 1999; see Table 2).

In order to compare our approach to previous modeling efforts, we estimated walking cost for the A.L. 288 *A. afarensis* specimen. Body mass of 28 kg for A.L. 288 was taken from McHenry (1992). V_{muscle} , and thus COT, was estimated over a range of EMA and l_{fasc} , from a chimpanzee-like boundary condition to a human-like boundary condition. Boundary condition parameters were estimated assuming geometric scaling as with the 30 kg human and chimpanzee models and parameter values between these boundary conditions were calculated using Equation 11. Hip height was estimated from published femur and tibia length (McHenry, 1992), assuming knee flexion while standing was 155 degrees for the chimpanzee-like boundary condition (similar to chimpanzees in our sample) and 180 degrees for the human-like boundary condition. In all cases, 3 cm was added to femur + tibia length to account for the height of the foot, based on the ratio of lateral malleolus height to hip height for a sample of 10 humans (Pontzer, unpublished data). V_{muscle} was estimated using Equation 3 over the full range of hip height, EMA, and l_{fasc} values, from 100% chimpanzee-like to 100% human-like, and estimated COT was compared to that estimated for 30 kg chimpanzees and humans. This enabled us to determine the degree to which l_{fasc} or EMA for A.L. 288 would need to change from a primitive, chimpanzee-like condition to a derived human-like condition in order to decrease walking cost below that of similarly sized quadrupedal chimpanzees. Results were also compared to previous cost estimates for this specimen. Finally, we examined the sensitivity of our results to changes in anatomical and postural variables.

Results

Active muscle volume and locomotor cost

As predicted, the mass-specific COT ($\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) in our comparative sample was strongly correlated with the estimated volume of muscle activated per meter traveled (\dot{V}_{muscle}/m ; Fig. 2).

Further, active muscle volume was a better predictor of cost than other commonly used parameters. With bobwhite quail removed from the regression to eliminate the disproportionate influence of this smallest species, and the degrees of freedom limited to reflect the number of separate species in the analysis, \dot{V}_{muscle}/m explains 91% of the variance in COT ($r^2 = 0.91$, $df = 5$ species, $p < 0.001$), outperforming body mass ($r^2 = 0.68$, $df = 5$, $p = 0.012$), L_{step} ($r^2 = 0.59$, $df = 5$, $p = 0.021$), and hip height ($r^2 = 0.81$, $df = 5$, $p = 0.006$; Fig. 2). This holds when bobwhite quail are included in the analysis, although r^2 values increase for all comparisons: body mass = 0.85; $L_{step} = 0.94$; hip height = 0.94; $\dot{V}_{muscle}/m = 0.98$ (Fig. 2).

Walking COT for humans (mean = $0.08 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$), which was equivalent to the minimum COT values measured in these subjects, was lower than mean minimum COT values in some previous studies (see Rubenson et al., 2007). This lower estimate is partly a function of the method used to calculate COT. Here, we subtracted the intercept value of the speed/cost relationship to determine COT in order to keep methods for humans and chimpanzees similar, whereas in other human studies the resting rate of oxygen consumption is typically subtracted to calculate net cost. Our approach lowered mean COT for humans by $0.015 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ compared to the COT calculated by subtracting resting cost.

Importantly, results of the model test are not sensitive to between-study variation in COT or V_{muscle} . Increasing cost to match the mean COT published in a recent meta-analysis of human walking cost (COT = 0.10; Rubenson et al., 2007), or decreasing it to match the human COT from our previous study (COT = 0.05; Sockol et al., 2007), has a negligible effect on the overall fit of the model (r^2 of 0.90 to 0.91 for all comparisons), and the \dot{V}_{muscle}/m remains the best predictor (highest r^2 value) for COT. Similarly, increasing active muscle volume to match values from previous work ($\dot{V}_{muscle}/m = 17.90$; Biewener et al., 2004) does not affect the fit or relative performance of our model. Finally, the fit of the model is unchanged ($r^2 = 0.91$) when bird species with estimated ratios of l_{fasc}/EMA are removed.

Effects of l_{fasc} , EMA, and hip height

Given the strong correlation between \dot{V}_{muscle}/m and COT, we can use the model to parse the independent contributions of l_{fasc} , EMA, and hip height to overall differences in cost between species and gaits. When size is accounted for by comparing expected COT for geometrically scaled 30 kg subjects, differences in locomotor cost between humans and bipedal chimpanzees are nearly evenly distributed among EMA, l_{fasc} , and hip height (Fig. 3). That is, the increased economy of human walking is nearly equally a function of posture, limb length, and muscle length. Further, the difference in COT between bipedal and quadrupedal chimpanzees was equally a function of the greater contact times afforded by quadrupedal walking and the decreased EMA in these chimpanzees during bipedal trials (Table 2).

Estimating walking cost for A.L. 288

Estimated walking costs for A.L. 288 range considerably depending on the assumptions made regarding posture and muscle fiber length. Our maximum estimate, using a chimpanzee-like EMA and muscle fascicle length, is $0.19 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ or $3.78 \text{ J kg}^{-1} \text{ m}^{-1}$. In contrast, the lowest estimated cost, assuming human-like EMA and l_{fasc} , was $0.10 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ or $1.94 \text{ J kg}^{-1} \text{ m}^{-1}$. Intermediate values produced an estimate of $0.14 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ or $2.85 \text{ J kg}^{-1} \text{ m}^{-1}$ (Fig. 4). Generally, estimates of COT fall below the estimated walking cost for a quadrupedal chimpanzee of similar mass (Fig. 4). A modest change of only 6% from the chimpanzee-like boundary condition toward the

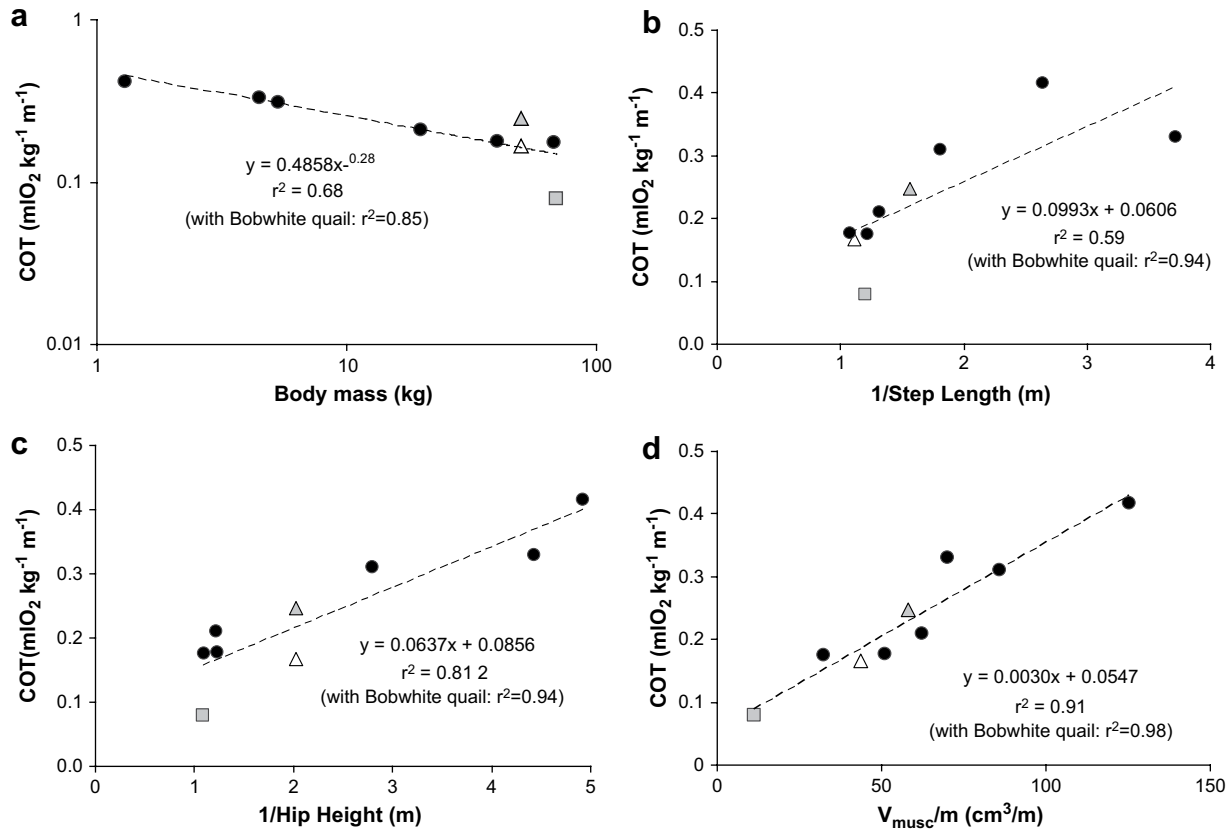


Fig. 2. Cost of transport (COT) versus a) Body mass, b) 1/Step length, c) 1/Hip height, and d) V_{muscle} . Black circles = comparative data (Table 1); gray squares = human walking; gray triangles = bipedal chimpanzees; white triangles = quadrupedal chimpanzees.

human-like condition in EMA and l_{fasc} lowers estimated COT for A.L. 288 below that of quadrupedal chimpanzees. When EMA and l_{fasc} are considered separately, an 18% change in EMA toward the human-like, fully extended condition, or a 10% change in l_{fasc} , results in lower COT than expected for similarly sized quadrupedal chimpanzees (Fig. 4). However, because hip height is shorter for A.L. 288, estimated COT was always greater than expected for a 30 kg human, even at the extreme human-like boundary conditions of EMA and l_{fasc} .

Our estimates of COT for A.L. 288 accord well with previous forward dynamics models of this specimen, which have produced COT estimates of $0.14 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ (Sellers et al., 2005) and $0.13 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ (Nagano et al., 2005). However, while COT estimates from these studies were most similar to our intermediate estimates, the gaits produced by these forward-dynamics studies were most similar to our human-like boundary condition. Thus, COT estimates following our approach are generally lower than those of forward-dynamics models; for a given gait, the V_{muscle}

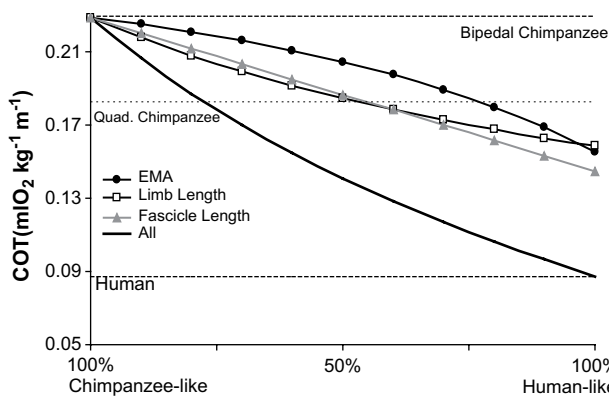


Fig. 3. Changes in estimated cost of transport (COT; $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) for a 30 kg bipedal hominin with changes in EMA (black line, circles), hind limb length (black line, squares), muscle fascicle length (gray line, triangles), and all parameters combined (black line) between chimpanzee-like and human-like boundary conditions. Estimated cost for 30 kg bipedal chimpanzees, 30 kg quadrupedal chimpanzees, and 30 kg humans are shown for comparison (dotted lines).

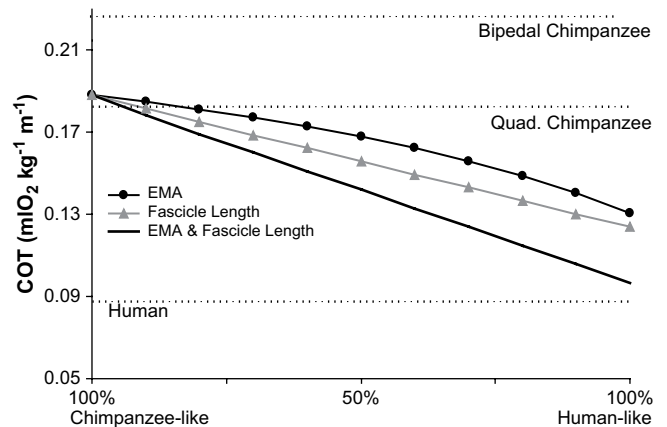


Fig. 4. Estimated cost of transport (COT; $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) for A.L. 288 over a range of EMA (black line, circles), muscle fascicle length (gray line, triangles), and both parameters combined (black line), between chimpanzee-like and human-like boundary conditions. Estimated cost for 30 kg bipedal chimpanzees, 30 kg quadrupedal chimpanzees, and 30 kg humans are shown for comparison (dotted lines).

approach used here produced a lower COT estimate. Mechanical-work approaches for estimating cost for *A. afarensis* ($0.03 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$; Fig. 9 in Kramer 1999; $0.06 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$; Wang et al., 2004) fall below the lowest estimates from our model.

Sensitivity analysis

The sensitivity of our models of early hominin locomotor cost to differences in anatomical or postural variables can be calculated directly using Equation 3. For both a hypothetical 30 kg hominin and for A.L. 288, estimated active muscle volume increases directly with l_{fasc} and R . Thus, a 20% increase in either of these variables for all joints will lead to a corresponding 20% increase in $\dot{V}_{\text{muscle}}/m$. Similarly, since $\dot{V}_{\text{muscle}}/m$ is inversely proportional to L_{step} and r , changes in these variables are inversely proportional to their effect on COT; a 20% increase in either of these variables leads to a 25% decrease in COT. When joints are considered separately, the sensitivity of our models of hominin cost are dependent on the overall reconstruction of morphology and posture. For the “100% Chimpanzee-like” boundary condition, changes at the hip have the greatest effect on COT; a 20% change in l_{fasc} or R at the hip leads to a 14% change in COT, while similar changes in these variables in the knee or ankle lead to a 3% increase in COT. In contrast, for the “100% Human-like” boundary condition, changes at the ankle have the largest effect, with a 20% increase in l_{fasc} or R leading to a 14% increase in COT, while a similar change at the knee or hip increases COT by 5% or 4%, respectively. This context dependency reflects postural differences between humans and chimpanzees and is consistent with previous work showing the ankle and hip engaging the largest muscle volumes in humans (Biewener et al., 2004) and chimpanzees (Sockol et al., 2007) respectively. The crouched posture of chimpanzees leads to large moments and muscle volumes at the hip, while the extended posture of humans leads to the highest moments and volumes at the ankle. Changes in these joints, thus, have large effects on $\dot{V}_{\text{muscle}}/m$, and hence COT, in chimpanzee- versus human-like reconstructions.

Discussion

Gait, anatomy, and walking cost in humans and chimpanzees

Our results support the hypothesis that the rate of muscle activation provides a reliable measure of locomotor cost. The volume of muscle activated per meter traveled ($\dot{V}_{\text{muscle}}/m$) explained a greater proportion of the variance in COT both between species and between gaits, than any other predictor used here, including body mass. When bobwhite quail are included in the analysis, $\dot{V}_{\text{muscle}}/m$ explained a remarkable 98% of the variation in COT (Fig. 2). The model has such broad applicability because, by explicitly incorporating step length, EMA, and fascicle length, it accounts for effects of body size, speed, posture, and gait. This is consistent with work indicating that these biomechanical variables underlie the scaling of locomotor cost for terrestrial animals (Kram and Taylor, 1990; Roberts et al., 1998a,b; Pontzer, 2007a,b). The success of the model suggests that V_{muscle} may be useful for comparing locomotor cost and efficiency when oxygen consumption cannot be measured directly, as in fossil species or untrained primates. This approach provides a more reliable estimate of locomotor cost than allometric estimates, and also provides a means of linking metabolic cost directly to muscular and skeletal anatomy.

The link between $\dot{V}_{\text{muscle}}/m$ and COT is consistent with variation in gait and cost in adult chimpanzees noted previously (Sockol et al., 2007). Subject C4 in Sockol et al., (2007) used 28% greater hip flexion and 17% greater knee flexion during quadrupedal walking compared to the other chimpanzees. Bipedal joint angles were similar to other chimpanzees (see Sockol et al., 2007, their Fig. 4),

but contact times for this individual were 5% longer during bipedal trials, while all other chimpanzees used longer steps during quadrupedal walking. While force plate data were not collected for this individual, when percentage differences in minimum hip and knee angles are converted into proportional differences in R and active muscle volumes are calculated following Equation 3, estimated $\dot{V}_{\text{muscle}}/m$ during quadrupedal walking ($84.0 \text{ cm}^3 \text{ kg}^{-1} \text{ m}^{-1}$) is 27% greater than for bipedal walking ($61.8 \text{ cm}^3 \text{ kg}^{-1} \text{ m}^{-1}$). Given the necessary estimation of R , this difference in muscle activation corresponds reasonably well to the 44% greater COT during quadrupedal walking for this individual.

The COT value for walking humans in this study ($0.08 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) is within the range (0.08–0.13), but below the mean (0.10) of previous estimates of walking COT reported in a recent meta-study of human locomotor cost (Rubenson et al., 2007). The COT value in our previous report (Sockol et al., 2007) was lower still (0.05), further highlighting the potential effect of individual and between-study variation in comparisons of locomotor performance. These differences are likely due in part to the relatively small sample sizes used, and the intercept-subtraction approach used here and in our previous study (Sockol et al., 2007) to calculate net cost. Importantly, lower COT for humans do not affect the overall fit of the model; r^2 values remained above 0.94 when estimates of COT or $\dot{V}_{\text{muscle}}/m$ from previous human studies were used, and active muscle volume remains the best predictor of differences in COT between species and gaits for humans and chimpanzees. Still, given the variation in COT observed across human studies (Rubenson et al., 2007) and within a sample of adult chimpanzees (Sockol et al., 2007), broad comparisons across species should be tempered with an understanding of the underlying variation in locomotor performance. For example, depending on the individuals or samples used for comparison (Rubenson et al., 2007; Sockol et al., 2007), humans have COTs that are between ~40%–80% lower than chimpanzees.

Differences in walking cost between gaits and species were attributable nearly equally to differences in posture, limb length, and muscle fascicle length. In particular, the importance of l_{fasc} in determining locomotor cost is notable. Most previous considerations of differences in human, ape, and fossil hominin locomotor performance have focused on gait (Jenkins, 1972; Stern and Susman, 1983; Crompton et al., 1998) or limb length differences (Jungers, 1982; Kramer, 1999). While these aspects of locomotor anatomy and gait are clearly important, our results indicate that muscle morphology must be considered as well, in order to develop a complete reconstruction of locomotor performance. Recent work on muscle morphology of apes (Thorpe et al., 1999; Payne et al., 2006a,b) may prove critical in moving locomotor comparisons of living and extinct hominoids beyond skeletal comparisons. Further, future work might improve on the accuracy of estimating $\dot{V}_{\text{muscle}}/m$ and COT by taking non-invasive measures of these parameters for individual subjects, rather than relying on scaled measurements taken from cadaveric specimens.

Limitations of the model

As noted above, a number of approaches have been used to estimate locomotor costs for extinct hominins. The novel method we propose here has the advantage of explicitly linking locomotor anatomy to cost using a model that can be verified across a range of gaits and species. However, as with any modeling study, the results are only as reliable as the underlying assumptions. Perhaps most critically, our approach uses estimated muscle force production and active muscle volume to predict metabolic cost. While this approach is strongly supported by previous empirical work (Kram and Taylor, 1990; Taylor, 1994; Roberts et al., 1998a,b; Pontzer, 2005, 2007a) and explains over 90% of the variance in cost in this data set

(Fig. 2), it does not directly consider mechanical work or collisional energy losses, which must also contribute to cost (see Minetti et al., 1999; Donelan et al., 2002). Incorporating collisional losses and mechanical work may improve the fit of the model, and could potentially affect our results.

One important assumption we used in estimating cost for A.L. 288 and 30 kg chimpanzees and humans is that EMA and I_{fasc} scale isometrically. This assumption has the effect of decreasing estimated cost, since the ratio of r to R remains constant if both scale with $(\text{body mass})^{0.33}$. In contrast, empirical data for the scaling of r and R indicate that EMA scales with $(\text{body mass})^{0.26}$ (Biewener, 1989). As a result, our estimated costs for 30 kg chimpanzees and humans are near the observed COT for our larger-bodied subjects, in contrast to the expectation of increasing COT with smaller body size. This departure from the empirically based expectation for EMA is suitable for this investigation, since we seek to model explicitly chimpanzee-like and human-like boundary conditions. However, future work might explore the effect of different scaling regimes on \dot{V}_{musc}/m and COT.

Another important simplification in our model is the calculation and use of a single measure of I_{fasc} , r , and R for each joint and extensor group. This approach has been used before (e.g., Roberts et al., 1998b) and produces estimates of active muscle volume that correspond well with locomotor cost (Fig. 2), but it condenses a great deal of variation in musculoskeletal anatomy (e.g., Thorpe et al., 1999). Future work might improve upon our model by accounting for the relationship between joint angle and r , or by testing the assumption that each muscle's contribution in extensor force is proportional to its PCSA. Further, while the approach we used in estimating R has the advantage of incorporating the segmental inertia and the effects of two-joint muscles into estimates of active muscle volume, it is a departure from the simplest means of calculating this variable (e.g., Fig. 1). The more involved approach is useful here, as it enables the model to capture changes in segmental inertia and two-joint muscles between the chimpanzee-like and human-like boundary conditions. Still, since R was not significantly different when calculated using either method ($p = 0.07$, Student's two-tailed paired t -test), and since calculating R using the simpler approach (Fig. 1) does not affect the fit of the model (r^2 remains 0.95), the computationally simpler method may be preferred in some studies. Regardless, the effects of different approaches to estimating R warrant future investigation, since sensitivity analyses indicate that changes in R are directly proportional to changes in estimated muscle activation and cost.

While long-term bipedal training may affect locomotion in habitual quadrupeds (Preuschoft et al., 1988; Nakatsukasa et al., 1995), the effect of bipedal training on chimpanzee walking kinematics and cost in this data set are likely small. As facultative bipeds, the chimpanzees in this study did not need to be trained to walk bipedally per se. Rather, the training regimen was directed toward acclimating the chimpanzees to the treadmill and to walking for adequately long duration to measure steady-state oxygen use (Sockol et al., 2007). The percentage of each day spent walking or standing bipedally for these chimpanzees was not measured, but is likely quite low. Even for the duration of the Sockol et al. (2007) study, training sessions rarely exceeded an hour, and only a small portion of each session was spent engaged in bipedal walking, with multiple rest breaks interspersed between treadmill trials; chimpanzees spent the great majority of their day walking as they chose, usually quadrupedally. Still, since the chimpanzees in this data set perform occasionally for commercial purposes, they likely spend more time bipedally over the course of their lives than do wild chimpanzees (Hunt, 1992). Therefore, while joint angles and ground force patterns appear broadly similar to those reported for untrained chimpanzees (e.g., Kimura, 1991), the chimpanzees in

this study may be more accustomed to walking bipedally than their wild counterparts.

The use of chimpanzees as a model for the human–chimpanzee LCA affects our analysis by setting a chimpanzee-like boundary condition for our reconstructions of hominin anatomy, posture, and cost. However, our approach is flexible, and can be adapted to other models of the human–chimpanzee LCA by using anatomical data from other apes (e.g., Payne et al., 2006a,b) or otherwise modifying these variables. For example, Payne and colleagues (2006a,b) report shorter fascicle length and longer moment arms for the hip flexors of orangutans as compared to chimpanzees. This, in addition to the more extended hind limb postures reported for orangutans (Thorpe et al., 2007), would presumably lead to lower estimates of cost for an orangutan-like model of a proto-hominin, although differences in step length and other extensor groups would need to be considered. More kinetic and kinematic data from other apes, as well as more anatomical data for late Miocene apes, may help improve and refine models of the human–chimpanzee LCA.

Walking cost in early hominins

Our approach produces estimates of COT for A.L. 288 that correspond reasonably well with previous forward-dynamics models of this specimen. Given the different sets of assumptions that go into these different modeling approaches, the similarities in estimated cost are notable. Interestingly, COT estimates produced by computer simulations (Nagano et al., 2005; Sellers et al., 2005) are somewhat higher than those produced by our human-like boundary condition, the condition that most closely resembles the gait of these forward-dynamics models. This difference in COT between computer-modeling and experimentally-based estimates has been noted previously (Sellers et al., 2005). As discussed by Sellers and colleagues (2005), the increased COT from computer simulations may be due to the absence of common energy-saving mechanisms in these computer models, such as elastic energy storage in the tendons. While these energy saving mechanisms are not explicitly modeled using \dot{V}_{musc}/m to predict COT, using the ratio of \dot{V}_{musc}/m to COT borne from experimental data may effectively account for them by assuming, implicitly, that the same energy saving mechanisms used by extant species are available to the modeled fossil species.

Mechanical work estimates of walking cost (Kramer, 1999; Wang et al., 2004) in *A. afarensis* are well below our estimates based on \dot{V}_{musc}/m . This is perhaps unsurprising, as mechanical work is typically a poor predictor of metabolic cost (Cavagna and Kaneko, 1977; Heglund et al., 1982). Still, while some have previously cautioned against using mechanical work to estimate the metabolic cost of walking (Wang et al., 2004), estimates of mechanical work are often used as measures of efficiency and energy savings, particularly in walking gaits. These estimates of work may be useful for comparisons of gait, but they cannot be translated directly to metabolic cost because of the inherent inefficiency of muscle and the complex ways in which metabolic power is related to mechanical power in musculoskeletal systems.

Walking cost and the evolution of hominin bipedalism

Estimates of walking cost for the A.L. 288 specimen are generally lower than those expected for a similarly sized quadrupedal chimpanzee. Modest changes of less than 10% of the morphospace between chimpanzee- and human-like boundary conditions were sufficient to bring estimated COT below that for quadrupedal chimpanzees (Fig. 4). Therefore most, if not all, reconstructions of gait and posture in this species (Stern and Susman, 1983; Latimer, 1991; Stern, 2000) would result in lower walking costs relative to quadrupedal apes. While the degree to which the posture of

A. afarensis was crouched is not typically specified in studies proposing a bent-hip, bent-knee gait for this species (Stern and Susman, 1983; Stern, 1999, 2000), the more dorsally projecting ischial attachment for the hamstrings (Robinson, 1972; Stern and Susman, 1983) suggests a less crouched posture than that seen in chimpanzees. Any change toward a more extended posture, in conjunction with the longer hind limbs of A.L. 288 relative to chimpanzees, would result in a lower cost of walking than seen in quadrupedal apes. In contrast, because the hind limb of A.L. 288 is short relative to modern humans (Jungers, 1982), estimated walking cost remains above the human-like boundary condition even when human-like values of l_{fasc} and EMA are used (Fig. 4). These results, in addition to similar estimates of walking cost for A.L. 288 from forward dynamics models (Nagano et al., 2005; Sellers et al., 2005), suggest that, at least by 3 million years ago hominin bipedalism was more economical than that of our ape-like quadrupedal forebears, but not as economical as that of modern humans.

A lack of adequate postcranial evidence makes it more difficult to test hypotheses regarding walking cost in the earliest hominins. The substantial, independent effects of l_{fasc} , EMA, and hip height on differences in COT between bipedal and quadrupedal chimpanzees (Fig. 3) indicate that there are a number of morphological and postural modifications that would have lowered the walking cost of an early, ape-like bipedal hominin below that of a quadrupedal ape. Further, these changes would not need to be dramatic to lower the cost of hominin bipedalism below that of quadrupedal apes. Interestingly, changes in EMA are expected to have a smaller initial effect on COT than changes in l_{fasc} or hind limb length (Fig. 3), suggesting that any selection for lower walking cost might be expected to act on muscle morphology and limb length ahead of posture. However, the relative lability and heritability of these traits is unknown.

Overall, our analyses indicate that no adaptive hurdle would need to be overcome during the transition to bipedalism. While the three chimpanzees studied here had greater bipedal walking costs, our modeling of V_{musc} and COT indicates that relatively minor changes in gait, muscle morphology, and hind limb length, equivalent to approximately 25% of the morphospace between human- and chimpanzee-like boundary conditions, would have lowered the cost of bipedal walking below that of quadrupedalism (Fig. 3). Further, the observed variation in gait and cost in adult chimpanzees (Sockol et al., 2007; see above) suggests that bipedalism in even the earliest, most primitive hominins could have been more economical than quadrupedalism. Our results also suggest that locomotor economy was an important selective force shaping anatomy in early hominins. By 3 million years ago, with *A. afarensis*, hominin walking cost was likely well below that of quadrupedal apes (Figs. 3 and 4) due to increased hind limb length and pelvic changes allowing greater hip and knee extension. Postcranial evidence for earlier species is needed to test whether these same adaptations are apparent in the earliest hominins.

At least 30 distinct skeletal features have been used to argue for the efficiency or inefficiency of walking in *A. afarensis* (see Stern, 2000; their Tables 1 and 2), although most have yet to be linked empirically to locomotor speed or cost. The model employed here identifies limb length, posture and muscle moment arm length (EMA), and muscle length (l_{fasc}) as the primary variables determining locomotor cost. Despite the broad range of gaits and locomotor anatomies represented in our comparative sample, these four variables captured 98% of the variation in locomotor cost suggesting that while other features undoubtedly affect walking efficiency, they likely play a relatively smaller role. As such, functional analyses of hominin locomotor anatomy may do well to take an explicitly hierarchical approach, placing greatest weight on the anatomical variables known to account for the largest amount of

variation in performance. For example, quantitatively tying anatomical traits such as ischial orientation to posture would greatly improve our ability to model early hominin costs. Such an approach might advance the current debate regarding terrestrial and arboreal adaptations in *A. afarensis* and other early hominins.

Biomechanical analyses and reconstructions can only demonstrate how the performance of a structure evolved, and perhaps provide clues to its evolutionary success. But even if bipedalism in early hominins was more economical, this need not be why it evolved initially. Hominin bipedalism may have originated in a different behavioral context in which energetic advantages were not critical (see Thorpe et al., 2007). Indeed, morphological solutions for decreasing locomotor cost, including increased hind limb length, improved EMA, and shorter muscle fibers, are presumably available to quadrupedal apes and would not require a transition to bipedalism. The maintenance of long muscle fibers, short hind limbs, and crouched postures in chimpanzees may suggest that competing selection pressures, such as safety in the canopy (Pontzer and Wrangham, 2004), outweigh selection for locomotor economy in this species, and perhaps in the other non-human apes. In contrast, the absence of an energetic hurdle to bipedalism, combined with evidence that the earliest hominins may well have reaped energy benefits (Fig. 3) and that hominins had undergone selection for walking economy beyond that of quadrupedal apes by the mid-Pliocene (Fig. 4), suggests that locomotor energy economy was important in the success and persistence of the hominin radiation.

Acknowledgements

A.A. Biewener, D.E. Lieberman, J. Jones, and P. Rodman generously provided necessary equipment for this study. Three anonymous reviewers provided useful comments. This project was supported by grants from the National Science Foundation BCS-0424092 to M.D.S. and the L.S.B. Leakey Foundation.

References

- Biewener, A.A., 1989. Scaling body support in mammals: limb posture and muscle mechanics. *Science* 245, 45–48.
- Biewener, A.A., 2003. *Animal Locomotion*. Oxford University Press.
- Biewener, A.A., Farley, C.T., Roberts, T.J., Temaner, M., 2004. Muscle mechanical advantage of human walking and running: implications of energy cost. *J. Appl. Physiol.* 97, 2266–2274.
- Carey, T.S., Crompton, R.H., 2005. The metabolic costs of “bent-hip, bent-knee” walking in humans. *J. Hum. Evol.* 48, 25–44.
- Cavagna, G.A., Kaneko, M., 1977. Mechanical work and efficiency in level walking and running. *J. Physiol.* 268, 467–481.
- Collins, S., Ruina, A., Tedrake, R., Wisse, M., 2005. Efficient bipedal robots based on passive dynamic walkers. *Science* 307, 1082–1085.
- Crompton, R.H., Li, Y., Wang, W.J., Gunther, M.M., Savage, R., 1998. The mechanical effectiveness of erect and “bent-hip, bent-knee” bipedal walking in *Australopithecus afarensis*. *J. Hum. Evol.* 35, 55–74.
- Dart, R.A., 1925. *Australopithecus africanus*: the man-ape of South Africa. *Nature* 115, 195–199.
- Darwin, C., 1871. *The Descent of Man and Selection in Relation to Sex*. John Murray, London. reprinted by Princeton University, 1981.
- Donelan, J.M., Kram, R., Kuo, A.D., 2002. Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. *J. Exp. Biol.* 205, 3717–3727.
- Fedak, M.A., Rome, L., Seeherman, H.J., 1981. One-step N_2 -dilution technique for calibrating open-circuit VO_2 measuring systems. *J. Appl. Physiol.* 51, 772–776.
- Galik, K., Senut, B., Pickford, M., Gommery, D., Treil, J., Kuperavage, A.J., Eckhardt, R.B., 2004. External and internal morphology of the BAR 1002 '00 *Orrorin tugenensis* femur. *Science* 305, 1450–1453.
- Griffin, T.M., Kram, R., Wickler, S.J., Hoyt, D.F., 2004. Biomechanical and energetic determinants of the walk-trot transition in horses. *J. Exp. Biol.* 207, 4215–4223.
- Heglund, N.C., Fedak, M.A., Taylor, C.R., Cavagna, G.A., 1982. Energetics and mechanics of terrestrial locomotion IV: total mechanical energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* 79, 57–66.
- Hildebrand, M., 1985. Walking and running. In: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B. (Eds.), *Functional Vertebrate Morphology*. Harvard University, pp. 38–57.

- Hoyt, D.F., Wickler, S.J., Cogger, E.A., 2000. Time of contact and step length: the effect of limb length, running speed, load carrying, and incline. *J. Exp. Biol.* 203, 221–227.
- Hunt, K.D., 1992. Positional behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *Am. J. Phys. Anthropol.* 87, 83–107.
- Hutchinson, J.R., 2004. Biomechanical modeling and sensitivity analysis of bipedal running ability. I. Extant taxa. *J. Morphol.* 262, 421–440.
- Jenkins Jr., F.A., 1972. Chimpanzee bipedalism: cineradiographic analysis and implications for the evolution of gait. *Science* 178, 877–879.
- Jungers, W.L., 1982. Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis* (A.L. 288-1). *Nature* 297, 676–678.
- Kimura, T., 1991. Voluntary bipedal walking in infant chimpanzees. *Hum. Evol.* 6, 377–390.
- Kram, R., Taylor, C.R., 1990. Energetics of running: a new perspective. *Nature* 346, 265–267.
- Kramer, P.A., 1999. Modelling the locomotor energetics of extinct hominids. *J. Exp. Biol.* 202, 2807–2818.
- Kramer, P.A., Eck, G.G., 2000. Locomotor energetics and leg length in hominid bipedality. *J. Hum. Evol.* 38, 651–666.
- Latimer, B., 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Coppens, Y., Senut, B. (Eds.), *Origine(s) de la bipédie chez les Hominides*. CRNS Editions, Paris, pp. 169–176.
- Leonard, W.R., Robertson, M.L., 1997. Rethinking the energetics of bipedality. *Curr. Anthropol.* 38, 304–309.
- Marsh, R.L., Ellerby, D.J., Carr, J.A., Henry, H.T., Buchanan, C.I., 2004. Partitioning the energetics of walking and running: swinging the limbs is expensive. *Science* 303, 80–83.
- McHenry, H.M., 1992. Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 87, 407–431.
- Minetti, A.E., Ardigo, L.P., Reinach, E., Saibene, F., 1999. The relationship between mechanical work and energy of locomotion in horses. *J. Exp. Biol.* 202, 2329–2338.
- Nagano, A., Umberger, B.R., Marzke, M.W., Gerritsen, K.G., 2005. Neuromusculoskeletal computer modeling and simulation of upright, straight-legged, bipedal locomotion of *Australopithecus afarensis* (A.L. 288-1). *Am. J. Phys. Anthropol.* 126, 2–13.
- Nakatsukasa, M., Hayama, S., Preuschoft, H., 1995. Postcranial skeleton of a macaque trained for bipedal standing and walking and implications for functional adaptation. *Folia Primatol.* 64, 1–29.
- Nakatsukasa, M., Hirasaki, E., Ogihara, N., 2006. Energy expenditure of bipedal walking is higher than that of quadrupedal walking in Japanese macaques. *Am. J. Phys. Anthropol.* 131, 33–37.
- Nakatsukasa, M., Ogihara, N., Hamada, Y., Goto, Y., Yamada, M., Hirakawa, T., Hirakasi, E., 2004. Energetic costs of bipedal and quadrupedal walking in Japanese macaques. *Am. J. Phys. Anthropol.* 124, 248–256.
- Payne, R.C., Crompton, R.H., Isler, K., Savage, R., Vereecke, E.E., Gunther, M.M., Thorpe, S.K., D'Aout, K., 2006a. Morphological analysis of the hind limb in apes and humans. I. Muscle architecture. *J. Anat.* 208, 709–724.
- Payne, R.C., Crompton, R.H., Isler, K., Savage, R., Vereecke, E.E., Gunther, M.M., Thorpe, S.K., D'Aout, K., 2006b. Morphological analysis of the hind limb in apes and humans. II. Moment arms. *J. Anat.* 208, 725–742.
- Pilbeam, D.R., 1996. Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. *Mol. Phylogenet. Evol.* 5, 155–168.
- Pontzer, H., 2005. A new model predicting locomotor cost from limb length via force production. *J. Exp. Biol.* 208, 1513–1524.
- Pontzer, H., 2007a. Predicting the cost of locomotion in terrestrial animals: a test of the LiMb model in humans and quadrupeds. *J. Exp. Biol.* 210, 484–494.
- Pontzer, H., 2007b. Limb length and the scaling of locomotor cost in terrestrial animals. *J. Exp. Biol.* 210, 1752–1761.
- Pontzer, H., Wrangham, R.W., 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *J. Hum. Evol.* 46, 315–333.
- Preuschoft, H., Hayama, S., Günther, M.M., 1988. Curvature of the lumbar spine as a consequence of mechanical necessities in Japanese macaques trained for bipedalism. *Folia Primatol.* 50, 42–58.
- Raichlen, D.A., 2004. Convergence of forelimb and hind limb natural pendular periods in baboons (*Papio cynocephalus*) and its implication for the evolution of primate quadrupedalism. *J. Hum. Evol.* 46, 719–738.
- Richmond, B.G., Begun, D.R., Strait, D.S., 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. *Am. J. Phys. Anthropol.* S33, 70–105.
- Richmond, B.G., Strait, D.S., 2000. Evidence that humans evolved from a knuckle-walking ancestor. *Nature* 404, 382–385.
- Roberts, T.J., Marsh, R.L., Weyand, P.G., Taylor, C.R., 1997. Muscular force in running turkeys: the economy of minimizing work. *Science* 275, 1113–1115.
- Roberts, T.J., Kram, R., Weyand, P.G., Taylor, C.R., 1998a. Energetics of bipedal running: I. metabolic cost of generating force. *J. Exp. Biol.* 201, 2745–2751.
- Roberts, T.J., Chen, M.S., Taylor, C.R., 1998b. Energetics of bipedal running: II. limb design and running mechanics. *J. Exp. Biol.* 201, 2753–2762.
- Robinson, J.T., 1972. *Early Hominid Posture and Locomotion*. Chicago University Press.
- Rodman, P.S., McHenry, H.M., 1980. Bioenergetics and the origin of hominid bipedalism. *Am. J. Phys. Anthropol.* 52, 103–106.
- Rubenson, J., Heliam, D.B., Maloney, S.K., Withers, P.C., Lloyd, D.G., Fournier, P.A., 2007. Reappraisal of the comparative cost of human locomotion using gait-specific allometric analyses. *J. Exp. Biol.* 210, 3513–3524.
- Ruvolo, M., 1997. Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Mol. Biol. Evol.* 14, 248–265.
- Schmitt, D., 1999. Compliant walking in primates. *J. Zool. Lond.* 248, 149–160.
- Sellers, W.L., Cain, G.M., Wang, W., Crompton, R.H., 2005. Stride lengths, speed, and energy costs in walking of *Australopithecus afarensis*: using evolutionary robotics to predict locomotion of early human ancestors. *J. R. Soc. Interface* 22, 431–441.
- Sellers, W.L., Dennis, L.A., Crompton, R.H., 2003. Predicting the metabolic energy costs of bipedalism using evolutionary robotics. *J. Exp. Biol.* 206, 1127–1136.
- Sockol, M.D., Raichlen, D.A., Pontzer, H., 2007. Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc. Natl. Acad. Sci.* 30, 12265–12269.
- Stern, J.T., 1999. The cost of bent-knee, bent-hip bipedal gait: a reply to Crompton, et al. *J. Hum. Evol.* 36, 567–570.
- Stern, J.T., 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. *Evol. Anthropol.* 9, 113–133.
- Stern, J.T., Susman, R.L., 1983. Locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60, 279–317.
- Stuedel-Numbers, K., 2003. The energetic cost of locomotion: humans and primates compared to generalized endotherms. *J. Hum. Evol.* 44, 255–262.
- Stuedel-Numbers, K.L., Tilken, M.J., 2004. The effect of lower limb length on the energetic cost of locomotion: implications for fossil hominins. *J. Hum. Evol.* 47, 95–109.
- Susman, R.L., Stern, J.T., Jungers, W.L., 1984. Arboreality and bipedality in the hadar Hominids. *Folia Primatol.* 43, 113–156.
- Taylor, C.R., 1994. Relating mechanics and energetics during exercise. *Comparative vertebrate exercise physiology: unifying physiological principles*. *Adv. Vet. Sci. Comp. Med.* 38, 181–215.
- Taylor, C.R., Heglund, N.C., McMahon, T.A., Looney, T.R., 1980. Energetic cost of generating muscular force during running: a comparison of large and small animals. *J. Exp. Biol.* 86, 9–18.
- Taylor, C.R., Heglund, N.C., Maloiy, G.M.O., 1982. Energetics and mechanics of terrestrial locomotion: I. metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* 97, 1–21.
- Taylor, C.R., Rowntree, V.J., 1973. Running on two or on four legs: which consumes more energy? *Science* 179, 186–187.
- Thorpe, S.K.S., Crompton, R.H., Gunther, M.M., Ker, R.F., Alexander, R.M., 1999. Dimensions and moment arms of the hind- and forelimb muscles of common chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* 110, 179–199.
- Thorpe, S.K., Holder, R.L., Crompton, R.H., 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* 316, 1292–1294.
- Umberger, B.R., Gerritsen, K.G.M., Martin, P.E., 2003. A model of human muscle energy expenditure. *Comput. Methods. Biomech. Biomed. Engin.* 6, 99–111.
- Wang, W., Crompton, R.H., Carey, T.S., Gunther, M.M., Li, Y., Savage, R., Sellers, W.L., 2004. Comparison of inverse-dynamics musculo-skeletal models of A.L. 288-1 *Australopithecus afarensis* and KNM-WT 15000 *Homo ergaster* to modern humans, with implications for the evolution of bipedalism. *J. Hum. Evol.* 47, 453–478.
- Ward, C.V., 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *Yearb. Phys. Anthropol.* 45, 185–215.
- Ward, C.V., Leakey, M.D., Walker, A., 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *J. Hum. Evol.* 41, 255–368.
- Washburn, S.L., 1967. Behaviour and the origin of man. The Huxley Memorial Lecture. *Proc. R. Anthropol. Inst. Gr. Br. Ireland.* 3, 21–27.
- White, T.D., Suwa, G., Asfaw, B., 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371, 306–312.
- Wickler, S.J., Hoyt, D.F., Cogger, E.A., Hirschbein, M.H., 2000. Preferred speed and cost of transport: the effect of incline. *J. Exp. Biol.* 203, 2195–2200.
- Willems, P.A., Cavagna, G.A., Heglund, N.C., 1995. External, internal, and total work in human locomotion. *J. Exp. Biol.* 198, 379–393.
- Winter, D.A., 2005. *Biomechanics and Motor Control of Human Movement*, third ed. Wiley, New York.
- Zollhofer, C.P.E., Ponce de Leon, M.S., Lieberman, D.E., Guy, F., Pilbeam, D., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2005. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature* 434, 755–759.