

# The Biomechanical and Energetic Advantages of a Mediolaterally Wide Pelvis in Women

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## ABSTRACT

Here, we argue that two key shifts in thinking are required to more clearly understand the selection pressures shaping pelvis evolution in female hominins: (1) the primary locomotor mode of female hominins was loaded walking in the company of others, and (2) the periodic gait of human walking is most effectively explained as a biomechanically controlled process related to heel-strike collisions that is tuned for economy and stability by properly-timed motor inputs (a model called dynamic walking). In the light of these two frameworks, the evidence supports differences between female and male upper-pelvic morphology being the result of the unique reproductive role of female hominins, which involved moderately paced, loaded walking in groups. *Anat Rec*, 300:764–775, 2017. © 2017 Wiley Periodicals, Inc.

**Key words:** sexual dimorphism; obstetrical dilemma; pelvis; dynamic walking; load carrying

## INTRODUCTION

In considering hominin locomotor adaptations, the question at hand is, do differences in male and female pelvic morphology represent “solutions” to the exact same locomotor “problem”? Under the obstetrical dilemma paradigm, the anatomy of the human female pelvis is generally viewed as a compromise between selective pressures favoring safer parturition and those reducing energy expenditure during a particular style of locomotion (Krogman, 1951; Washburn, 1960; Lovejoy, 1981, 1988); the style of locomotion typically used by modern human male foragers: unloaded, solitary, rapid-pace walking (Marlowe, 2005; Cashdan et al., 2012; Wagnild and Wall-Scheffler, 2013). What is the evidence that this style of locomotion is typical of female foragers, or even of now-extinct hominin males? Similarly, reduced energy expenditure alone may not be the primary criterion for “effective” locomotion, given the importance of other selection pressures (e.g., regulation of core temperature, water balance). It is clear when perusing the non-human literature that there are multitudes of ways to optimize locomotion, including reducing heat load, reducing injuries, and maximizing agility. Locomotor optimality can involve

tradeoffs between speed and maneuverability (Clemente and Wilson, 2015; Moore and Biewener, 2015) or between speed and accuracy (Wheatley et al., 2015), as well as balancing rate-related costs with energy efficiency (energetic cost for a given distance) (O’Neill, 2012).

The non-human literature is also full of examples where sex-differences in foraging strategies are proposed as correlates of different morphological adaptations. Large body size is found among female spotted hyenas

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who eats first (thus consuming higher quality meat) and more aggressively (Mills, 1989). Larger wings and bills found among male Magellanic woodpeckers are selected for foraging on larger substrates and at different tree heights than females (Chazarreta et al., 2012). Larger head sizes among female water snakes is similarly due to selection for larger prey types and deep-water utilization (Shine, 1986). In our own Order, numerous studies have shown that sex differences in foraging and feeding behavior correlate with morphological differences, an argument elegantly and clearly laid out by Zihlman (1993) who notes significant differences in dietary composition, feeding time, feeding priorities, and travel routes between the sexes of Indriids, Titi Monkeys, Gelada Baboons, Mangabeys, Guenons, Patas Monkeys, and Orang-Utans.

Here, we claim that there was a locomotor advantage for bipedal hominin females in having a medio-laterally (M-L) broad pelvis, given the selection pressures that these females actually faced (Wall-Scheffler and Myers, 2013). Given the availability of developmental mechanisms to selectively modify specific parts of the pelvis (Grabowski, 2013; Reno, 2014) we further believe that selection can precisely act on the M-L dimensions, while still maintaining other dimensions of the pelvis for other functions. We focus here on pelvic measures in the M-L dimension because the literature generally treats M-L measures as a source of obstetrically-related locomotor “constraints” on females, or on any hominin with a relatively broad pelvis (Ruff, 1995; Richmond and Jungers, 2008). It is important to recognize, however, that the obstetrical dilemma of parturition is more related to anterior-posterior (A-P) dimensions of the pelvis (Rosenberg, 1992; Rosenberg and Trevathan, 2002; Brown, 2011) (though see Kurki (2007, 2011, 2013) for population variation in A-P dimensions as well), or even simply the lower pelvic region (Gruss and Schmitt, 2015). Thus, our argument takes two essential forms, namely that females perform locomotor primarily when loaded (and in the company of others), and that investigators of the locomotor-constraint side of the obstetrical dilemma have erred by considering the proposed effects of morphological changes in isolation, rather than looking at how the neuromuscular timing and related metabolic cost of the whole stride are influenced by dimorphisms. In other words, we need to consider that any energetic cost resulting from a small increase in the moment arm along the pelvis, and thus muscular activity at the pelvis, might very well be compensated for at other parts of the gait cycle (Kuo et al., 2005; Lee et al., 2013). Therefore, we suggest that sexual dimorphism in the M-L dimensions of the pelvis have emerged as a consequence of loading behavior during walking.

In the first instance, ethnographic data on modern human foragers suggest that women worldwide carry items most of the time, beginning with the basic reproductive loads which follow a cyclical pattern among non-contraceptive using populations. Reproductive-aged women sling or carry nursing babies anteriorly (Whiting, 1994; Konner, 2005; Harris, 2010), in a similar manner to the load of pregnancy (Wall-Scheffler and Myers, 2013); this load can be 20% of a woman’s mass (Prentice and Goldberg, 2000; Rasmussen et al., 2009) and is carried for a substantial proportion of a woman’s life as children transition to slings after birth. When children

gain the necessary motor skills (e.g., strong neck), they are moved into a side-sling while moving and foraging (Tanaka, 1980). Also on the side (same or opposite as the child) will be satchels loaded with food, such as underground storage organs (USOs, or tubers) (Lee, 1979). To both forage and manage their reproductive loads, women are thus mixing and matching the locations of children, food, and household items, locating items on their bodies, in their arms, and on their heads. Data on the!Kung and the Ache document women carrying containers of food, water, firewood, or other household items on their back, while also carrying satchels for tools, babies, and larger food items on their side; older toddlers may also be placed in the pouch on the back or on the shoulders (Lee, 1979; Hurtado et al., 1985). Alternatively, women have also been shown to use tump-lines to carry plant-based resources on their back (Maloiy et al., 1986; National Geographic Society and Agland, 1988; Panter-Brick, 1992; Hilton and Greaves, 2004; Bastien et al., 2005). As the primary carriers in most populations (Bentley, 1985; Hurtado et al., 1985; Brightman, 1996; Hawkes et al., 1997; Hilton and Greaves, 2004, 2008; Wall-Scheffler, 2012a; Wall-Scheffler and Myers, 2013) women tend to carry burdens of a larger amount of mass than men, both relatively and absolutely, in the majority of foraging populations, and across the lifespan (Bentley, 1985; Goodman et al., 1985; Blurton Jones et al., 1989; Brightman, 1996; Hilton and Greaves, 2004, 2008). Thus, the importance of understanding the role of carrying loads seems integral to the understanding and interpretation of female locomotor morphology (Rosenberg et al., 2004; Wall-Scheffler et al., 2007; DeSilva, 2011).

Carrying loads does not simply change the mass of the carrier (meaning that cost would simply increase in a linear fashion): clearly there will be interactions with the rest of the locomotor system. Studies on these interactions between load carrying and walking show that carrying loads significantly impacts self-selected walking speeds, generally by making walking speeds slower, if that is an option (Bentley, 1985; Hurtado et al., 1985; Marlowe, 2006; Lloyd et al., 2010; Wall-Scheffler and Myers, 2013). Yet, data also clearly suggest that such slowing down is not always an option, and that during times when groups must either travel long distances, or when the group needs to travel more quickly, this is exactly when women are more likely to pick up older (i.e., heavier) children in order to maintain the pace of the entire group (Kramer, 1998, 2004); in these circumstances, slowing down at the child’s self-selected (and often slower or more meandering) pace is not an available recourse. Thus, the interplay between burden and speed may be moderated by other aspects of daily life, including transport distance (Hilton and Greaves, 2004). Given the interactive effects of load (mass) and speed on locomotor energetics and biomechanics (Griffin et al., 2003; Kramer, 2010; Wall-Scheffler and Myers, 2013), any investigation into the importance of locomotor morphology must also consider the speed at which the walker is likely to move.

How does a full consideration of the locomotor tasks likely to have occupied female hominins influence our interpretation of their pelvic morphology? Apart from the overwhelming ethnographic evidence of females as the burden-bearing sex, what evidence suggests that females are good at carrying loads, perhaps even more

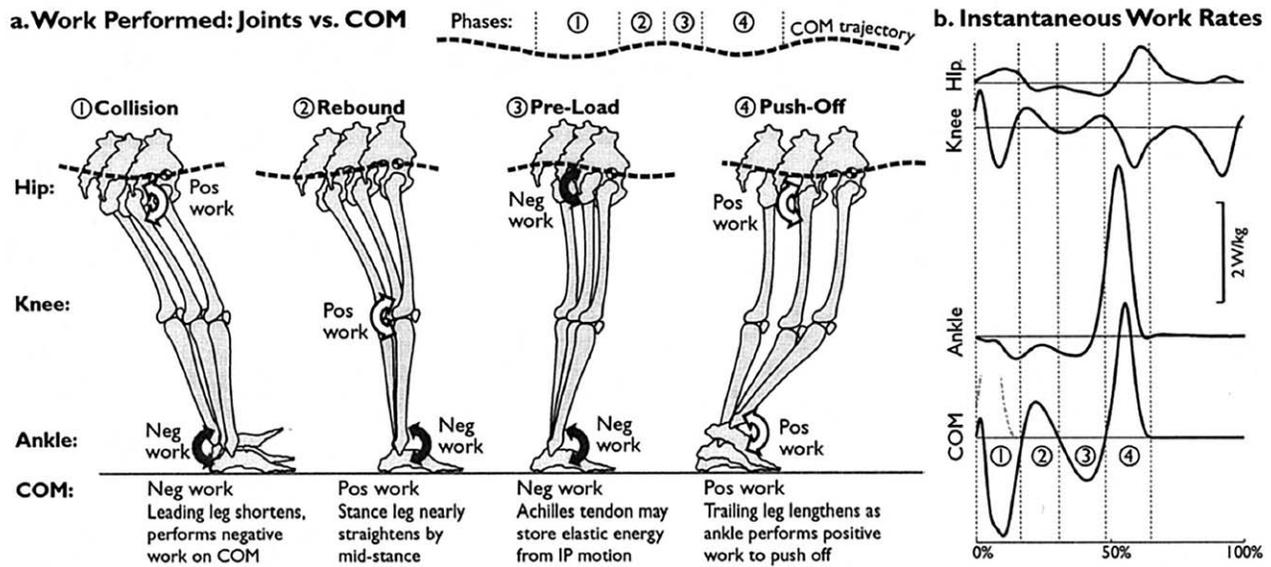


Fig. 1. A conceptualization of the work performed at lower limb joints during stance phase (part a.) and then throughout the entire gait (part b.) Stance phase is divided into four phases as the lower limb collides with the ground; the action of the hip musculature during these four phases, and then during swing phase is investigated in this paper. This Figure is taken from Figure 6 of Kuo et al. 2005 and used here with permission.

effective than males? Such data come from multiple studies (Gruss et al., 2009; Myers et al., 2011; Wall-Scheffler, 2012b, 2012a; Wall-Scheffler and Myers, 2013; Wall-Scheffler, 2014). Metabolic data suggest that women with a relatively wide bitrochanteric breadth use less energy to carry loads (Wall-Scheffler et al., 2007), and that women with a relatively wide bi-iliac breadth have more metabolically comparable speed options when carrying loads than women with more narrow measures (Wall-Scheffler and Myers, 2013). Speed flexibility, demonstrated by a flatter cost of transport curve, is clearly important given that women walk with companions ranging widely in size and age, and also minimize heat loads by moderating their speed in proportion to the intensity of their task (e.g., size of burden, incline level of path) (Wall-Scheffler, 2012b; Wall-Scheffler and Myers, 2013; Myers et al., 2014; Wall-Scheffler, 2015).

We also explore whether the overly simplistic model commonly used to infer metabolic cost from biomechanical/morphological differences (but particularly developed for large phylogenetic comparisons (e.g., Biewener, 2003)) is what leads to the misinterpretation that female locomotion is less economical, or less efficient, or less adaptive than male locomotion. Many papers on the obstetrical dilemma, at least implicitly, use a model that assumes any morphological change that decreases the effective mechanical advantage of a muscle group at one point in the stride *must* increase the metabolic cost of each stride (e.g., Lovejoy, 1981; Richmond and Jungers, 2008) (though see Kramer, 1999). That is, these are additive models of pluses and minuses that do not recognize the interactions within parts of the body and between parts of the stride that occur in biological systems, particularly in comparisons between members of the same species. Even in unloaded walking, a variety of “interactive” biomechanical arguments support an idea

that females (generally with a relatively broader M-L pelvis width) show an increased ability to achieve M-L stability than males (Mazza et al., 2009), and that not achieving M-L stability, especially on uneven terrain has a metabolic cost (e.g., Donelan et al. 2004; Voloshina et al. 2013). Part of this increased stability comes from the proportional increase in mass of the pelvic area in females that comes from more bone and musculature there (Wall-Scheffler et al., 2006), thus driving down the center of mass (COM) and increasing stability. Furthermore, increased stability through actions of the hip adductors (which comes with a broader pelvis (Wall-Scheffler et al., 2010)), may decrease the overall cost of walking (Kuo, 1999; Kuo et al., 2005; Kuo, 2007). Such a result is consistent with the dynamic walking model, where the emphasis is on the muscular work done to redirect the COM following energy-dissipating collisions with the ground (Fig. 1). Hence, actions at one part of the stride, that reduce collisional losses later in the stride, can reduce the overall metabolic cost of locomotion. Under this model, it is possible that actions caused by increased muscular action at the pelvis prior to the collision with the ground (that is, at the end of swing phase), might reduce the energy lost in that collision, and thus the muscular work required to redirect the COM after the collision. As illustrated in Video 1: [http://players.brightcove.net/656326989001/default\\_default/index.html?videoId=5291030505001](http://players.brightcove.net/656326989001/default_default/index.html?videoId=5291030505001), there are clear differences in the typical gait of human men and women. Likewise, the muscle activity patterns shown in Figure 2 highlight multiple possibilities as to how the muscular and skeletal systems interact to create a coherent system that is effective for both sexes. For example, multiple muscle groups have increased activity at the end of swing (e.g., Fig. 4 in (Wall-Scheffler et al., 2010)). These contractions may act to coordinate the timing and direction of the ground

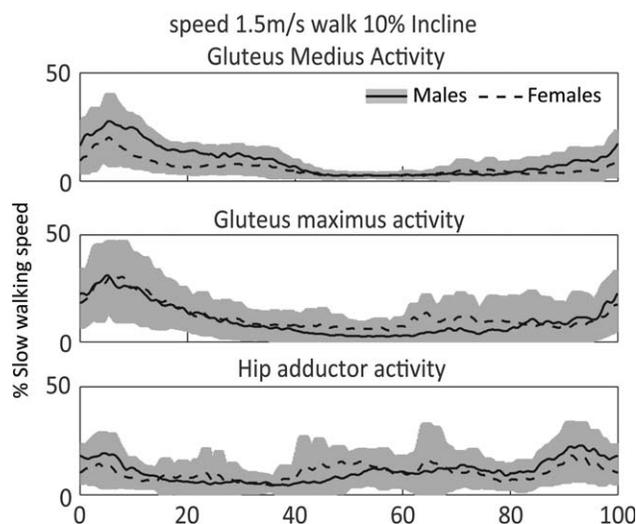


Fig. 2. The mean activity of muscle groups with origins on the pelvis across the gait cycle. The solid line represents the mean activity at a 10% grade and  $1.5\text{ms}^{-1}$  for males; the dotted line represents mean activity for females. The gray band represents the standard deviations for the entire sample, both males and females. The y-axis represents the percentage increase in muscle activity normalized to slow, level walking.

collision so as to reduce the energy lost, and thus the amount of energy required to redirect the center of mass after the collision. While we expect there to be changes in the timing and amount of muscle group activity during load carrying, it is also possible that there are morphological correlates that support these changes, including a broader pelvis (Chumanov et al., 2008; Wall-Scheffler, 2012b; Wall-Scheffler and Myers, 2013; Wall-Scheffler, 2014).

Thus, our argument demands two key shifts in thinking to more accurately understand the selection pressures shaping the differential pelvis evolution among female hominins: (1) the primary locomotor mode of female hominins was loaded walking in the company of others, and (2) the periodic gait of human walking is most effectively explained as a biomechanically controlled process related to heel-strike collisions that is tuned for economy and stability by properly-timed motor inputs (a model called dynamic walking). In the light of these two frameworks, the evidence supports differences between female and male upper-pelvic morphology being the result of the specific reproductive role of female hominins, which involved moderately paced, loaded walking in groups.

## MATERIALS AND METHODS

### Study One: Sex Differences in Walking Electromyography (EMG)

The methods describing the collection of these data have been previously published (Wall-Scheffler et al., 2010), but a brief summary follows. We collected data on 34 human subjects (17 males and 17 females), between the ages of 18–37 (mean = 22.9); each signed a written informed consent form approved by the UW-Madison

IRB. Male mass was  $79.8\text{kg} \pm 13.0$ ; female mass was  $60.1\text{kg} \pm 5.9$ . Male bitrochanteric breadth was  $31.0\text{ cm} \pm 2.1$ ; female was  $30.2\text{ cm} \pm 2.1$ ; females had significantly broader bitrochanteric breadth relative to body mass ( $P < 0.001$ ). The protocol consisted of walking on a treadmill at a series of randomly ordered speeds (1.2, 1.5, and  $1.8\text{ ms}^{-1}$ ) at a 10% incline. The incline was chosen to represent a gentle grade that would have some evolutionary meaning regarding the terrain with which most hominins would be interacting regularly (compare for example that  $>50\%$  grade is used when discussing Neanderthal-specific morphology (Higgins and Ruff, 2011)). The speeds were chosen to represent a wide range of comfortable speeds for both males and females; the analyses were run at all speeds, but only shown here for  $1.5\text{ ms}^{-1}$  as all patterns of muscle activation were the same across the speeds.

Each subject had electromyography surface electrodes placed on seven thigh and hip muscle groups following Basmajian's protocol (Basmajian and Blumenstein, 1989) which ensured each EMG reading is coming from the muscle of interest (Clancy et al., 2002; Rainoldi et al., 2004). Once placed, these electrodes were secured with athletic tape and not moved for the duration of the trial ensuring consistent and comparable readings for each individual. The muscle groups included the hamstring muscles (biceps femoris and medial hamstrings (which include semitendinosus and semimembranosus)), two quadriceps muscles (vastus lateralis and rectus femoris), hip adductors, hip abductors (gluteus medius) and the gluteus maximus. We decided to consider two groups of hamstrings and two of quadriceps to assess differences in activation between two muscles that have somewhat similar anatomical locations.

All EMG signals were first full-wave rectified and low pass filtered using a sixth order Butterworth filter with a cutoff frequency of 50 Hz. For each participant, the mean activity for each muscle was found during the slowest walking speed ( $1.2\text{ ms}^{-1}$ ) on a level surface; this value was then used as the normalization factor. Approximately 10 s of data (a minimum of five strides) were recorded for each condition. The choice to use five gait cycles was based on Kadaba et al. (1989) who demonstrated repeatable kinematic, kinetic and EMG data during locomotion from as few as three gait cycles (Kadaba et al., 1989). Our kinematic data varied less than  $2.5^\circ$  within each condition for all measured angles leading us to conclude that five strides for each condition was sufficient to accurately characterize the locomotion pattern.

Our statistical analysis consisted of comparing, using independent *t*-tests, the muscle activation patterns of men and women during the quartiles of swing phase (particularly the final 25%, the preparation for the Collision phase) with the quartiles of stance phase (Collision, Rebound, Pre-Load, Push-Off) (Fig. 1). We focused on these parts of the gait cycle to detail potential differences between men and women in their overall muscle activation patterns that could tradeoff effectively in reducing the costs of recovering from collisions. All analysis was done in SPSS 23.

In light of concerns over the binary use of *P*-values in hypothesis testing (Greenland et al., 2016; Wasserstein and Lazar, 2016), we focus here on effect sizes and patterns of differences and report specific *P*-values as a tool

for readers in judging the level of evidence consistency between the evidence presented and proposed models.

### Study Two: Sex Differences in Level, Loaded Walking

We collected data on 12 nonsmoking, physically active human subjects (6 males and 6 females), between the ages of 21–45 (mean = 27.1); each signed a written informed consent form approved by the University of St Catherine IRB. Full body anthropometrics were collected, including mass, stature, lower limb length (greater trochanter to lateral malleolus), bitrochanteric breadth, bi-iliac breadth, and biacromial breadth. Male mass was  $88.6 \text{ kg} \pm 6.8$ ; female mass was  $57.7 \text{ kg} \pm 5.1$ . Male bitrochanteric breadth was  $33.2 \text{ cm} \pm 2.6$ ; female was  $29.9 \text{ cm} \pm 2.4$ . Females had significantly broader bitrochanteric breadth relative to body mass ( $P < 0.001$ ). Whole-body and segment tissue composition was determined by DEXA scans.

On each of two days, participants walked around the perimeter of a gym carrying an 11 kg toddler manikin on their hip at four randomly ordered walking speed directives: Slow Walk, Walk-all-Day, Brisk Walk, and Fast Walk. Actual walking speed and stride frequency were determined from video recordings using a stopwatch. Stride length was calculated by dividing walking speed by stride frequency.

Breath by breath values for the rate of oxygen consumption and carbon dioxide production were collected using a COSMED K4b2 portable metabolic unit as participants walked at the directed speed until their metabolic rate leveled off (5 min at minimum). These rates were used to calculate metabolic power (W) using the Weir (1949) equation. Steady-state metabolic power (Cost of Locomotion, CoL) was calculated as the average of the last 3 min of each trial; both testing sessions of a participant were averaged to determine the CoL for each of the four speed directives. Cost per distance, or Cost of Transport (CoT) for each speed directive was computed by dividing CoL by actual walking speed. Cost per stride for each speed directive was computed by dividing CoL by stride frequency. Two-tailed, independent *t*-tests were used to compare differences between sexes in self-selected walking speed and cost measures at each speed directive. Regression models were used to model variation in stride length and to test for sex differences between kinematic variables as a function of walking speed (Minitab 17).

## RESULTS

### Study One: The Potential for Differential Muscle Activity and Gait Cycle Patterns within Dimorphic Anatomy

In our analysis of EMG data of the pelvis and lower limb areas of males ( $N = 17$ ) and females ( $N = 17$ ) during walking at three different speeds at a slight incline, we found substantial, and often significant, differences between sexes in the timing of muscle activation. The differences in timing particularly related to the period before the collision with the ground (that is, the end of swing phase), and the recovery from the collision. Given that this sample followed the general human trend of women having relatively larger bitrochanteric breadths

than men, our overarching hypothesis was that increased activation of the muscles (originating on the pelvis) during the end of swing could offset the muscular force necessary to recover from the collision with the ground. We also ran the same analyses using relative bitrochanteric breadth as the comparative variable instead of sex and found nearly identical results; these are shown in Figure 3 alongside the sex-based results.

We found that females activated their hamstrings significantly more at the end of swing (45.4%,  $P = 0.05$ ), whereas males activated their hamstrings more at the beginning of stance (39.7%,  $P = 0.16$ ) (Fig. 3A). In hip abduction, males also showed a substantial trend for more activation than women, with their gluteus medius activity being 37% higher than females during recovery from the collision (Pre-Load) (large standard deviations, so  $P = 0.40$ ) (Fig. 3B). In contrast, females activated their gluteus medius more than males at the initiation of swing (53.4%,  $P = 0.012$ ), possibly due to resisting pelvic drop on the contralateral side as it moves through a greater angle of rotation when elongating the stride (Fig. 3B)

We also found that males increased hip adductor activity 40.6% more than females at the end of swing ( $P = 0.12$ ), whereas females increased hip adductor activity 44.2% more at the end of stance, the final push off and recovery from the collision ( $P = 0.11$ , Fig. 3C).

### Study Two: The Potential for Metabolic Economy and Efficiency during Load Carrying

In our analysis of women and men carrying an 11 kg toddler model on their hips, we found that women were from 20% to 35% more economical across the walking speeds (Cost of Locomotion) than males ( $P$ -values ranging from 0.03 to 0.16). In addition, we scaled costs in a variety of standard ways across a range of four submaximal speeds (Fig. 4A–D). We found that females were 29% to 63% more efficient on a cost per distance basis than males at all speeds (Fig. 4A,  $P$ -values ranged from 0.002 to 0.02), but used almost the same energy per meter when scaled by total mass at slow and moderate speeds ( $P$ -values ranged from 0.24 to 0.83), with females trending higher than males at the highest speed (Fig. 4C,  $P = 0.13$ ). Likewise, when scaled by the stride, females were 32% to 58% more efficient on a cost per stride basis than males at all speeds (Fig. 4B,  $P$ -values ranged from 0.003 to 0.03), but had very similar costs/stride per kg of total load (Fig 4D), with females trending lower at slowest speed ( $P = 0.38$ ) and higher than males at the higher speeds ( $P$ -values range from 0.38 to 0.48). In large part, the absolute cost differences per distance or stride are due to the size differential: males were 51% larger than females by total body mass. On a relative task basis, females are performing the same absolute task as males (hip-carrying an 11 k toddler) even though the muscle mass of females (generally, and in our sample) is much smaller than in males; males in our sample have 1.6 times more lean body mass ( $P < 0.0001$ ) and 1.7 times more lean lower limb mass ( $P < 0.0001$ ) than the females, who are thus doing a substantially harder relative task. The females in our study also had significantly broader bitrochanteric breadths relative to mass than males ( $P < 0.001$ ).

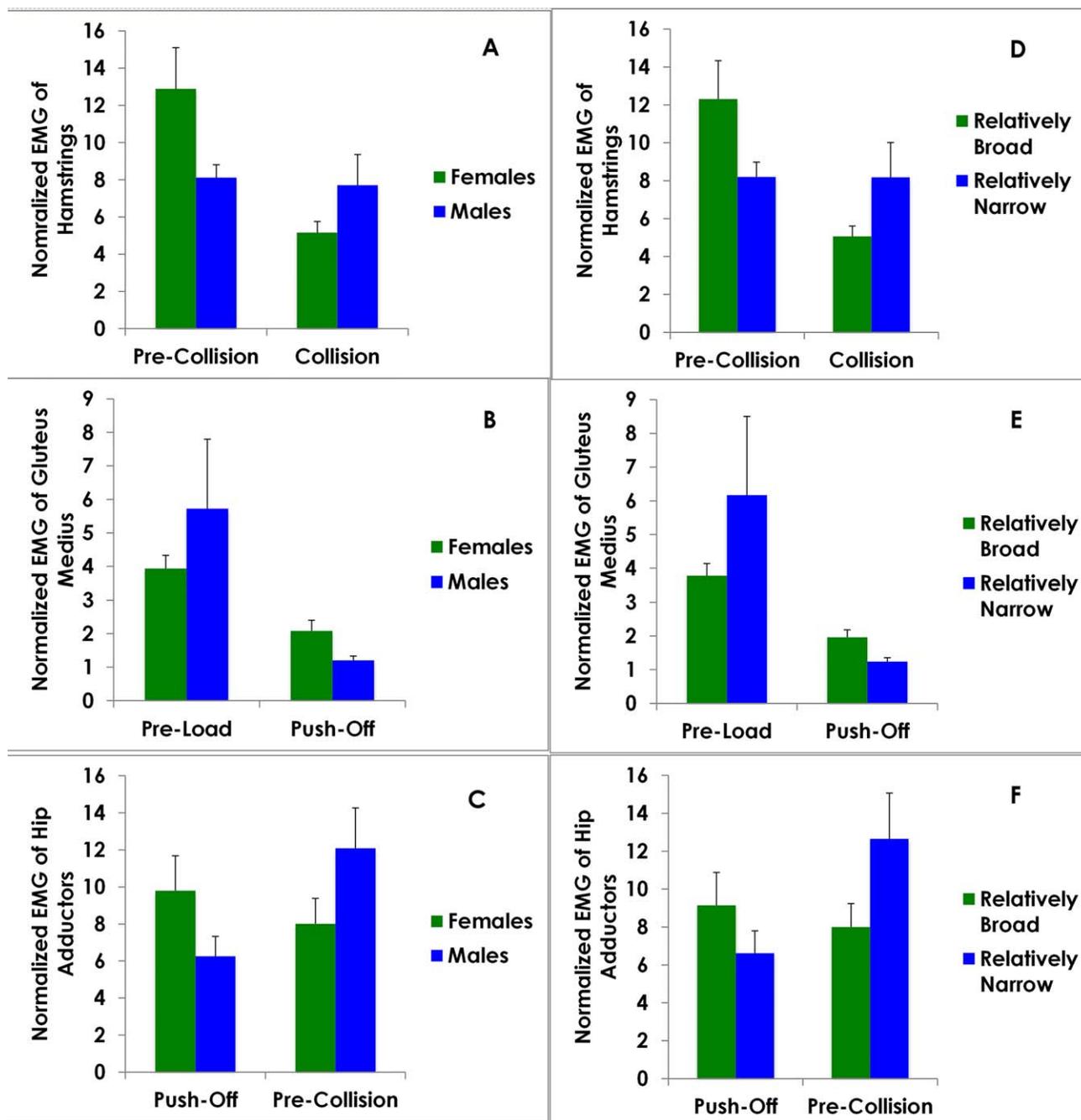


Fig. 3. The different activity between males and females at the different phases of the gait cycle (See Fig. 1). In all cases, the y-axis represents muscle activation patterns at a 10% grade and 1.5 ms<sup>-1</sup> (the same condition as Fig. 2). In all cases, a corresponding graph using the criteria of “relatively broad bitrochanteric breadth” and “relatively narrow bitrochanteric breadth” is used to show how much of the male and female differences are due to this anatomical feature alone, and not some other aspect of sexual dimorphism. In part A, Females have significantly more activation than men at the end of Swing in their (medial) hamstrings (45.4%,  $P=0.05$ ). Males have more 39.7% activation at the onset of Collision in their mid-hamstrings (biceps femoris)

( $P=0.16$ ); see part D for the graphs due to pelvic measures. In part B, in which males have increased activity in gluteus medius activity during the Pre-Load phase (37% more, but with a large standard deviation, so  $P=0.40$ ), and females have increased activity during Push-Off (53.4%,  $P=0.012$ ) (possibly due to resisting pelvic drop on the contralateral side during swing of the relatively heavier limb through a greater angle of rotation); see part E for the graphs due to pelvic measures. Part C shows that males have 40.6% more hip adductor (HADD) activation at the end of swing (Pre-Collision) ( $P=0.12$ ). Females have a 44.2% increase in HADD at Push-Off ( $P=0.11$ ); see part F for the graphs due to pelvic measures.

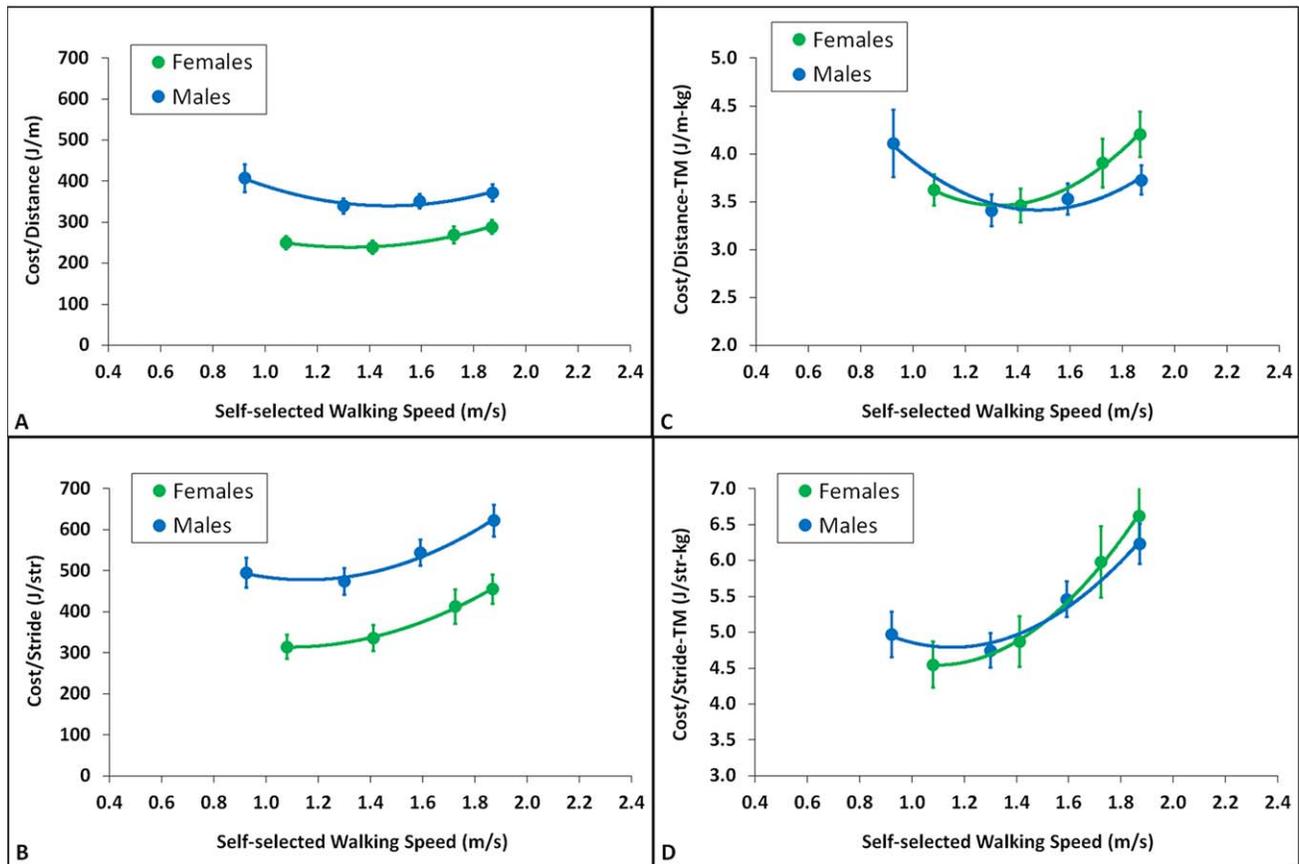


Fig. 4. Costs for six females and six males as a function of self-selected walking speed while carrying an 11 kg toddler manikin at the hip, scaled by (A) cost per distance traveled, (B) cost per stride, (C) cost/distance per kg of total load (person plus toddler load), and (D) cost/stride per kg of total load. Points represent average costs within each sex for four speed directives: Slow Walk, Walk All Day, Brisk Walk, and Fast Walk. Error bars are  $\pm 1$  SE.

There were also small but systematic sex differences in spatiotemporal variables (Fig. 5A–C): females carried the hip load using higher stride frequencies (Fig. 5A,  $P = 0.02$ ) and shorter stride lengths (Fig. 5B,  $P = 0.005$ ) than males, yet tended toward longer relative stride lengths (SL/lower limb length) at a given speed (Fig. 5C,  $P = 0.15$ ). In response to our speed directives, females also chose faster walking speeds overall than males ( $P = 0.05$ ), with the selected speeds converging at the faster speed (“Fast Walk”).

Thus, the females in our study showed absolutely better economy and efficiency, with mostly comparable costs on a total mass basis, and chose faster submaximal walking speeds than their male counterparts, despite the fact that the mass of the toddler manikin was 1.5 times larger relative to the average female body mass. The fact that females carrying loads achieve a longer stride length relative to their lower limb length suggests that they are able to lengthen their stride more than males through hip/pelvis rotation.

To distinguish which kinematic and anthropometric characteristics could explain the observed sex related differences in stride length, Table 1 shows several regression models of stride length variation. Of the 2-

factor models shown, speed and body mass account for the largest percent of variation in stride length (90.8%), with speed and bitrochanteric breadth as the next best 2-factor model (89.5%). Models 7 and 8 are the best 3-factor models ( $R^2 = 92.6\%$ ) and show that, with speed and body mass already in the model, bitrochanteric breadth explains a very similar part of additional variation as does sex (the sex effect becomes negative when body mass is in the model, meaning when size is taken into account, “maleness” has a negative effect on stride lengths). These results are consistent with females having relatively wider bitrochanteric widths than males (on a mass basis) and females getting a longer SL out of a given limb length by translating their hips further through a longer rotation of their wider pelvis. Biacromial breadth and biiliac breadth, though significant contributors to the model ( $P = 0.002$  and  $P = 0.001$  respectively) contributed only 1% to the model  $R^2$ .

## DISCUSSION

The energetic costs pertaining to locomotion come from a number of different places, including the cost of swinging the lower limb (Myers and Steudel, 1985) and

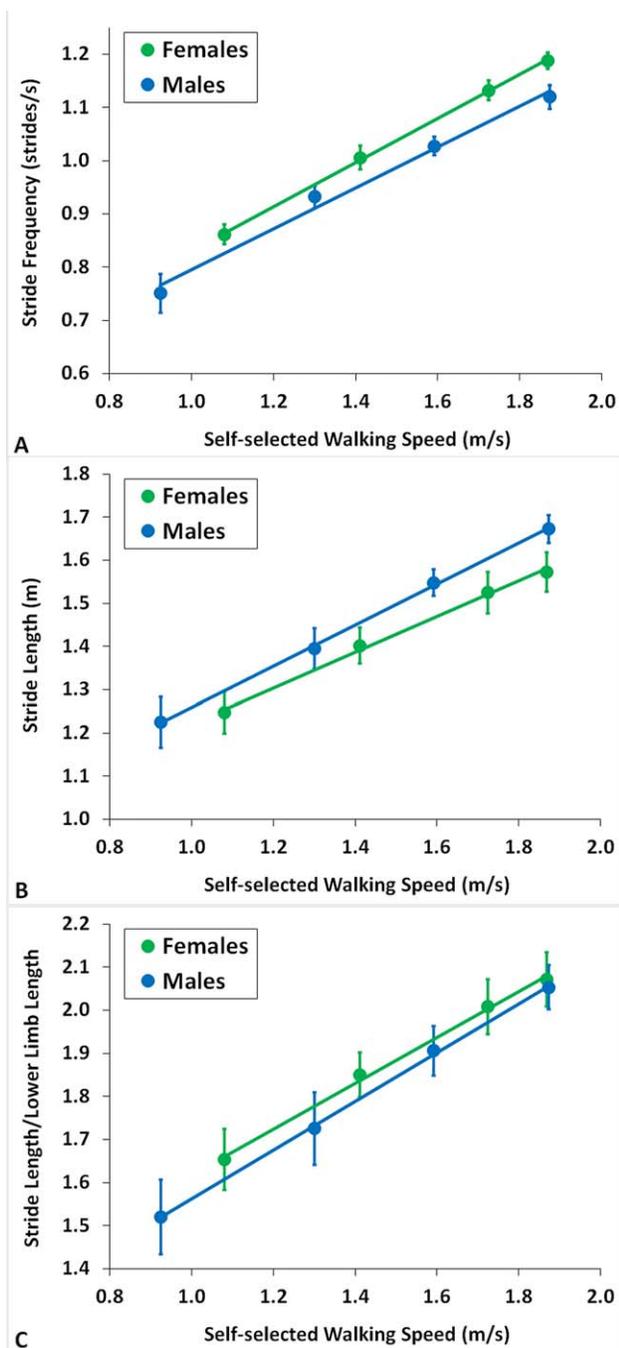


Fig. 5. Stride frequency (A), stride length (B), and relative stride length (SL/Lower Limb Length) (C) for six females and six males as a function of self-selected walking speed while carrying an 11 kg toddler manikin at the hip. Points represent average speeds within each sex for four speed directives: Slow Walk, Walk All Day, Brisk Walk, and Fast Walk. Error bars are  $\pm 1$  SE.

the cost of rebounding from the collision during stance phase (Kuo and Donelan, 2010). There are additional costs of maintaining one's physiological processes during activity, and of regulating body temperature, but many of the costs that occur during walking occur within a single gait cycle, and thus, when a person is traveling a given distance it will cost that person less energy if she

can reduce the total number of strides she is taking (Donelan et al., 2002; Kuo et al., 2005; Weyand et al., 2010). If that person is small, (to reduce the energy to build somatic tissue, to increase relative surface area, to use absolutely less energy on physiological tasks), then some compensation must be made with limb proportions and kinematics in order to maximize stride length when walking; we are arguing here that one of the key morphological adjustments for human females (and in fact all hominins except for *Homo sapiens* males), is widening the pelvis in the medio-lateral direction (Stringer, 1986; Rosenberg et al., 2006; Simpson et al., 2008; DeSilva, 2011). Multiple lines of evidence show that for a given speed, women are rotating their pelvis through a greater angle than men, increasing their stride length, and reducing the number of strides they need to take to go a given distance (Wall-Scheffler et al., 2007; Whitcome et al., 2012; Wall-Scheffler and Myers, 2013). With a relatively larger pelvis, women can increase their stride length through rotation alone (Rak, 1991). Without this additional horizontal translation, a person would have to generate stride length with additional lower limb length (which would have to be grown) or additional propulsion from thigh musculature. Alternatively, and quite uneconomically (Donelan et al., 2001; Donelan et al., 2004), they could avoid rotating their pelvis at all and just have a very wide step width. Women are able to keep a narrower (that is, typical) step width while maintaining stride length and walking speed by getting more translation of the pelvis for a given rotation angle (Whitcome et al., 2012; Gruss et al., this issue), but this action is particularly marked during load carrying (Wall-Scheffler et al., 2007; Wall-Scheffler and Myers, 2013). In fact, when women carry loads, they are more likely to use this method than when they are not carrying loads (Wall-Scheffler et al., 2007; Wall-Scheffler and Myers, 2013), likely because multiple feedback loops related to the rate of energy usage tightens the constraints around speed during load carrying. Women with wider bitrochanteric breadths have longer step lengths than women with more narrow bitrochanteric breadths particularly when carrying, and as a result use less energy to carry their load (Wall-Scheffler et al., 2007).

Additionally, the part of the cost of walking that occurs during swing phase is strongly influenced by the speed at which the lower limb swings. We have found that people with shorter limbs swing their limbs more quickly, which might be part of the reason for people with relatively short limbs to have a higher metabolic cost of walking (Stuedel-Numbers and Tilkens, 2004). Using pelvic rotation to translate the hip forward prior to lower limb swing is a potential means for a smaller person to limit the distance through which limb must be actively swung, aiding in energy savings.

The widening of the pelvis also allows for increased stability by increasing the amount of heavy tissue (i.e., bone and muscle) lower in the person. For example, compared to the males in our load carrying study, females have 3% more of their total body mass in their lower limbs and 5% less in their arms and trunk (based on DEXA scans). In females, the effect of this is a lower COM; this has quite clearly been shown to increase stability of gait, in a manner that reduces the energetic cost of walking (Donelan et al., 2004; Voloshina et al., 2013).

**TABLE 1. Regression models for stride length during asymmetrical hip carrying of an 11 kg toddler manikin**

Model	Design variable	Anthropometric variable	Coefficient direction	P-value	Model R <sup>2</sup>
1	Speed		Positive	<0.0001	85.3%
2	Speed	Sex	Positive Positive	<0.0001 0.018	87.0%
3	Speed	Body mass	Positive Positive	<0.0001 <0.0001	90.8%
4	Speed	Lower limb length	Positive Positive	<0.0001 0.230	85.7%
5	Speed	Height	Positive Positive	<0.0001 0.021	87.0%
6	Speed	Bitrochanteric breadth	Positive Positive	<0.0001 <0.0001	89.5%
7	Speed	Body mass Sex	Positive Positive Negative	<0.0001 <0.0001 0.002	92.6%
8	Speed	Body Mass Bitrochanteric breadth	Positive Positive Positive	<0.0001 <0.0001 0.003	92.6%

A “participant” term was included in all regression models. The Coefficient Direction column shows the sign of each regression coefficient. Model R<sup>2</sup> column is % of variation explained by each regression model.

## CONCLUSION

The results of our studies allow the conclusion of a number of key points about human locomotion. First, even unloaded, men and women have different muscle activation patterns (Chumanov et al., 2008; Sizer and James, 2014), and they may become even more pronounced during load carrying (Simpson et al., 2011), though potentially only in pelvic musculature, and in studies that are focusing on the precollision versus post-collision responses (so, contra Silder et al., 2013). The sex differences in muscle activation patterns are consistent with predictions based on the dynamic walking model (Bertram, 2005; Kuo et al., 2005; Ruina et al., 2005), namely that there can be tradeoffs in a gait cycle allowing for a reduction in the collision with the ground which will reduce the energy required to rebound from this collision. Here, we have shown that greater activation in women’s hip abduction and hamstring activity across swing phase transitions allow for reduced muscular activity during stance phase, and in the recovery from the collision with the ground. Future work will investigate sex differences in muscle activation patterns during load carrying and determine if these correspond to differences in the braking and propulsive forces involved in collisional losses and redirecting the center of mass.

Second, we have shown quite clearly that women are in no way at a disadvantage either in terms of metabolic costs, or in terms of speed selection, during walking with loads. Numerous studies find that women, partly because of their smaller size, use absolutely less energy to walk than men (Browning et al., 2006; Wall-Scheffler, 2012b), a trait that selection can act upon. We demonstrate here that women and men carrying hip loads have comparable costs of transport on a total mass (load plus body mass) basis at slow and moderate speeds, and that women chose faster speeds for a given speed directive, even though the load carried was a significantly

higher proportion of their lean ( $1.6\times$ ,  $P < 0.0001$ ) and total body mass ( $1.5\times$ ,  $P < 0.0001$ ).

Finally, it is impossible to consider only the pelvis when thinking of all aspects of sexual dimorphism relevant to locomotion, particularly important is the overall smaller size of female hominins. As noted in the introduction, there are numerous reasons for females to be smaller than males (Frayser and Wolpoff, 1985; Zihlman, 1993), including promoting heat loss in aid of core temperature regulation (Wall-Scheffler, 2015), but better locomotor economy is surely among the most compelling (Aiello and Key, 2002). Given that the cost of locomotion is integrally tied to mass, as well as speed, it is useful to consider the evolutionary relevance of having a relatively broad pelvis *within the context* of being small.

There are two ways of considering *Homo sapiens* sexual dimorphism, either within the current context of human females always being between 7% and 12% smaller than human males or within a longer view that considers the range of hominin size and dimorphism across time and space. There seems to be stronger evidence for more variation between populations (Gabunia et al., 2000; Antón, 2003; Antón and Swisher, 2004; Antón et al., 2007) than within populations (Frayser and Wolpoff, 1985; Reno et al., 2010), and little consensus as to how selection might act to make males larger and females consistent, or males consistent and females smaller. The longer view pattern is variable and extremely complex (Frayser and Wolpoff, 1985), but the species specific pattern is quite clear: regardless of absolute size, niche, and terrain, females remain somewhat smaller (in mass and stature) than males, and this needs an explanation.

We conclude that one of the key ways women have evolved to be such excellent (as in both economical and efficient) load carriers while staying small is through the maintenance of a relatively medio-laterally (M-L) broad pelvis. While historically the M-L width was not considered part of the obstetrical dilemma, multiple

researchers have used sex differences in M-L width to suggest reduced efficiency (or economy) in the locomotion of females and/or extinct hominins. Clearly a wide M-L width, and its benefits for load carrying, pertain to women's reproduction, but not necessarily to parturition, and clearly a wide M-L width provides women with specific adaptations to their locomotor niche.

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### LITERATURE CITED

- Aiello LC, Key C. 2002. Energetic consequences of being a *Homo erectus* female. *Am J Hum Biol* 14:551–565.
- Antón SC. 2003. Natural History of *Homo erectus*. *Yrbk Phys Anthropol* 46:126–169.
- Antón SC, Spoor F, Fellmann CD, Swisher CCI. 2007. Defining *Homo erectus*: Size considered. In: Henke W, Tattersall I, editors. *Handbook of Paleoanthropology: Volume III, Phylogeny of Hominids*. Berlin: Springer. p 1655–1693.
- Antón SC, Swisher CC. III. 2004. Early dispersals of *Homo* from Africa. *Annu Rev Anthropol* 33:271–296.
- Basmajian JV, Blumenstein R. 1989. *Electrode placement in electromyographic biofeedback*. 3rd ed. Baltimore: Williams and Wilkins.
- Bastien GJ, Willems PA, Schepens B, Heglund NC. 2005. Effect of load and speed on the energetic cost of human walking. *Eur J Appl Physiol* 94:76–83.
- Bentley GR. 1985. Hunter-gatherer energetics and fertility: A reassessment of the!Kung San. *Hum Ecol* 13:79–109.
- Bertram JE. 2005. Constrained optimization in human walking: Cost minimization and gait plasticity. *J Exp Biol* 208:979–991.
- Biewener AA. 2003. *Animal locomotion*. Oxford: Oxford University Press.
- Blurton Jones N, Hawkes K, O'Connell JF. 1989. Modelling and measuring costs of children in two foraging societies. In: Standen V, Foley RA, editors. *The behavioural ecology of humans and other mammals*. Oxford: Blackwell Scientific Publications. p 367–390.
- Brightman R. 1996. The sexual division of foraging labor: Biology, taboo, and gender politics. *Comp Stud Soc Hist* 38:687–729.
- Brown KM. 2011. Obstetrical adaptation in the human bony pelvis: A three-dimensional morphometric approach. In: Department of Functional Anatomy & Evolution. Baltimore: Johns Hopkins University.
- Browning RC, Baker EA, Herron JA, Kram R. 2006. Effects of obesity and sex on the energetic cost and preferred speed of walking. *J Appl Physiol* 100:390–398.
- Cashdan E, Marlowe FW, Crittenden A, Porter C, Wood BM. 2012. Sex differences in spatial cognition among Hadza foragers. *Evolution and Human Behavior* 33:274–284.
- Chazarreta L, Ojeda V, Lammertink M. 2012. Morphological and foraging behavioral differences between sexes of the Magellanic Woodpecker (*Campephilus magellanicus*). *Ornitologia Neotropical* 23:529–544.
- Chumanov ES, Wall-Scheffler CM, Heiderscheidt BC. 2008. Gender differences in walking and running on level and inclined surfaces. *Clin Biomech* 23:1260–1268.
- Clancy EA, Morin EL, Merletti R. 2002. Sampling, noise-reduction and amplitude estimation issues in surface electromyography. *J Electromyogr Kinesiol* 12:1–16.
- Clemente CJ, Wilson RS. 2015. Balancing biomechanical constraints: Optimal escape speeds when there is a trade-off between speed and maneuverability. *Integr Comp Biol* 55:1142–1154.
- DeSilva JM. 2011. A shift toward birthing relativizing large infants early in human evolution. *Proc Natl Acad Sci U S A* 108:1022–1027.
- Donelan JM, Kram R, Kuo AD. 2001. Mechanical and metabolic determinants of the preferred step width in human walking. *Proc R Soc Lond B Biol Sci* 268:1985–1992.
- Donelan JM, Kram R, Kuo AD. 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.
- Donelan JM, Shipman DW, Kram R, Kuo AD. 2004. Mechanical and metabolic requirements for active lateral stabilization in human walking. *J Biomech* 37:827–835.
- Frayser DW, Wolpoff MH. 1985. Sexual dimorphism. *Annu Rev Anthropol* 14:429–473.
- Gabunia L, Vekua A, Lordkipanidze D, Swisher CC, III, Ferring R, Nioradze M, Tvalchrelidze M, Antón SC, Bosinski G, Joris O, et al. 2000. Earliest Pleistocene cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting, and age. *Science* 288:1019–1025.
- Goodman MJ, Griffin PB, Estioko-Griffin AA, Grove JS. 1985. The compatibility of hunting and mothering among the Agta hunter-gatherers of the Philippines. *Sex Roles* 12:1199–1209.
- Grabowski MW. 2013. Hominin obstetrics and the evolution of constraints. *Evol Biol* 40:57–75.
- Greenland S, Senn SJ, Rothman KJ, Carlin JB, Poole C, Goodman MJ, Altman DG. 2016. Statistical tests, p values, confidence intervals, and power: A guide to misinterpretations. *Eur J Epidemiol* 31:337–350.
- Griffin TM, Roberts TJ, Kram R. 2003. Metabolic cost of generating muscular force in human walking: Insights from load-carrying and speed experiments. *J Appl Physiol* 95:172–183.
- Gruss LT, Gruss R, Schmitt D. 2017. Pelvic breadth and locomotor kinematics in human evolution. *Anatomical Record* 300:739–751.
- Gruss LT, Schmitt D. 2015. The evolution of the human pelvis: Changing adaptations to bipedalism, obstetrics and thermoregulation. *Philos Trans R Soc Lond B Biol Sci* 370:20140063.
- Gruss LT, Wall-Scheffler CM, Malik N. 2009. Infant carrying in humans: Interactions between morphometric and gait parameters. *Am J Phys Anthropol* S48:182–183.
- Harris LJ. 2010. Side biases for holding and carrying infants: Reports from the past and possible lessons for today. *Laterality* 15:56–135.
- Hawkes K, O'Connell JF, Blurton Jones NG. 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Curr Anthropol* 38:551–577.
- Higgins RW, Ruff CB. 2011. The effects of distal limb segments shortening on locomotor efficiency in sloped terrain: Implications for Neandertal locomotor behavior. *Am J Phys Anthropol* 146:336–345.
- Hilton CE, Greaves RD. 2004. Age, sex and resource transport in Venezuelan foragers. In: Meldrum DJ, Hilton CE, editors. *From biped to strider: The emergence of modern human walking, running and resource transport*. New York: Kluwer Academic/Plenum Publishers. p 163–181.
- Hilton CE, Greaves RD. 2008. Seasonality and sex differences in travel distance and resource transport in Venezuelan foragers. *Curr Anthropol* 49:144–153.
- Hurtado AM, Hawkes K, Hill K, Kaplan H. 1985. Female subsistence strategies among Ache hunter-gatherers of Eastern Paragay. *Hum Ecol* 13:1–28.
- Kadaba MP, Ramakrishnan HK, Wootten ME, Gaine J, Gorton G, Cochran GV. 1989. Repeatability of kinematic, kinetic, and electromyographic data in normal adult gait. *J Orthop Res* 7:849–860.

- Konner M. 2005. Hunter-gatherer infancy and childhood: The!Kung and others. In: Hewlett BS, Lamb ME, editors. *Hunter-Gatherer childhoods*. New Brunswick: Aldine Transaction. p 19–64.
- Kramer PA. 1998. The costs of human locomotion: Maternal investment in child transport. *Am J Phys Anthropol* 107:71–85.
- Kramer PA. 1999. Modeling the locomotor energetics of extinct hominids. *J Exp Biol* 202:2807–2818.
- Kramer PA. 2004. The behavioral ecology of locomotion. In: Meldrum DJ, Hilton CE, editors. *From biped to strider: The emergence of modern human walking, running and resource transport*. New York: Plenum Publishers. p 101–115.
- Kramer PA. 2010. The effect of energy expenditure of walking on gradients or carrying burdens. *Am J Hum Biol* 22:497–507.
- Krogman WM. 1951. The scars of human evolution. *Sci Am* 1951: 54–57.
- Kuo AD. 1999. Stabilization of lateral motion in passive dynamic walking. *Int J Robot Res* 18:917–930.
- Kuo AD. 2007. Choosing your steps carefully: Trade-offs between economy and versatility in dynamic walking bipedal robots. *IEEE Robot Autom Mag* 14:18–29.
- Kuo AD, Donelan JM. 2010. Dynamic principles of gait and their clinical implications. *Phys Ther* 90:157–174.
- Kuo AD, Donelan JM, Ruina A. 2005. Energetic consequences of walking like an inverted pendulum: Step-to-step transitions. *Exerc Sport Sci Rev* 33:88–97.
- Kurki HK. 2007. Protection of obstetric dimensions in a small-bodied human sample. *Am J Phys Anthropol* 133:1152–1165.
- Kurki HK. 2011. Pelvic dimorphism in relation to body size and body size dimorphism in humans. *J Hum Evol* 61:631–643.
- Kurki HK. 2013. Skeletal variability in the pelvis and limb skeleton of humans: Does stabilizing selection limit female pelvic variation? *Am J Hum Biol* 25:795–802.
- Lee RB. 1979. *The!Kung San: Men, women, and work in a foraging society*. Cambridge: Cambridge University Press.
- Lee DV, Comanescu TN, Butcher MT, Bertram JE. 2013. A comparative collision-based analysis of human gait. *Proc R Soc Lond B Biol Sci* 280:20131779.
- Lloyd R, Parr B, Davies S, Cooke C. 2010. Subjective perceptions of load carriage on the head and back in Xhosa women. *Appl Ergon* 41:522–529.
- Lovejoy CO. 1981. The origin of man. *Science* 211:341–350.
- Lovejoy CO. 1988. Evolution of Human Walking. *Sci Am* 256:118–125.
- Maloiy GM, Heglund NC, Prager LM, Cavagna GA, Taylor CR. 1986. Energetic cost of carrying loads: Have African women discovered an economic way? *Nature* 319:668–669.
- Marlowe FW. 2005. Hunter-gatherers and human evolution. *Evol Anthropol* 14:54–67.
- Marlowe FW. 2006. Central place provisioning: The Hadza as an example. In: Hohmann G, Robbins M, Boesch C, editors. *Feeding ecology in apes and other primates*. Cambridge: Cambridge University Press. p 359–377.
- Mazza C, Iosa M, Picerno P, Cappozzo A. 2009. Gender differences in the control of the upper body accelerations during level walking. *Gait Posture* 29:300–303.
- Mills MGL. 1989. Comparative behavioral ecology of hyenas. In: Gittleman JL, editor. *Carnivore behavior, ecology, and evolution*. Ithaca: Cornell University Press. p 125–142.
- Moore TY, Biewener AA. 2015. Outrun or outmaneuver: Predator-prey interactions as a model system for integrating biomechanical studies in a broader ecological and evolutionary context. *Integr Comp Biol* 55:1188–1197.
- Myers MJ, Lovstad M, Kennedy A, Wall-Scheffler CM. 2014. Thermoregulatory and mobility consequences for reproductive age women carrying loads in an indigenous pack basket. *Am J Phys Anthropol* 153:192.
- Myers MJ, Myhre A, Kpanquoi M, Stearns L, Wall-Scheffler CM. 2011. Self-selected walking speeds: Do females and males carrying children choose differently? *Am J Phys Anthropol* 144:222.
- Myers MJ, Steudel K. 1985. Effect of limb mass distribution on the energetic cost of running. *J Exp Biol* 116:363–373.
- National Geographic Society US, Agland P. 1988. *Baka: People of the forest*. In: Washington: National Geographic Society.
- O'Neill M. 2012. Gait-specific metabolic costs and preferred speeds in ringtailed lemurs (*Lemur catta*), with implications for the scaling of locomotor costs in primates. *Am J Phys Anthropol* 149:356–364.
- Panther-Brick C. 1992. The energy cost of common tasks in rural Nepal: Levels of energy expenditure compatible with sustained physical activity. *Eur J Appl Physiol* 64:477–484.
- Prentice AM, Goldberg GR. 2000. Energy adaptations in human pregnancy: Limits and long-term consequences. *Am J Clin Nutr* 71:1226S–1232S.
- Rainoldi A, Melchiorri G, Caruso I. 2004. A method for positioning electrodes during surface EMG recordings in lower limb muscles. *J Neurosci Methods* 134:37–43.
- Rak Y. 1991. Lucy's pelvic anatomy: Its role in bipedal gait. *J Hum Evol* 20:283–290.
- Rasmussen KM, Catalano PM, Yaktine AL. 2009. New guidelines for weight gain during pregnancy: What obstetrician/gynecologists should know. *Curr Opin Obstet Gynecol* 21:521–526.
- Reno PL. 2014. Genetic and developmental basis for parallel evolution and its significance for hominoid evolution. *Evol Anthropol* 23:188–200.
- Reno PL, McCollum MA, Meindl RS, Lovejoy CO. 2010. An enlarged postcranial sample confirms *Australopithecus afarensis* dimorphism was similar to modern humans. *Philos Trans R Soc Lond B Biol Sci* 365:3355–3363.
- Richmond BG, Jungers WL. 2008. *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science* 319: 1662–1665.
- Rosenberg K. 1992. The evolution of modern human childbirth. *Yrbk Phys Anthropol* 35:89–124.
- Rosenberg K, Trevathan W. 2002. Birth, obstetrics and human evolution. *BJOG* 209:1199–1206.
- Rosenberg KR, Golinkoff RM, Zosh JM. 2004. Did australopithecines (or early *Homo*) sling? *Behav Brain Sci* 27:522.
- Rosenberg KR, Zuné L, Ruff CB. 2006. Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China. *Proc Natl Acad Sci U S A* 103:3552–3556.
- Ruff CB. 1995. Biomechanics of the hip and birth in early *Homo*. *Am J Phys Anthropol* 98:527–574.
- Ruina A, Bertram JE, Srinivasan M. 2005. A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *J Theor Biol* 237:170–192.
- Shine R. 1986. Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* 69: 260–267.
- Silder A, Delp SL, Besier TF. 2013. Men and women adopt similar walking mechanics and muscle activation patterns during load carriage. *J Biomech* 46:2522–2528.
- Simpson KM, Munro BJ, Steele JR. 2011. Backpack load affects lower limb muscle activity patterns of female hikers during prolonged load carriage. *J Electromyogr Kinesiol* 21:782–788.
- Simpson SW, Quade J, Levin NE, Butler R, Dupont-Nivet G, Everett M, Semaw S. 2008. A female *Homo erectus* pelvis from Gona, Ethiopia. *Science* 322:1089–1092.
- Sizer PS, James CR. 2014. Considerations of sex differences in musculoskeletal anatomy. In: Robert-McComb JJ, Norman RL, Zumwalt M, editors. *The active female*, 2nd ed. New York: Springer. p 33–60.
- Steudel-Numbers K, Tilkens M. 2004. The effect of lower limb length on the energetic cost of locomotion: Implications for fossil hominins. *J Hum Evol* 47:95–109.
- Stringer KR. 1986. An archaic character in the Broken Hill innominate E. 719. *Am J Phys Anthropol* 71:115–120.
- Tanaka J. 1980. *The San, Hunter-Gatherers of the Kalahari: A study in ecological anthropology*. Tokyo: University of Tokyo Press.
- Voloshina AS, Kuo AD, Daley MA, Ferris DP. 2013. Biomechanics and energetics of walking on uneven terrain. *J Exp Biol* 216: 3963–3970.

- Wagnild JM, Wall-Scheffler CM. 2013. Energetic consequences of human sociality: Walking speed choices among friendly dyads. *PLoS ONE* 8:e76576.
- Wall-Scheffler CM. 2012a. Energetics, locomotion and female reproduction: Implications for human evolution. *Annu Rev Anthropol* 41:71–85.
- Wall-Scheffler CM. 2012b. Size and shape: Morphology's impact on human speed and mobility. *J Anthropol* 2012:1–9.
- Wall-Scheffler CM. 2014. The balance between burden carrying, variable terrain, and thermoregulatory pressures in assessing morphological variation. In: Carlson KJ, Marchi D, editors. *Reconstructing mobility: Environmental, behavioral, and morphological determinants*. New York: Springer. p 173–192.
- Wall-Scheffler CM. 2015. Sex differences in incline-walking among humans. *Integr Comp Biol* 55:1155–1165.
- Wall-Scheffler CM, Chumanov ES, Steudel-Numbers K, Heiderscheit BC. 2010. EMG activity across gait and incline: The impact of muscular activity on human morphology. *Am J Phys Anthropol* 143:601–611.
- Wall-Scheffler CM, Geiger K, Steudel-Numbers K. 2007. Infant carrying: The role of increased locomotory costs in early tool development. *Am J Phys Anthropol* 133:841–846.
- Wall-Scheffler CM, Myers MJ. 2013. Reproductive costs for everyone: How female loads impact human mobility strategies. *J Hum Evol* 64:448–456.
- Wall-Scheffler CM, Myers MJ, Steudel-Numbers K. 2006. The application to bipeds of a geometric model of lower limb segment inertial properties. *J Hum Evol* 51:320–326.
- Washburn SL. 1960. Tools and human evolution. *Sci Am* 203:3–15.
- Wasserstein RL, Lazar NA. 2016. The ASA's statement on p-values: Context, process, and purpose. *Am Stat* 70:129–133.
- Weir JV. 1949. New methods for calculating metabolic rate with special reference to protein metabolism. *J Physiol* 109:1–9.
- Weyand PG, Smith BR, Puyau MR, Butte NF. 2010. The mass-specific energy cost of human walking is set by stature. *J Exp Biol* 213:3972–3979.
- Wheatley R, Angilletta MJ, Niehaus AC, Wilson RS. 2015. How fast should an animal run when escaping? An optimality model based on the trade-off between speed and accuracy. *Integr Comp Biol* 55:1166–1175.
- Whitcome KK, Lopez J, Miller EE, Burns JL. 2012. Revisiting the human obstetrical dilemma: Effect of pelvic rotation on stride length. *Am J Phys Anthropol* 54:302.
- Whiting J. 1994. Environmental constraints on infant care practices. In: Chasdi EH, editor. *Culture and human development: The selected papers of John Whiting*. Cambridge: Cambridge University Press. p 107–134.
- Zihlman A. 1993. Sex differences and gender hierarchies among primates: An evolutionary perspective. In: Miller BD, editor. *Sex and gender hierarchies*. Cambridge: Cambridge University Press. p 32–56.



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