

RESEARCH ARTICLE

The loss of the 'pelvic step' in human evolution

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ABSTRACT

Human bipedalism entails relatively short strides compared with facultatively bipedal primates. Unique non-sagittal-plane motions associated with bipedalism may account for part of this discrepancy. Pelvic rotation anteriorly translates the hip, contributing to bipedal stride length (i.e. the 'pelvic step'). Facultative bipedalism in non-human primates entails much larger pelvic rotation than in humans, suggesting that a larger pelvic step may contribute to their relatively longer strides. We collected data on the pelvic step in bipedal chimpanzees and over a wide speed range of human walking. At matched dimensionless speeds, humans have 26.7% shorter dimensionless strides, and a pelvic step 5.4 times smaller than bipedal chimpanzees. Differences in pelvic rotation explain 31.8% of the difference in dimensionless stride length between the two species. We suggest that relative stride lengths and the pelvic step have been significantly reduced throughout the course of hominin evolution.

KEY WORDS: Locomotion, Bipedal, Chimpanzee, Stride length, Hominin

INTRODUCTION

The human walking stride is generally characterized as having a low metabolic cost compared with other mammals (Rubenson et al., 2007), including our closest living relatives (Pontzer et al., 2014; Sockol et al., 2007). A suite of musculoskeletal traits appearing throughout the course of hominin evolution have been interpreted as adaptations towards reducing the cost of walking. Paramount among them is elongation of the lower limbs, which is argued to have allowed some fossil hominin species – including, ultimately, humans – to increase stride length, average walking speed and overall walking economy (e.g. Jungers, 1982; Minetti et al., 1994; Pontzer, 2017; Steudel-Numbers, 2006). Consequently, it is perhaps paradoxical that short-legged apes and monkeys have longer dimensionless stride lengths than humans at matched dimensionless speeds (O'Neill et al., 2018).

In walking, human relative stride lengths fall at the lower end of quadrupedal primates (Reynolds, 1987) and well below those of facultative bipeds, including chimpanzees (O'Neill et al., 2015), macaques (O'Neill et al., 2018), gibbons (Vereecke et al., 2006) and capuchins (Demes, 2011). During quadrupedalism, the longer strides of primates are primarily due to their large sagittal-plane

angular joint excursions (Larson et al., 2001; Reynolds, 1987). That humans maintain relatively short strides even when compared with other primate bipeds may be due to reduction in the three-dimensional (3-D) motion of our pelvis and lower limbs (O'Neill et al., 2018). In particular, transverse plane pelvic rotations, long identified as a non-sagittal-plane determinant of human bipedal mechanics (Saunders et al., 1953), may play an outsized role in this difference. Pelvic rotation involves swing-side hip translation that, when timed with swing-limb protraction, can increase stride length, termed the 'pelvic step' (Ducroquet et al., 1965). Chimpanzees and macaques use pelvic rotations during bipedalism that are similar in timing to humans, but involve ranges of motion 2–3 times larger than those of humans (Kinoshita et al., 2021; O'Neill et al., 2015, 2018; Thompson et al., 2015). In humans, the effect of the pelvic step is small, and accounts for only 2–5% of stride length at moderate-to-fast walking speeds (Liang et al., 2014; Whitcome et al., 2017). The substantial pelvic rotations of bipedal chimpanzees and macaques raise the possibility that the pelvic step may contribute to the relatively longer stride lengths of facultative bipeds as compared with humans. If so, a large pelvic step may have characterized the walking stride of the *Pan-Homo* last common ancestor and the earliest hominins.

Here, we collected 3-D kinematic data from bipedal chimpanzees and humans over a wide speed range to investigate the contribution of pelvic rotation to stride lengths. We sought to determine (1) to what extent does pelvic rotation contribute to stride length, and (2) to what extent does a human-like reduction in pelvic rotation explain the short dimensionless stride lengths of humans?

MATERIALS AND METHODS

Participants

All human experimental protocols were approved by The New York Institute of Technology's Internal Review Board and participants provided informed written consent prior to experiments. Three-dimensional kinematic data were recorded on 10 human participants (five females, five males; body mass=67.1±16.2 kg; age=24.8±0.9 years) during walking. All participants walked on a treadmill over a speed range of 0.3–2.0 m s⁻¹ in 0.1 m s⁻¹ increments. Speeds were randomized and participants were given time to adjust to a new speed prior to data recording. Five strides for each speed were collected for each subject. Chimpanzee kinematic data are from previously published studies (Thompson et al., 2015, 2018) on two male subadult chimpanzees (body mass=34.8±1.2 kg; age=7.1±0.1 years) walking bipedally at self-selected speeds along a runway. Chimpanzee data collection protocols were approved by the Stony Brook University Institutional Animal Care and Use Committee. Both chimpanzees were over the ages at which adult-like locomotor characteristics are expected (Kimura, 1996; Kimura and Yaguramaki, 2009; Pontzer et al., 2014). Aside from methodological limitations common to all 3-D kinematic studies (e.g. Della Croce et al., 2005), one limitation of the present study is that our chimpanzee data are derived from two individuals. While a

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small sample, our previous work has shown that chimpanzee bipedal kinematic data are largely stereotypic even with small sample sizes (O'Neill et al., 2015). Twenty-three strides were included for chimpanzees (subject 1: $n=11$ strides, $0.83\text{--}1.04\text{ m s}^{-1}$; subject 2: $n=12$ strides, $0.91\text{--}1.12\text{ m s}^{-1}$).

Data collection and analysis

All human kinematic data were collected using a 12-camera Vicon motion capture system (Vicon Motion Systems Ltd., Oxford, UK). Motion data were collected at 150 frames s^{-1} using the full-body Plug-In Gait marker set (based on the Newington/Helen Hayes gait model; Davis et al., 1991; Kadaba et al., 1990). Marker positions were filtered using a generalized cross-validated spline (i.e. 'Woltring filter'; Woltring, 1986). Pelvic rotation was calculated using the default Plug-In Gait analysis and were taken directly from Vicon Nexus (v2.9, Vicon Motion Systems) and compiled in ProCalc (Vicon Motion Systems) for further analysis. Chimpanzee data were collected on a 4-camera Xcitex motion capture system (Xcitex Inc., Woburn, MA, USA) at 150 frames s^{-1} , and the methods for calculating pelvic rotation were as in Thompson et al. (2015, 2018). Briefly, marker clusters (≥ 3 markers) were placed on the pelvis and rotations were calculated in the global coordinate system using Cardan angles and a standard tilt, list, rotation sequence of rotations.

For both chimpanzees and humans, in order to calculate the contribution of pelvic rotation to stride length, it was necessary to estimate the bi-acetabular breadth for each subject. For humans, the bi-acetabular breadth was taken as the distance between the estimated hip joint centers as calculated using the Plug-In Gait/Newington–Gage model (Davis et al., 1991). For chimpanzees, bi-acetabular

breadth (between the centers of each femoral head) was measured from pelvic X-rays that were taken within 6 months of data collection. These measurements were increased by an additional amount ($1.1\text{--}3.2\%$) to account for additional growth between the X-ray date and experimental date. This amount was determined based on growth rates derived from a large chimpanzee radiological dataset (Thompson et al., 2020; see Tables S1 and S2, and Fig. S1 for details).

To calculate anterior translation of the swing-side hip over the stride, we used a model similar to one that has been used previously (Liang et al., 2014; Whitcome et al., 2017). For a stride, the pelvic angle (relative to the neutral position) at the contralateral ($\angle\text{CTD}$) and second ipsilateral ($\angle\text{IP2}$) touchdowns were noted (Fig. 1A). The linear translation of the hip joint centers due to pelvic rotation and given the bi-acetabular breadth (B) was:

$$D = B \times \sin(\angle\text{CTD}) - B \times \sin(\angle\text{IP2}), \quad (1)$$

where D is the total linear translation of the hip joint centers over a stride, or, as illustrated in Fig. 1A:

$$D = d_1 + d_2, \quad (2)$$

where d_1 and d_2 are the linear translation of the contralateral and ipsilateral hip joint centers, respectively. The contribution that this distance made to the stride was calculated by dividing D by stride length and multiplying by 100.

Stride length in both species was calculated by taking the fore–aft distance between the positions of a heel marker at two consecutive ipsilateral heel strikes. It was made dimensionless by dividing by effective limb length (ELL). ELL was calculated as the distance of the greater trochanter from the ground during standing (humans) or

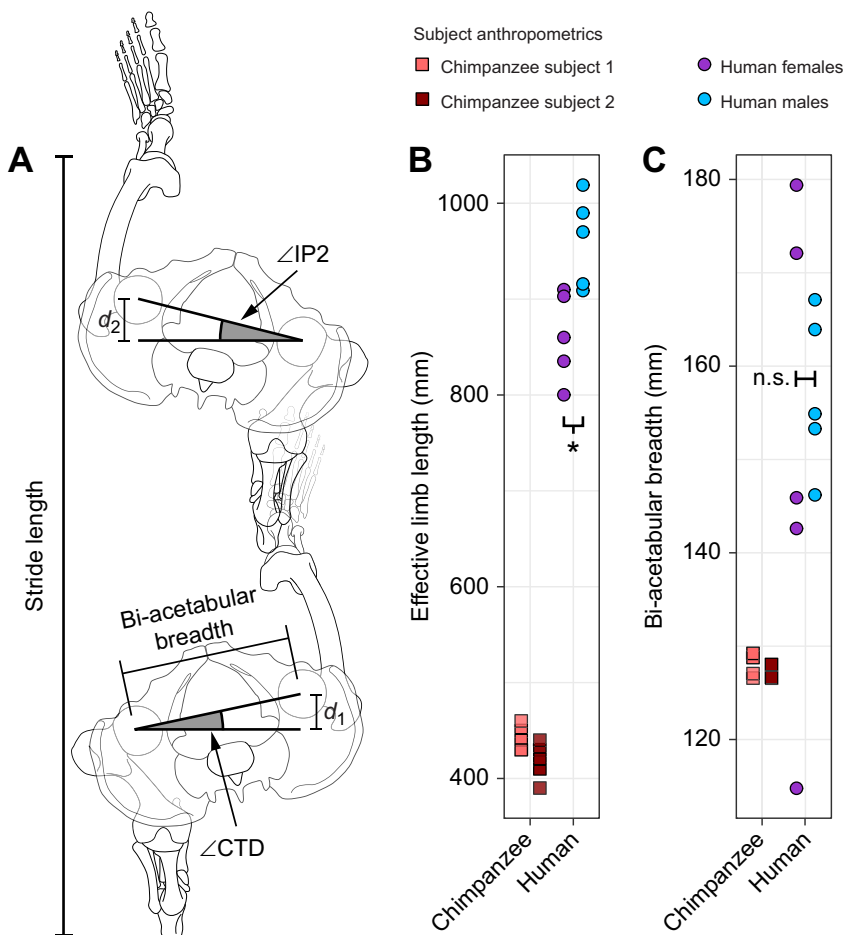


Fig. 1. Pelvic step model and subject anthropometric data. (A) Model for calculating the contribution of pelvic rotation to stride length ('pelvic step contribution'). Pelvic rotation at contralateral touchdown ($\angle\text{CTD}$) and second ipsilateral touchdown ($\angle\text{IP2}$) and bi-acetabular breadth were used to calculate the forward translations (D) of the swing-side hip ($d_1 + d_2$). Pelvic rotation magnitude is exaggerated for clarity. (B) Effective limb length (ELL) and (C) bi-acetabular breadth for participants. For chimpanzees, individual trials are shown (light and dark red shaded squares), and for humans, individual participants are shown (females, purple circles; males, blue circles). Statistics refer to differences between males and females in the human sample (* $P < 0.05$; n.s., not significant). Differences between humans and chimpanzees are significant at the $P < 0.01$ level.

when the greater trochanter was vertically positioned above the foot during a stride (chimpanzees).

Statistical analysis

Differences in anthropometric variables (ELL, bi-acetabular breadth and height) between species, or between sexes within humans, were tested via Welch's two-sample *t*-test in R version 3.6.1 (<https://www.r-project.org/>) to account for unequal variance. The biomechanical variables investigated were expected to vary with speed. Therefore, to investigate differences between species, and between sexes in humans, we used linear mixed models (LMMs) where dimensionless speed was a predictor variable in all analyses. Comparisons at similar dimensionless speeds across species also minimizes the effect of differences owing to body size on gait dynamics (Alexander and Jayes, 1983). Dimensionless speed was calculated as $v \times (9.81 \times \text{ELL})^{-0.5}$, where *v* is walking speed.

For each biomechanical variable of interest, two sets of LMM models were created using the package lme4 (Bates et al., 2015). The first set tested whether, within humans, the outcome variable differed between sexes. The second set tested for differences between chimpanzees and humans irrespective of sex. For all variables, within-human LMMs including a second-degree polynomial function for the effect of dimensionless speed better approximated the distribution of the data and outperformed first-degree polynomials, as determined via a lower Akaike information criterion score (Akaike, 1974). Therefore, for all models (including those in chimpanzees), a second-order polynomial function was included. In both sets of LMMs, subject identity was included as a correlated random effect with variable slopes and *y*-intercepts. For the first set of LMMs, sex was included as a fixed effect, and then evaluated for significance against a null model omitting the effect of sex in an ANOVA. If the model including the effect of sex did not significantly outperform the null model, the null model was accepted. In the second set of LMMs (interspecific comparisons), species was included as a random factor with correlated random slopes and *y*-intercepts. Sex was not included as a factor as the two chimpanzees were male. Models were then tested for significance against a null model that omitted the effect of species.

In the figures, the response of the model for the predictor of dimensionless speed is shown and was plotted using the packages ggeffects (Lüdtke, 2018) and ggplot2 (Wickham, 2016). All plots show the results of the LMM comparing species, except when sex was a significant predictor within humans, in which case the within-human model (including sex) is also shown.

Modeled dimensionless stride lengths

To calculate the magnitude of the effect of pelvic rotation on dimensionless stride length, we recalculated chimpanzee dimensionless stride lengths, but assuming a human-like magnitude of pelvic rotation. This was done by: (1) taking the chimpanzee stride lengths, (2) subtracting the linear distance contributed by pelvic rotation ($D_{\text{chimpanzee}}$), (3) calculating the estimated human-like pelvic rotation range of motion for that specific dimensionless speed from the LMM, (4) recalculating the distance contributed by pelvic rotation (D_{human}) as if the chimpanzee pelvis of that size underwent a human-like degree of pelvic rotation, and (5) re-adding this distance to the stride length. Following this, another LMM was performed as above with the modeled data and including species as a factor.

RESULTS

Within humans, male participants were 14% taller than female participants (ELL: males: 960.8 ± 7.5 mm, females: 861.6 ± 46.3 mm;

$P < 0.05$; Fig. 1B, Table S1). However, the bi-acetabular breadths of the male participants fell completely within the range of the female participants (males: 157.1 ± 8.4 mm, females: 151.0 ± 25.8 mm; n.s.; Fig. 1C). Humans had significantly longer ELLs (112%) and larger bi-acetabular breadths (20%) than chimpanzees (ELL, $P < 0.001$; bi-acetabular breadth, $P < 0.01$; Table S1).

Dimensionless stride lengths, the percent contribution of pelvic rotation to stride length, and pelvic range of motion (ROM) against dimensionless speed are all shown in Fig. 2. For all three variables, humans and chimpanzees were significantly different. A significant difference between males and females within the human sample was only detected for dimensionless stride length (Fig. 2A; see Scripts 1–4 in Supplementary Materials & Methods).

At comparable dimensionless speeds (0.40–0.55), chimpanzees used 26.7% (range: 21.7–31.1%) longer dimensionless strides than humans (Fig. 2A). Within humans, the dimensionless stride lengths of males were longer than those of females by 0.1 (see Script 1 in Supplementary Materials & Methods).

Pelvic rotation ROM in humans followed a distinct parabolic shape, with the lowest ROMs (LMM minimum of 7.9 deg) occurring at a dimensionless speed of 0.3 (Fig. 2B). Chimpanzee pelvic rotation ROM averaged 41.8 deg (range: 28.4–61.0 deg) and was, on average 3.8 (range: 3.5–3.9) times larger than in humans at comparable dimensionless speeds.

The contribution of the pelvic step to stride length varied with speed in humans (Fig. 2C). At low speeds, the pelvic step contribution was slightly negative. This indicates that the swing-side hip was not protracted at ipsilateral heel strike; pelvic rotation actually detracted from stride length. At the highest dimensionless speed (0.64), the average contribution was 2.7%, with the maximum amount for any stride being 4.5%. In chimpanzees, pelvic rotation contributed 9.6% (6.6–14.2%) to stride length. This corresponds to pelvic step contributions in chimpanzees that are on average 5.4 (range: 5.0–6.0) times greater than in humans at the comparable dimensionless speed range (0.40–0.55).

Chimpanzee dimensionless stride lengths, and those recalculated stride lengths modeled with a human-like degree of pelvic rotation, are shown in Fig. 3. The difference between the original LMM effect (solid line of Fig. 2A) and that of the modeled LMM (dashed line of Fig. 3) was used to calculate how much of the difference between human and chimpanzee dimensionless stride lengths can be explained by differences in pelvic rotation ROM. Over the comparable speed range, differences in pelvic rotation ROM account for 31.8% (range: 25.4–35.7%) of the difference in relative stride length between humans and chimpanzees at the comparable dimensionless speed range (0.40–0.55).

DISCUSSION

Here, we sought to determine how much of humans' relatively short strides are due to small pelvic rotations and a reduced pelvic step compared with bipedal chimpanzees. Our results show that bipedal chimpanzees have 26.7% (21.7–31.1%) longer dimensionless stride lengths, and the contribution of pelvic rotation to a stride is 5.4 (5.0–6.0) times greater than in humans. Of the difference in dimensionless stride length between humans and chimpanzees, 31.8% (25.4–35.7%) can be attributed solely to the effect of larger pelvic rotations in chimpanzees. In humans, the small (and at slow speeds, negative) contribution of the pelvic step strongly suggests that it is of only minor functional significance. Even at moderate dimensionless speeds the contribution of pelvic rotation to stride length is less than 2.5% in humans, similar to levels measured elsewhere (Liang et al., 2014; Whitcome et al., 2017). A pelvic step larger than that of

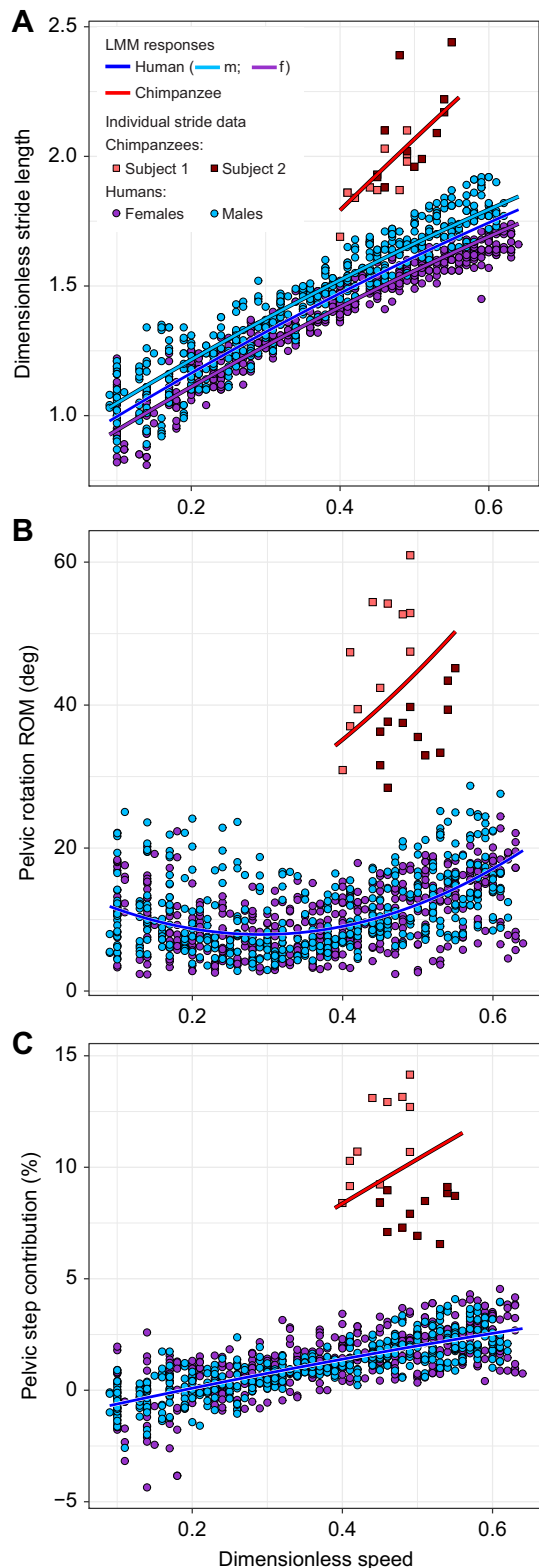


Fig. 2. Kinematic data for humans and chimpanzees. (A) Dimensionless stride length, (B) pelvic rotation range of motion (ROM) and (C) the contribution of pelvic step to stride length against dimensionless speed for all trials. Circles are humans (female, purple; male, blue) and squares are chimpanzees (subject 1, light red; subject 2, dark red). Blue and red lines indicate model responses from the linear mixed models (LMMs) for humans and chimpanzees, respectively. In cases where sex had a significant effect (A), the response for females and males are also shown in purple and light blue, respectively.

humans is also likely present in bipedal macaques, who have relative stride lengths similar to those of chimpanzees, albeit with slightly smaller pelvis rotation ROMs (O'Neill et al., 2018).

Given that large pelvic rotations characterize both chimpanzees and macaques, it is likely the case that large pelvic rotations, and large pelvic steps, were present in the last common ancestor of humans and chimpanzees and perhaps the earliest hominins. Although the bipedal walking gait of the earliest hominins has been argued to be critically influenced by iliac height, lumbar column length and facultative lordosis (Lovejoy and McCollum, 2010; Lovejoy et al., 2009), recent quantitative comparisons indicate that bipedal chimpanzees and bipedal macaques are nearly the same in 3-D pelvis and hind limb kinematics, despite marked differences in these traits (O'Neill et al., 2018). There is current disagreement as to the primitive conditions of the earliest hominin pelvis and hind limbs (e.g. Almécija et al., 2021; Lovejoy et al., 2009; Pilbeam and Lieberman, 2017). Nevertheless, based on the available data, we suggest that the last common ancestor of humans and chimpanzees and the earliest hominins would have likely walked with large pelvis rotations and pelvic steps. This would indicate that it is within hominins that pelvis rotation, as well as the pelvic step, have been reduced. Yet, hominins are also widely thought to have been under selective pressure to increase stride length, as evidenced primarily through lower limb elongation (Jungers, 1982, 2009; Jungers et al., 2016; Minetti et al., 1994; Pontzer, 2007, 2017; Steudel-Numbers, 2006; Steudel-Numbers and Tilkens, 2004). This ultimately raises the question, if hominins were under selective pressure to increase stride length, why not retain a large pelvic step? Humans are clearly capable of walking with very large pelvic rotations. Race walking, which optimizes stride length and speed without using an aerial phase (Hanley et al., 2013), involves pelvic rotation magnitudes that are 70–90% larger than in walking at preferred speeds and are within the range of bipedal chimpanzees and macaques (Cairns et al., 1986; Murray et al., 1983; O'Neill et al., 2018; Thompson et al., 2015). But normal human walking favors smaller pelvic rotation ROMs, particularly at low-to-preferred speeds, as shown by the U-shaped relationship between pelvic rotation ROM and speed found here (Fig. 2B) and elsewhere (Bruijn et al., 2008; Liang et al., 2014; van Emmerik and Wagenaar, 1996; van Emmerik et al., 2005). Therefore, it seems likely that constraints on pelvis rotation in hominins outweighed benefits of lengthening the stride via the pelvic step. However, the specific biomechanical constraints on pelvic rotation are unknown. In other words, what possible factors determine the optimal amount of (reduced) pelvic rotations for modern humans?

Classically, it was thought that pelvis rotation reduced vertical oscillations of the center of mass (vCOM) and, thus, the cost of locomotion (Saunders et al., 1953). This line of reasoning has also been applied to fossil hominins. Rak (1991) proposed that small-bodied hominins with wide pelves could use relatively longer pelvic steps to help reduce otherwise large vCOM arising from short lower limbs (Gruss et al., 2017; Rak, 1991). Yet, experimental data show that the effect of pelvis rotation on vCOM excursion is small (Della Croce et al., 2001; Kerrigan et al., 2001). Additionally, reducing vCOM excursion increases, rather than decreases, metabolic cost of locomotion (Gordon et al., 2009; Massaad et al., 2007; Ortega and Farley, 2005; Wurdeman et al., 2017), and vCOM excursions are expected in efficient pendular-like walking to help minimize mechanical work during the stride (Kuo, 2007; Srinivasan and Ruina, 2006). Thus, the reduction in pelvic rotation within humans is likely unrelated to reducing vCOM oscillations.

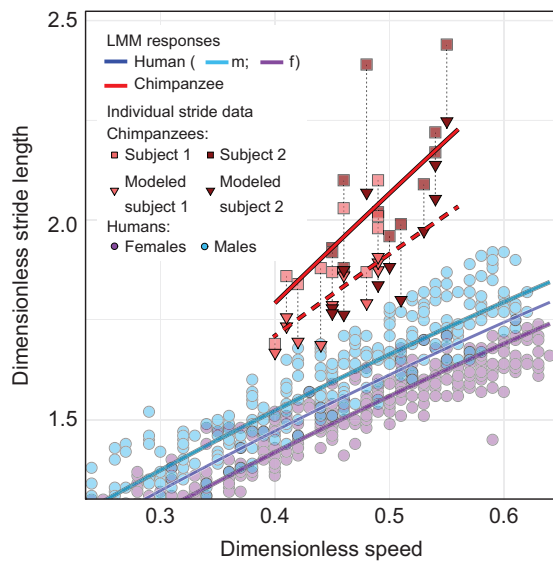


Fig. 3. Actual and modeled dimensionless stride lengths for chimpanzees. Modeled stride lengths (triangles) are those that were recalculated using a human-like degree of pelvic rotation. Vertical dashed lines indicate the difference between the actual and modeled dimensionless stride length for each chimpanzee stride. The dashed red line indicates the chimpanzee model response from the LMM for the modeled data as compared with the original data (solid red line). All other symbols follow Fig. 2.

One possible mechanical constraint that may predict the decrease in pelvic rotations in hominin evolution is conservation of whole-body angular momentum. In general, humans walk in a way that reduces extraneous angular momentum and angular acceleration of body segments (Herr and Popovic, 2008). Within the trunk, the thorax and pelvis rotate out of phase, which in turn allows the angular momentum of the swinging upper limbs to offset that of the lower limbs (Bruijn et al., 2008; Collins et al., 2009; Elftman, 1939; Herr and Popovic, 2008). This facilitates energetically efficient arm swing (Collins et al., 2009; Pontzer et al., 2009; Umberger, 2008; Yegian et al., 2019). One key aspect of this system may be the human-like out-of-phase rotations of the thorax and pelvis, a feature not seen in bipedal chimpanzees (Thompson et al., 2015) nor in bipedal macaques (Kinoshita et al., 2021; Ogihara et al., 2010). A reduction in pelvic rotation throughout hominin evolution may have been a prerequisite to achieve this out-of-phase pattern (Thompson et al., 2015) and lower extraneous angular momentum. This may have some benefits for reducing the energetic cost of walking; however, it is unclear exactly where the cost savings arise from possessing efficient arm-swing, or how overall minimization of angular momentum may be related to overall muscle mechanics and energy expenditure. Studies of human locomotion with absent or non-normal arm swing suggest angular momentum considerations might account for approximately 5–26% of the cost of walking and running (Arellano and Kram, 2011, 2014; Collins et al., 2009; Umberger, 2008). This could serve as an estimate of the ‘upper limit’ of energetic benefits arising from angular momentum balance. However, such studies consider different arm-swing conditions in humans that already display an out-of-phase thorax–pelvis coordination; any energetic benefits resulting from the out-of-phase condition itself (i.e. changes in rotational power at the hip) are yet to be determined. The importance of angular momentum balance may also be gait specific (Bramble and Lieberman, 2004). For instance, during the aerial phase of running, whole-body angular momentum must be conserved

because no external forces are applied (Hinrichs, 1987), but a study of asymmetric loading shows that angular momentum balance may not always be controlled in walking (Thielemans et al., 2014). Nevertheless, factors related to angular momentum conservation may be one plausible reason for why humans decreased pelvic rotations. If so, this effect may have outweighed the modest effect of large pelvic rotations on increasing stride length. However, more work is needed to make clear how angular momentum compares between humans and facultative bipeds.

Whether and how a reduction in pelvic rotation is related to pelvic anatomy is also unclear. Despite recognition of a suite of derived pelvic and hip morphologies in humans and some early hominins (Gruss and Schmitt, 2015; Stern, 2000, among others), linking these to specific characteristics of pelvic and/or hip motion has still proven elusive. For instance, in chimpanzees, laterally expanded, dorsally oriented iliac blades may contribute to the magnitude of axial pelvic rotation (O’Neill et al., 2015). However, macaques, who differ from apes in their precise ilia orientation (Middleton et al., 2017; Waterman, 1929), also walk with large pelvis rotations (O’Neill et al., 2018). This suggests that additional traits may have a role, or that the relationship between ilia orientation and pelvis motion is simply robust to the differences in ilia orientation between chimpanzees and macaques. Furthermore, humans are capable of walking with chimpanzee-like large pelvic rotations (Cairns et al., 1986; Murray et al., 1983) and chimpanzees are anatomically capable of generating smaller pelvic rotations. Indeed, the smallest chimpanzee pelvic rotation measured here was similar to the largest value recorded in humans (Fig. 2B). Together, this suggests that there is likely not a straightforward correlation between pelvic rotation and a specific anatomical trait. Differences in pelvic rotation may therefore represent different optimization criteria for bipedalism on short limbs with flexed, abducted hips and flexed knees (O’Neill et al., 2015). Whether this is due to changes in angular momentum criteria (as described above), overall differences in strategies to maintain body stability while bipedal (Thompson et al., 2018), or some other kinematic or mechanical factors remains to be determined.

Regardless of the underlying mechanical or anatomical causation, the results reported here indicate that it was likely within the hominin lineage that pelvic rotations, and the pelvic step, were reduced. It may therefore be that stride length in early hominins was not under as strong of a selective pressure as previously considered. Indeed, long lower limbs are not consistently seen in the fossil record until after the appearance of *Homo* (Jungers, 2009; Jungers et al., 2016; Morwood et al., 2005; Pontzer et al., 2010), several million years after the origin of the hominin lineage and bipedalism. Co-occurrence of *Australopithecus afarensis* specimens with both long and short lower limb lengths has also been argued as evidence that lower limb elongation was of limited adaptive significance, at least in early hominins (Haile-Selassie et al., 2010). A reduction of the pelvic step during human evolution would be consistent with this view, but not necessarily exclusive evidence in support of it. It must also be considered that although humans have relatively short strides compared with other primate bipeds, long lower limbs still result in absolutely long strides. Therefore, lower limb elongation, particularly in *Homo* and some earlier large-bodied hominins (e.g. KSD-VP-1/1) would have still led to absolutely longer strides, regardless the magnitude of the pelvic step mechanism. The evolution of absolutely long lower limbs and concomitant stride lengths may have in some ways obviated the need for a large pelvic step, allowing hominins a somewhat different strategy for achieving stride length. This may be the case if there is some optimum for stride length, in which case the

combination of pelvis rotation and longer limb length would simply exceed that value. If correct, this would imply a trade-off between limb length and pelvis rotation.

Finally, differences in pelvic rotation alone account for ~32% of the difference in relative stride length between humans and chimpanzees. This represents a sizable portion of the difference for a single kinematic factor, but leaves ~68% of the difference in stride length unexplained. This likely primarily represents the effects of hip extension and overall excursion, knee extension and ultimately, differences in leg and total lower limb length. Thus, understanding when and why a reduction in the pelvic step occurred will require a more nuanced view of the specific factors constraining modern humans to reduced pelvic rotation magnitudes, as well as more detailed predictions of 3-D walking kinematics encompassing all factors that contribute to stride length. Nevertheless, the results here show that bipedal chimpanzees use pelvic rotations to increase stride length to a much greater degree than humans. Despite largely being considered to be under selective pressure for long strides, we suggest that hominins have abandoned the pelvic step as a mechanism to lengthen strides.

Conclusions

Here, we show that a reduced pelvic step accounts for 31.8% of the difference in stride length between humans and chimpanzees. A large pelvic step is also likely common to facultative bipeds. We propose that hominins decreased pelvic rotation and the contribution of the pelvic step throughout human evolution, despite possible selective pressure for longer strides and lower limb elongation. Other mechanical constraints on pelvic motion (e.g. angular momentum balance) may be of greater consequence for restricting pelvic rotations in humans. Evolutionarily, these constraints likely outweighed the minor increase in stride length resulting from a larger pelvic step.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.E.T., B.D., S.G.L.; Methodology: N.E.T., B.D., S.G.L.; Software: N.E.T.; Validation: N.E.T., D.R., W.P., M.A.B.; Formal analysis: N.E.T., D.R., W.P., M.A.B.; Investigation: N.E.T., D.R., W.P., M.A.B.; Resources: N.E.T., B.D., S.G.L.; Data curation: N.E.T., D.R., W.P., M.A.B.; Writing - original draft: N.E.T., M.C.O.; Writing - review & editing: N.E.T., B.D., S.G.L., M.C.O.; Visualization: N.E.T.; Supervision: N.E.T.; Project administration: N.E.T.; Funding acquisition: N.E.T.

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Data availability

Original data are available from the Dryad digital repository (Thompson et al., 2021): dryad.0p2ngf21x.

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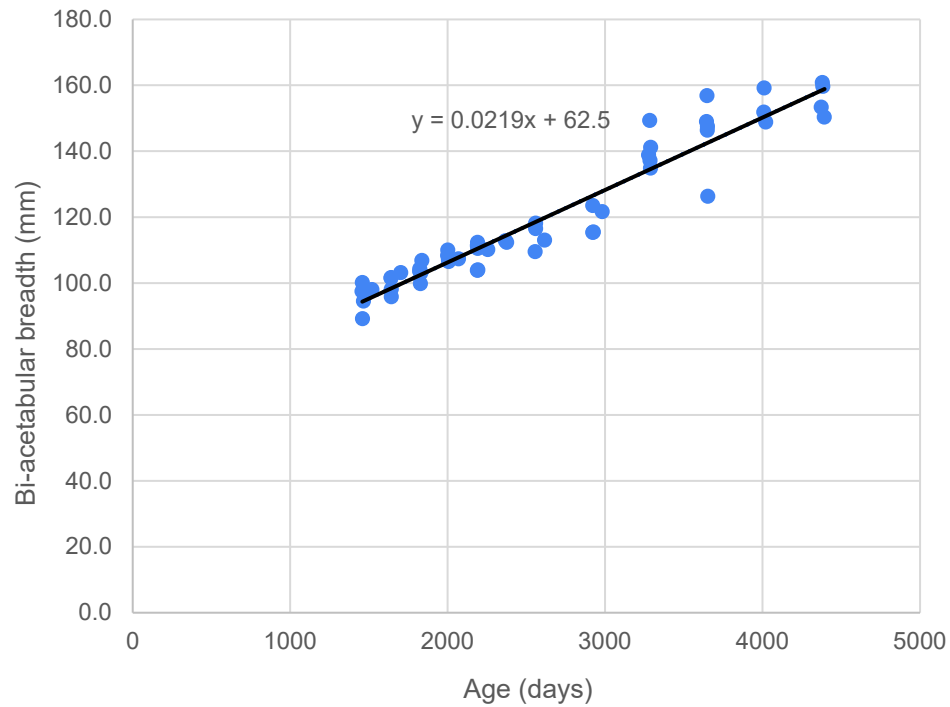


Fig. S1. Chimpanzee bi-acetabular breadth growth curve. Data are derived from an x-ray dataset of nine, laboratory-reared chimpanzees in a historical radiological study (see Thompson et al., 2020 for more details). Raw data shown in Table S2. Due to unequal and small sample sizes, simple linear regression was used to calculate a single growth rate (0.0219 mm/day). This growth rate generally led to only small increases to measured bi-acetabular size (1.1–3.2%).

Supplementary Materials & Methods

Script 1. Linear mixed model code and results for differences in dimensionless stride length versus dimensionless speed between sexes within humans.

The following is the summary of a model (m103.2.2) which incorporates only the human data, with sex as fixed effect and subject as a random effect (light blue and purple curves of Figure 2a).

```
summary(m103.2.2)

## Linear mixed model fit by REML ['lmerMod']
## Formula: DimensionlessStrideLength ~ DimSpeed + I(DimSpeed^2) + Sex +
##      (DimSpeed | Subject)
## Data: rotation_data[which(rotation_data$Species == "Human"), ]
## Control: lmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+05))
##
## REML criterion at convergence: -2805.8
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -3.7322 -0.5911  0.0159  0.6299  3.6588
##
## Random effects:
##   Groups    Name                Variance Std.Dev. Corr
##   Subject (Intercept)  0.011810  0.10867
##           DimSpeed     0.050467  0.22465  -0.88
##   Residual              0.002321  0.04817
## Number of obs: 900, groups: Subject, 10
##
## Fixed effects:
##              Estimate Std. Error t value
## (Intercept)    0.76744    0.03907  19.645
## DimSpeed       1.80666    0.08974  20.133
## I(DimSpeed^2) -0.44727    0.07478  -5.981
## SexM           0.10458    0.03272   3.196
##
## Correlation of Fixed Effects:
##              (Intr) DimSpd I(DS^2
## DimSpeed     -0.744
## I(DimSpd^2)   0.198 -0.600
## SexM         -0.418 -0.004  0.008
```

This model (m103.2.2) was tested against a null model, which is identical to m103.2.2, except without the including sex as an effect (m103.2.2_n). This null model resulting in a slightly lower, but nearly equivalent, AIC score. However, an ANOVA between the models shows that the model including sex significantly outperforms the model which does not include sex ($p = 0.008543$).

```
AIC(m103.2.2, m103.2.2_n)

##           df      AIC
## m103.2.2    8 -2789.781
## m103.2.2_n  7 -2790.619

anova(m103.2.2, m103.2.2_n)
```

```
## refitting model(s) with ML (instead of REML)

## Data: rotation_data[which(rotation_data$Species == "Human"), ]
## Models:
## m103.2.2_n: DimensionlessStrideLength ~ DimSpeed + I(DimSpeed^2) + (DimSpeed |
## m103.2.2_n: Subject)
## m103.2.2: DimensionlessStrideLength ~ DimSpeed + I(DimSpeed^2) + Sex +
## m103.2.2: (DimSpeed | Subject)
##      npar      AIC      BIC logLik deviance Chisq Df Pr(>Chisq)
## m103.2.2_n    7 -2803.3 -2769.7 1408.7 -2817.3
## m103.2.2      8 -2808.2 -2769.8 1412.1 -2824.2 6.916  1  0.008543 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Script 2. Linear mixed model code and results for differences in dimensionless stride length versus dimensionless speed between chimpanzees and humans

The following is the summary of a model (m103.2.2_s) which incorporates both human and chimpanzee data with species and subject as a random effects (red and blue curves of Figure 2a).

```
summary(m103.2.2_s)

## Linear mixed model fit by REML ['lmerMod']
## Formula: DimensionlessStrideLength ~ DimSpeed + I(DimSpeed^2) + (DimSpeed |
##      Species) + (DimSpeed | Subject)
## Data: chimp_human_data
## Control: lmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+05))
##
## REML criterion at convergence: -2771.4
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -3.5491 -0.5790  0.0091  0.6226  6.7741
##
## Random effects:
## Groups   Name                Variance Std.Dev. Corr
## Subject  (Intercept)  0.009083  0.09530
##          DimSpeed     0.049044  0.22146  -0.73
## Species  (Intercept)  0.023830  0.15437
##          DimSpeed     0.916419  0.95730  -1.00
## Residual                    0.002585  0.05085
## Number of obs: 923, groups: Subject, 12; Species, 2
##
## Fixed effects:
##              Estimate Std. Error t value
## (Intercept)   0.71183    0.11457   6.213
## DimSpeed      2.47903    0.68669   3.610
## I(DimSpeed^2) -0.44616    0.07879  -5.663
##
## Correlation of Fixed Effects:
##              (Intr) DimSpd
## DimSpeed    -0.980
## I(DimSpd^2)  0.076 -0.084
## convergence code: 0
## boundary (singular) fit: see ?isSingular
```

This model (m103.2.2_s) was tested against a null model, which is identical to m103.2.2_s, except without including species as an effect (m103.2.2_s_n). The model including species resulted in a lower AIC score, and significantly outperformed the null model ($p=0.002123$).

```
AIC(m103.2.2_s,m103.2.2_s_n)

##              df          AIC
## m103.2.2_s    10 -2751.398
## m103.2.2_s_n   7 -2740.052

anova(m103.2.2_s,m103.2.2_s_n)

## refitting model(s) with ML (instead of REML)
```



```
## Data: chimp_human_data
## Models:
## m103.2.2_s_n: DimensionlessStrideLength ~ DimSpeed + I(DimSpeed^2) + (DimSpeed |
## m103.2.2_s_n:      Subject)
## m103.2.2_s: DimensionlessStrideLength ~ DimSpeed + I(DimSpeed^2) + (DimSpeed |
## m103.2.2_s:      Species) + (DimSpeed | Subject)
##      npar      AIC      BIC logLik deviance  Chisq Df Pr(>Chisq)
## m103.2.2_s_n    7 -2751.1 -2717.3 1382.5  -2765.1
## m103.2.2_s     10 -2759.7 -2711.4 1389.9  -2779.7 14.668  3   0.002123 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Script 3. Linear mixed model code and results for differences in pelvic rotation range of motion versus dimensionless speed between chimpanzees and humans

The following is the summary of a model (m102.2.2_s) which incorporates both human and chimpanzee data with species and subject as a random effects (red and blue curves of Figure 2b).

```
summary(m102.2.2_s)

## Linear mixed model fit by REML ['lmerMod']
## Formula: PelvicRotationROM ~ DimSpeed + I(DimSpeed^2) + (DimSpeed | Species) +
##      (DimSpeed | Subject)
## Data: chimp_human_data
## Control: lmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+06))
##
## REML criterion at convergence: 4324.2
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -4.1086 -0.6621 -0.0276  0.5836  3.7481
##
## Random effects:
## Groups Name Variance Std.Dev. Corr
## Subject (Intercept) 36.650 6.054
##          DimSpeed 294.823 17.170 -0.79
## Species (Intercept) 0.000 0.000
##          DimSpeed 2166.785 46.549 NaN
## Residual 5.693 2.386
## Number of obs: 923, groups: Subject, 12; Species, 2
##
## Fixed effects:
##              Estimate Std. Error t value
## (Intercept) 16.129 1.917 8.414
## DimSpeed -23.747 33.532 -0.708
## I(DimSpeed^2) 96.726 3.699 26.150
##
## Correlation of Fixed Effects:
##              (Intr) DimSpd
## DimSpeed -0.137
## I(DimSpd^2) 0.215 -0.080
## convergence code: 0
## boundary (singular) fit: see ?isSingular
```

This model (m102.2.2_s) was tested against a null model, which is identical to m102.2.2_s, except without including species as an effect (m102.2.2_s_n). The model including species resulted in a lower AIC score, and significantly outperformed the null model ($p=0.008494$).

```
AIC(m102.2.2_s,m102.2.2_s_n)

##              df      AIC
## m102.2.2_s   10 4344.196
## m102.2.2_s_n  7 4352.280

anova(m102.2.2_s,m102.2.2_s_n)

## refitting model(s) with ML (instead of REML)
```

```
## Data: chimp_human_data
## Models:
## m102.2.2_s_n: PelvicRotationROM ~ DimSpeed + I(DimSpeed^2) + (DimSpeed | Subject)
## m102.2.2_s: PelvicRotationROM ~ DimSpeed + I(DimSpeed^2) + (DimSpeed | Species) +
## m102.2.2_s: (DimSpeed | Subject)
##      npar    AIC    BIC logLik deviance Chisq Df Pr(>Chisq)
## m102.2.2_s_n    7 4365.8 4399.6 -2175.9  4351.8
## m102.2.2_s    10 4360.1 4408.4 -2170.1  4340.1 11.698  3  0.008494 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```


Script 4. Linear mixed model code and results for differences in pelvic step contribution versus dimensionless speed between chimpanzees and humans

The following is the summary of a model (m101.2.2_s) which incorporates both human and chimpanzee data with species and subject as a random effects (red and blue curves of Figure 2c).

```
summary(m101.2.2_s)

## Linear mixed model fit by REML ['lmerMod']
## Formula: PelvicRot_Percent ~ DimSpeed + I(DimSpeed^2) + (DimSpeed | Species) +
##      (DimSpeed | Subject)
## Data: chimp_human_data
## Control: lmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 1e+05))
##
## REML criterion at convergence: 1809.4
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -5.1282 -0.5017 -0.0008  0.5364  3.3686
##
## Random effects:
## Groups   Name                Variance Std.Dev. Corr
## Subject  (Intercept)         1.2800   1.1314
##          DimSpeed           18.7460   4.3297  -0.92
## Species  (Intercept)         0.9943   0.9971
##          DimSpeed           98.2706   9.9132   1.00
## Residual                    0.3757   0.6130
## Number of obs: 923, groups: Subject, 12; Species, 2
##
## Fixed effects:
##              Estimate Std. Error t value
## (Intercept)   -0.6557    0.8059  -0.814
## DimSpeed       14.5722    7.1617   2.035
## I(DimSpeed^2)  -1.8063    0.9501  -1.901
##
## Correlation of Fixed Effects:
##              (Intr) DimSpd
## DimSpeed      0.781
## I(DimSpd^2)   0.132 -0.094
```

This model (m101.2.2_s) was tested against a null model, which is identical to m101.2.2_s, except without including species as an effect (m101.2.2_s_n). The model including species resulted in a lower AIC score, and significantly outperformed the null model ($p=0.0002871$).

```
AIC(m101.2.2_s,m101.2.2_s_n)

##              df      AIC
## m101.2.2_s    10 1829.398
## m101.2.2_s_n   7 1845.696

anova(m101.2.2_s,m101.2.2_s_n)

## refitting model(s) with ML (instead of REML)
```

```
## Data: chimp_human_data
## Models:
## m101.2.2_s_n: PelvicRot_Percent ~ DimSpeed + I(DimSpeed^2) + (DimSpeed | Subject)
## m101.2.2_s: PelvicRot_Percent ~ DimSpeed + I(DimSpeed^2) + (DimSpeed | Species) +
## m101.2.2_s:      (DimSpeed | Subject)
##      npar    AIC    BIC logLik deviance Chisq Df Pr(>Chisq)
## m101.2.2_s_n    7 1849.6 1883.4 -917.80   1835.6
## m101.2.2_s     10 1836.7 1885.0 -908.35   1816.7 18.898  3 0.0002871 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Table S1. Subject anthropometrics

	Subject	Sex	Height (mm)	Weight (kg)	Age (y)	Effective lower limb length (mm)	Bi-acetabular breadth (mm)
Humans	1	F	1575	59.7	26.6	860	143
	2	M	1710	72.1	23.7	909	164
	3	M	1780	74.1	24.6	916	146
	4	M	1820	83.0	24.2	970	167
	5	M	1800	74.4	24.8	990	153
	6	F	1462	42.6	24.3	800	146
	7	F	1600	50.5	23.8	835	115
	8	F	1640	66.0	25.5	910	179
	9	F	1652	52.6	25.9	903	172
	10	M	1915	96.2	24.7	1019	155
	male mean	-	1805	79.9	24.4	961	157
	male st. dev.	-	74	10.0	0.5	47	8
	female mean	-	1586	54.3	25.2	862	151
	female st. dev.	-	76	8.9	1.2	46	26
Chimpanzees^a	total mean	-	1695	67.1	24.8	911	154
	total st. dev.	-	135	16.2	0.9	68	18
	1 mean	M	1032	35.7	7.0	441	129
	1 st. dev.	-	3	0.8	0.1	9	1
	2 mean	M	1016	33.9	7.1	418	127
	2 st. dev.	-	5	1.0	0.1	13	1
	total mean	-	1023	34.8	7.1	429	128
	total st. dev.	-	9	1.2	0.1	16	1

Abbreviations: st. dev., standard deviation. ^aChimpanzee means and standard deviations are based on multiple experimental days.

Table S2. Growth curve data on chimpanzee bi-acetabular breadth

Subject	Sex	Morphosource subject ID	Subject ID	Image #	Age (days)	Bi-acetabular breadth (mm)
Ken	M	YLPB-55	55-19	549	2003	110.0
Ken	M	YLPB-55	55-24	784	3278	138.8
Ken	M	YLPB-55	55-25	145	3646	149.0
Ken	M	YLPB-55	55-26	429	4009	151.8
Ken	M	YLPB-55	55-27	690	4374	153.3
Art	M	YLPB-57	57-16	715	1521	98.0
Art	M	YLPB-57	57-17	52	1704	103.2
Art	M	YLPB-57	57-19	575	2071	107.3
Art	M	YLPB-57	57-21	66	2617	113.0
Art	M	YLPB-57	57-22	470	2983	121.7
Alf	M	YLPB-59	59-21	852	2192	112.3
Alf	M	YLPB-59	59-22	186	2560	118.2
Alf	M	YLPB-59	59-24	848	3291	141.2
Alf	M	YLPB-59	59-25	204	3651	146.3
Alf	M	YLPB-59	59-26	479	4022	148.8
Bard	M	YLPB-61	61-21	129	1460	100.2
Bard	M	YLPB-61	61-22	390	1642	101.5
Bard	M	YLPB-61	61-23	631	1825	104.3
Bard	M	YLPB-61	61-24	820	2007	107.2
Bard	M	YLPB-61	61-25	941	2194	111.5
Bard	M	YLPB-61	61-26	124	2376	112.3
Bard	M	YLPB-61	61-27	335	2560	116.5
Bard	M	YLPB-61	61-28	646	2923	123.5
Bard	M	YLPB-61	61-29	2	3287	137.2
Bard	M	YLPB-61	61-30	269	3652	147.5
Scarf	M	YLPB-65	65-30	871	1826	103.7
Scarf	M	YLPB-65	65-32	240	2193	110.5
Jed	M	YLPB-67	67-29	690 & 687	1461	89.2
Jed	M	YLPB-67	67-30	846 & 848	1644	95.8
Jed	M	YLPB-67	67-31	2	1829	99.8
Jed	M	YLPB-67	67-32	390	2191	103.8
Jed	M	YLPB-67	67-33	694	2557	109.5
Jed	M	YLPB-67	67-34	61 & 53	2927	115.5
Jed	M	YLPB-67	67-36	634	3654	126.3
Web	M	YLPB-79	79-23	464	1644	98.2
Web	M	YLPB-79	79-25	953 & 959	2194	104.0
Web	M	YLPB-79	79-26	239	2257	110.2
Web	M	YLPB-79	79-27	548	2923	115.3
Banka	F	YLPB-98	79-29	533	1467	94.5

Banka	F	YLPB-98	79-30	893	1831	103.0
Banka	F	YLPB-98	79-31	44 & 51	2008	106.5
Banka	F	YLPB-98	79-32	270	2196	111.2
Banka	F	YLPB-98	79-35	227	3290	134.8
Banka	F	YLPB-98	79-38	31	4394	150.3
Jenny	F	YLPB-90	90-22	141	1458	97.5
Jenny	F	YLPB-90	90-23	420	1643	101.7
Jenny	F	YLPB-90	90-24	636	1825	103.5
Jenny	F	YLPB-90	90-25	827	2001	108.3
Jenny	F	YLPB-90	90-26	949	2191	111.3
Jenny	F	YLPB-90	90-27	113	2368	112.8
Jenny	F	YLPB-90	90-30	13	3285	149.3
Jenny	F	YLPB-90	90-31	2868	3649	156.8
Jenny	F	YLPB-90	90-32	591	4011	159.2
Jenny	F	YLPB-90	90-33	843	4381	160.8
Jojo	F	YLPB-94	94-26	716	1838	106.8
Jojo	F	YLPB-94	94-27	7	2192	111.7
Jojo	F	YLPB-94	94-32	888	4384	159.7

Bi-acetabular breadth was measured in nine, laboratory-reared chimpanzees in a historical radiological study (see Thompson et al., 2020 for more details). Measurements were taken on all x-ray images where it was possible to visualize the center of the femoral head bilaterally. Subject ID's are as in Thompson et al. (2020). Bi-acetabular breadth is the average of three measurements.

Table S3. Application of growth curve data to measured chimpanzee bi-acetabular breadths

Chimpanzee	Image date	Experimental date	Days past imaging date	Expected additional growth (mm)	Original bi-acetabular measurement (mm)	Corrected bi-acetabular measurement (mm)	Increase (%)
Subject 1	6/11/2013	8/13/2013	63	1.38	125.2	126.6	1.1
Subject 1	6/11/2013	9/4/2013	85	1.86	125.2	127.1	1.5
Subject 1	6/11/2013	11/21/2013	163	3.57	125.2	128.8	2.9
Subject 1	6/11/2013	11/21/2013	163	3.57	125.2	128.8	2.9
Subject 1	6/11/2013	11/21/2013	163	3.57	125.2	128.8	2.9
Subject 1	6/11/2013	12/12/2013	184	4.03	125.2	129.2	3.2
Subject 1	6/11/2013	12/12/2013	184	4.03	125.2	129.2	3.2
Subject 1	6/11/2013	12/12/2013	184	4.03	125.2	129.2	3.2
Subject 1	6/11/2013	12/12/2013	184	4.03	125.2	129.2	3.2
Subject 1	6/11/2013	12/12/2013	184	4.03	125.2	129.2	3.2
Subject 1	6/11/2013	12/12/2013	184	4.03	125.2	129.2	3.2
Subject 2	6/6/2013	8/26/2013	81	1.77	124.8	126.6	1.4
Subject 2	6/6/2013	8/26/2013	81	1.77	124.8	126.6	1.4
Subject 2	6/6/2013	8/26/2013	81	1.77	124.8	126.6	1.4
Subject 2	6/6/2013	8/26/2013	81	1.77	124.8	126.6	1.4
Subject 2	6/6/2013	8/26/2013	81	1.77	124.8	126.6	1.4
Subject 2	6/6/2013	8/29/2013	84	1.84	124.8	126.6	1.4
Subject 2	6/6/2013	8/29/2013	84	1.84	124.8	126.6	1.4
Subject 2	6/6/2013	10/31/2013	148	3.24	124.8	126.6	1.5
Subject 2	6/6/2013	10/31/2013	148	3.24	124.8	126.6	1.5
Subject 2	6/6/2013	10/31/2013	148	3.24	124.8	128.0	2.6
Subject 2	6/6/2013	10/31/2013	148	3.24	124.8	128.0	2.6
Subject 2	6/6/2013	10/31/2013	148	3.24	124.8	128.0	2.6

The expected growth increases to bi-acetabular breadth are based on the growth rate (0.0219 mm/day, Fig. S1) measured herein and the number which passed between the previous measurement of the chimpanzees in this study.