



Bipedal and quadrupedal locomotion in chimpanzees

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ARTICLE INFO

Article history:

Received 12 December 2012

Accepted 18 October 2013

Available online 5 December 2013

Keywords:

Energetics
Biomechanics
Human evolution
Hominoid
Ranging ecology

ABSTRACT

Chimpanzees (*Pan troglodytes*) habitually walk both bipedally and quadrupedally, and have been a common point of reference for understanding the evolution of bipedal locomotion in early ape-like hominins. Here we compare the kinematics, kinetics, and energetics of bipedal and quadrupedal walking and running in a sample of five captive chimpanzees. Kinematics were recorded using sagittal-plane digital high-speed video of treadmill trials. Kinetics were recorded via a forceplate. Metabolic energy cost was measured via steady-state oxygen consumption during treadmill trials. Consistent with previous work on chimpanzees and other hominoids, we found that the spatiotemporal characteristics, joint angles, ground reaction forces, and metabolic cost of bipedal and quadrupedal locomotion are similar in chimpanzees. Notable differences include hip and trunk angles, which reflected a more orthograde trunk posture during bipedalism, and mediolateral ground reaction forces, which were larger during bipedal walking. Stride frequencies were also higher (and step lengths shorter) during bipedal trials. Bipodal and quadrupedal walking among chimpanzees was similar to that reported for bonobos, gibbons, and other primates. The similarity in cost between bipedal and quadrupedal trials suggests that the adoption of bipedal walking would have had no effect on walking costs for early ape-like hominins. However, habitual bipedalism may have favored modifications of the hip to allow a more orthograde posture, and of the hind limb abductor mechanisms to efficiently exert mediolateral ground forces.

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Introduction

The locomotor anatomy of chimpanzees (*Pan troglodytes*) reflects the varied demands of their evolved foraging strategy. As ripe fruit specialists (Wrangham et al., 1998) chimpanzees find most of their preferred foods in tree canopies, and must be adept at navigating complex three-dimensional arboreal environments in order to forage effectively. Yet chimpanzees also walk substantial distances on the ground, traveling 2–5 km each day between food patches (Pontzer and Wrangham, 2006). As a result, chimpanzees, like other apes, habitually employ a wide range of locomotor gaits, including bipedal and quadrupedal walking, in the trees and on the ground (Doran, 1997; Thorpe and Crompton, 2006). In this paper, we examine the kinematics, kinetics, and energy cost of bipedal and quadrupedal locomotion in chimpanzees and investigate the relationships among locomotor anatomy, gait, and energy expenditure in chimpanzees and other primates.

Studies of non-human primate locomotion have identified several features that, while not unique to the order, nonetheless distinguish their mechanics and kinematics from other mammals (see Schmitt et al., 2006). Many terrestrial mammals, especially cursorial species such as dogs, goats, and horses, typically use stiff-limbed walking gaits at slow speeds and more compliant, mass-spring running gaits at faster speeds (Biewener, 2003). In contrast, primates use compliant limbs even during walking (Larney and Larson, 2004), and also use relatively longer strides, lower stride frequencies, and greater limb excursion angles than typical quadrupeds (e.g., Alexander and Maloiy, 1984; Reynolds, 1987; Demes et al., 1991; Larson et al., 2001; Raichlen, 2005a; Schmitt et al., 2006; Demes and O'Neill, 2013). The degree of limb compliance and excursion in primates exceeds that of other mammals, with the notable exception of arboreal marsupials (Larney and Larson, 2004). Primates are also distinct in moving fluidly from a walk to an amble (a running gait with no aerial phase) as they increase speed (Schmitt et al., 2006), whereas non-primate mammals typically progress through walking, trotting, and galloping gaits, with discrete kinematic changes at each transition (Biewener, 2003). Ambling has been reported in elephants

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(Hutchinson et al., 2003) but is rare among non-primate mammals. Compliant limbs, ambling gaits, longer strides, and greater forelimb excursions are thought to aid travel along thin branches high in the canopy, as these locomotor strategies reduce peak limb forces and allow primates to maintain a point of contact at all times (Demes et al., 1991; Larson, 1998; Larson et al., 2000, 2001; Schmitt et al., 2006). These kinematic features may also be related to morphological differences among taxa (e.g., distal limb muscle mass for grasping hands and feet leading to long strides and low stride frequencies; Preuschoft and Günther, 1994; Raichlen, 2004, 2005a,b).

Primates also differ from most other mammals in using a diagonal sequence footfall pattern and in bearing more weight on their hind limbs than their forelimbs (Kimura et al., 1979; Reynolds, 1987; Demes et al., 1994; Schmitt, 1998, 1999, 2003; Cartmill et al., 2002; Schmitt and Lemelin, 2002; Schmitt and Hanna, 2004; Hanna et al., 2006). Both of these traits have been argued to promote safety during arboreal locomotion (Cartmill et al., 2002; Hanna et al., 2006), and similar locomotor traits among arboreal marsupials have been cited as evidence for evolutionary convergence under selection for fine-branch locomotion. This adaptive hypothesis remains a matter of debate, however, and others have offered alternative models for the development of diagonal sequence gaits and greater hind limb support in primates (Shapiro and Raichlen, 2005; Wallace and Demes, 2008; Raichlen et al., 2009; Young, 2012).

The available data on hominoid locomotion suggests their mechanics and kinematics are similar to those of other non-human primates. Measurements of ground reaction forces (GRF) in gibbons (*Hylobates lar*; Vereecke et al., 2006a,b), bonobos (*Pan paniscus*; D'Août et al., 2004), and chimpanzees (*Pan troglodytes*) (Kimura, 1991; Kimura and Yaguramaki, 2009) suggest that apes do not use inverted-pendulum mechanics at slow speeds, and achieve little or no exchange of potential and kinetic energy. Exchanging potential and kinetic energy throughout the stride cycle of pendular walking gaits is a common energy recovery strategy among terrestrial mammals that reduces fluctuations in total energy and thereby improves walking efficiency (Biewener, 2003). Vereecke et al. (2006a) examined voluntary bipedal overground walking in white-handed gibbons and calculated less than 25% energy recovery for most bouts. By comparison, humans typically obtain recovery rates of ~60% or more (Willems et al., 1995). Similarly, D'Août et al. (2004) examined GRF and kinematic data from bonobos and found no evidence for pendular walking mechanics. Further, both gibbons and bonobos transition smoothly into a 'running walk' as they increase speed bipedally, and neither displays a distinct gait transition nor develops an aerial phase as speed increases (D'Août et al., 2004; Vereecke et al., 2006a,b). Notably, running walks and compliant gaits with low energy recovery have recently been reported for tufted capuchin monkeys (*Cebus apella*; Demes and O'Neill, 2013), underscoring the locomotor similarities among hominoids and other primates.

Apes habitually use a variety of locomotor modes (quadrupedal, bipedal, tripedal) when on the ground (Doran, 1997; D'Août et al., 2004; Vereecke et al., 2006a,b), and studies of bonobo locomotion indicate a substantial degree of kinematic variation within quadrupedal and bipedal gaits (D'Août et al., 2004). Nonetheless, kinematic analyses have shown that limb segment and joint angles during bipedal walking are similar to those used in quadrupedal walking (bonobos: D'Août et al., 2004; gibbons: Vereecke et al., 2006b; chimpanzees: Jenkins, 1972; Kimura and Yaguramaki, 2009). Apes use a compliant 'bent-hip, bent-knee' gait during both bipedal and quadrupedal walking, and the primary kinematic differences between them are a more extended hip and shorter, more frequent steps when walking bipedally (D'Août et al., 2004;

Pontzer et al., 2009). From this perspective, bipedalism among hominoids is simply one, rather unremarkable, aspect of their locomotor versatility, which itself is an adaptation to the varied demands of their semi-arboreal lifestyle. Rather than being confined to a limited and well-defined set of stereotyped gaits, apes comfortably and habitually employ a diverse and variable range of gaits and movement patterns as they navigate terrestrial and arboreal environments.

The kinematic similarity of bipedal and quadrupedal walking in hominoids is reflected in the metabolic cost of these locomotor modes. Treadmill studies measuring oxygen consumption in chimpanzees have shown that bipedal and quadrupedal walking requires the same amount of metabolic energy (Taylor and Rowntree, 1973; Sockol et al., 2007). Biomechanical analyses of chimpanzee gait indicate that quadrupedalism and bipedalism are equally costly because they require a similar volume of muscle activation to support body weight (Sockol et al., 2007). Moreover, variation in bipedal and quadrupedal costs among individuals is explained by variation in gait and muscle activation; chimpanzees that use more crouched postures and shorter step lengths while bipedal have greater bipedal costs, and vice versa. These analyses have also shed light on an apparent trade-off in hominoid locomotor anatomy: compliant gaits, flexed limb postures, and associated anatomical traits result in higher terrestrial travel costs for apes compared with other mammals (Sockol et al., 2007; Pontzer et al., 2009) but may improve security in the canopy and increase hind limb force production during vertical climbing.

Much of the work that has been done on hominoid locomotion has focused on bipedal walking and running, with the goal of understanding the evolution of bipedalism in the earliest hominins (Jenkins, 1972; Taylor and Rowntree, 1973; Rodman and McHenry, 1980; Yamazaki and Ishida, 1984; Shapiro and Jungers, 1988; Kimura, 1991; Tardieu et al., 1993; Li et al., 1996; D'Août et al., 2002; Videan and McGrew, 2002; Thorpe et al., 2004, 2007; Sockol et al., 2007; Vereecke et al., 2006a,b; Raichlen et al., 2008; Kimura and Yaguramaki, 2009; Pontzer et al., 2009). The broad similarity between bipedal walking and other locomotor modes, particularly vertical climbing (e.g., Yamazaki and Ishida, 1984), combined with the observation that apes in the wild often use bipedalism in the trees (Stanford, 2006; Thorpe and Crompton, 2006; Thorpe et al., 2007; Crompton et al., 2010), has led several authors to suggest that early hominin bipedalism evolved as an outgrowth of habitual arboreal bipedalism in their Miocene ancestors, an idea that can be traced back to Keith (1903, 1923). The similarity of bipedal and quadrupedal cost for chimpanzees has been cited as evidence that the adoption of bipedalism by early hominins would not have affected travel cost (Taylor and Rowntree, 1973; Sockol et al., 2007). The relatively high energy cost of chimpanzee walking and of humans employing ape-like, compliant walking gaits (Carey and Crompton, 2005) suggests that adaptations for a more extended-limb, human-like gait would have conferred improved locomotor efficiency for fossil hominins (Rodman and McHenry, 1980; Sockol et al., 2007; Pontzer et al., 2009). Several studies have suggested that adaptations for an extended-limb walking gait are evident in *Australopithecus afarensis* (e.g., Latimer, 1991; Crompton et al., 1998, 2012; Sellers et al., 2005; Sockol et al., 2007; Raichlen et al., 2010), which would indicate a relatively efficient form of bipedalism for these hominins. Conversely, Stern and Susman (1983), Susman et al. (1984), and Stern (1999, 2000) have argued that the locomotor anatomy of *A. afarensis* indicates a compliant 'bent-hip, bent-knee' (BHBK) bipedal gait that would have been energetically inefficient.

In this paper, we examine the kinematics, kinetics, and energetics of bipedal and quadrupedal locomotion in chimpanzees. Our previous analyses of this dataset (Sockol et al., 2007; Raichlen et al.,

2008, 2009; Pontzer et al., 2009) have focused on joint moments and testing specific models of gait and cost, primarily during walking speeds. As such, those papers focused on speeds of 0.67–1.34 m s⁻¹. Here, we provide a more comprehensive analysis of locomotor kinematics and mechanics, with a larger range of speeds (up to 3.58 m s⁻¹) including some asymmetrical (galloping) gaits, and address three broad questions. First, how do the kinematics, kinetics, and energetics of bipedal locomotion compare with those of quadrupedal locomotion in chimpanzees? Second, how do bipedal and quadrupedal locomotion in chimpanzees compare with other hominoids? Third, how do the kinematics, kinetics, and energy costs of bipedalism and quadrupedalism in chimpanzees compare with terrestrial locomotion in other mammals? We also examine the implications of these analyses for reconstructions of early hominin locomotion.

Materials and methods

Subjects

Five chimpanzees (*P. troglodytes*, subspecies unknown; two male, three female; age 6–33 years; Table 1) were included in this study, which was conducted in 2005–2006. These chimpanzees were privately owned and used as trained animal actors for movie, television, and other entertainment purposes. As such, starting in infancy, they were trained through positive operant conditioning to respond to the voice commands and hand gestures of their trainer. Each of these chimpanzees spent their juvenile periods engaged in the entertainment industry; the two youngest subjects were still working at the time of this study, the three older subjects were retired. All five subjects were trained, during short weekly sessions over the course of approximately six months, to walk and run on a treadmill for this study. Three subjects also performed a set of

force-plate trials. Because they were adept at listening to voice commands, training for force-plate trials proved unnecessary and those trials were collected in one day.

Ethical statement

All federal and institutional guidelines for the use of primates in research were followed for this study. Institutional Animal Care and Use Committee (IACUC) permissions were obtained from the University of California (UC) Davis and Harvard University (the cognizant institutions at the time of data collection) prior to data collection. The chimpanzee facility was licensed by the United States Department of Agriculture (USDA). Further, it was (and remains) our impression that the chimpanzees at the facility were well cared for, and that training for this study, and for commercial work was performed using positive reinforcement techniques. The owners of the facility have since retired, and the chimpanzees moved to zoos accredited by the Association of Zoos and Aquariums.

Nonetheless, by employing a private chimpanzee facility, particularly one engaged in entertainment, to conduct this study, we failed to follow the best practices of our field. Other studies have collected similar measurements in zoo or sanctuary settings, using apes housed under conditions superior to those in this study (e.g., D'Août et al., 2004; Vereecke et al., 2006a,b; Kimura and Yaguramaki, 2009; Channon et al., 2010). Also, the use of apes in entertainment has been shown to adversely affect public attitudes toward the protection of ape populations in the wild (Ross et al., 2008, 2011). Regrettably, by employing a private facility engaged in entertainment, we indirectly supported and implicitly condoned this misuse of primates.

The primary reason we chose to work with a private entertainment facility was that no other chimpanzee facility in the U.S.

Table 1
Subject characteristics and metabolic data.

Subject	Mass (kg)	Hind limb (cm)	Age	Sex	Postural cost (mlO ₂ kg ⁻¹ s ⁻¹)	Speed (m s ⁻¹)	VO ₂ (mlO ₂ kg ⁻¹ s ⁻¹)					
							Bipedal			Quadrupedal		
							Mean	St. dev.	n	Mean	St. dev.	n
Jack	34.2	45.0	6	M	0.12	0.67	0.36	—	1	0.22	—	1
						0.89	0.33	0.07	6	0.28	0.02	6
						1.12	0.35	—	1	0.28	—	1
						1.34	0.46	0.13	8	0.39	0.08	3
						1.56	0.48	0.09	2	0.45	—	1
						1.79	0.51	0.08	5	0.50	0.02	4
Louie	52.8	52.5	9	M	0.09	0.67	0.30	—	1	0.22	0.05	2
						0.89	0.31	0.08	9	0.26	0.03	5
						1.12	0.34	0.03	3	0.27	—	1
						1.34	0.45	0.09	11	0.33	0.07	5
						1.56	0.53	0.02	2	0.44	—	1
						1.79	0.47	0.12	6	0.48	0.02	5
Lucy	66.3	40.5	33	F	0.11	0.67	0.17	—	1	0.27	0.06	3
						0.89	0.20	0.04	9	0.38	0.07	4
						1.12	0.32	0.12	4	0.34	0.06	4
						1.34	0.26	0.07	7	0.46	0.08	5
						1.56	0.30	0.06	4	0.47	—	1
						0.67	0.17	—	2	0.16	0.01	3
Lulu	84.8	41.3	27	F	0.09	0.89	0.20	0.04	3	0.21	0.03	4
						1.12	0.21	0.05	2	0.22	0.03	2
						1.34	—	—	—	0.31	0.06	3
						0.67	0.23	—	1	0.16	—	1
						0.89	0.24	0.03	6	0.22	0.03	4
						1.12	0.30	—	1	0.20	—	1
Sally	61.8	51.0	19	F	0.06	1.34	0.37	0.04	8	0.29	0.04	5
						1.56	0.39	0.03	4	0.27	—	1
						1.79	0.39	0.05	5	0.44	0.01	2

'Hind Limb' denotes effective limb length (Pontzer, 2007). Number of measurements, *n*, is given for each speed. Italics denotes standard deviations.

had the resources or interest to undertake the training needed to acclimate chimpanzees, particularly adults, to treadmill trials. However, as more zoos and sanctuaries adopt operant conditioning programs with their apes, and as methods for data collection improve and become less intrusive, the opportunities to collect detailed data on apes and other primates in these settings are increasing. We have committed ourselves to working with sanctuaries, zoos, and similar facilities in our future primate research. By making the data from this study fully available, we hope to support the greater use of zoos and sanctuaries in primate research by reducing the need to collect additional measurements of chimpanzee locomotor cost, one aspect of performance that remains difficult to measure in zoo and sanctuary settings.

Metabolic measurements

Measurements of locomotor energy expenditure were collected by Michael D. Sockol as part of his dissertation work at UC Davis (direct interaction with the chimpanzees was limited to their trainer). All subjects were able to walk and run quadrupedally and bipedally without any training, but training sessions were required to acclimate the subjects to the treadmill, and to achieve trials of sufficient duration (3–5 min) to measure steady-state oxygen consumption. Training sessions also allowed the chimpanzees to become accustomed to wearing a light plastic mask, which was used to collect expired air for respirometry.

In previous studies (Sockol et al., 2007; Pontzer et al., 2009), we limited our energetics analysis to speeds of 0.67–1.34 m s⁻¹, approximately the range of habitual walking speeds in chimpanzees in the wild (Hunt, 1989). Here, we examine speeds up to 1.79 m s⁻¹, the maximum speed for which energetics measurements were obtained, which is near the transition to asymmetrical ‘galloping’ gaits for chimpanzees in this sample (see Results, below). While the energetics protocol did not seek to determine the fastest possible speed for aerobic measurement, our impression, based on the chimpanzees’ heavy breathing after these faster bouts, was that 1.79 m s⁻¹ was near the maximum speed that chimpanzees in this sample could maintain for the required 3–5 min measurement period. Marginally faster speeds may have been possible for Jack and Louie, both young males (Table 1). Lucy and Lulu were not able to maintain 1.79 m s⁻¹ for a long enough period to obtain a reliable measurement (Table 1), perhaps due to age or, in Lulu’s case, obesity.

Metabolic cost was calculated from the rate of oxygen consumption, using open-flow methods described elsewhere (Fedak et al., 1981; Sockol et al., 2007). During a metabolic measurement trial, subjects wore a loose-fitting plastic mask attached via a long flexible hose to a vacuum system. The vacuum pulled air through the mask at a sufficiently high rate to collect all of the subject’s expired air, as well as some ambient air. Oxygen concentration in the vacuum air stream was monitored and recorded continuously. The difference in oxygen concentration between ambient air (measured immediately before the trial) and the vacuum air stream from the mask during steady-state locomotion was used to calculate the rate of oxygen consumption (mlO₂ s⁻¹) (Fedak et al., 1981), and then divided by the subject’s body mass to give the mass-specific rate of oxygen consumption, VO₂ (mlO₂ kg⁻¹ s⁻¹). The number of metabolic measurements at each speed for each subject is shown in Table 1. When multiple measurements were collected for a given subject at a given speed, the mean VO₂ was calculated and used in subsequent analyses. These VO₂ values are shown in Table 1.

To test whether bipedal or quadrupedal locomotion was more costly for each subject, paired *t*-tests (bipedal versus quadrupedal) were performed on VO₂ values for the range of speeds measured.

Differences were considered to be significant if the two-tailed *p*-value for these tests was less than 0.05. A paired *t*-test (bipedal versus quadrupedal) was also performed on the pooled VO₂ measurements from all subjects. We also performed a repeated measures ANOVA, as our approach generated several measurements for each subject.

For comparison with other studies (e.g., Taylor et al., 1982), we also calculated the bipedal and quadrupedal net cost of transport, COT (mlO₂ kg⁻¹ m⁻¹) for each subject. The COT is typically calculated as the slope of the VO₂/speed trendline (Taylor et al., 1982), and we followed the same approach in this study. To calculate a mean COT for bipedal and quadrupedal walking, we calculated the mean VO₂ at each speed, pooling VO₂ values from all subjects, and plotted group means for VO₂ against speed. The slope of the least-squares regression through these points provided the species COT values for bipedal and quadrupedal locomotion.

We modified this approach to calculate the COT values for individual subjects. First, VO₂ measurements were plotted against speed for each subject, and an ordinary least-squares trendline was calculated for the pooled sample of all trials, bipedal and quadrupedal combined (Excel®). The intercept of this trendline was used as the ‘postural’ cost of locomotion (see Taylor et al., 1982). Next, ordinary least-squares trendlines were calculated separately for bipedal and quadrupedal trials, with the intercept forced through the common postural cost value (Excel®). By requiring the bipedal and quadrupedal trendlines to use a common intercept, their relative slopes reflect measured differences in VO₂; that is, the locomotor mode with higher VO₂ values will also have a greater slope and hence a greater COT.

This modified approach for calculating individual COT values was done so that calculated COT values reflected observed differences in VO₂. For all five subjects, the intercept value for quadrupedal trials was somewhat lower than that of bipedal trials, while the slope for quadrupedal trials was somewhat greater. Since COT is measured as the slope of the VO₂/speed trendline, the erroneous implication of these greater slopes is that the cost of quadrupedalism is greater than bipedalism. In fact, for most subjects the cost of quadrupedal locomotion was somewhat lower (Fig. 1; Table 1), although the difference was not always statistically significant. Requiring a common intercept value for quadrupedal and bipedal trendlines avoids this problem. We discuss the limitations of this approach and the lower intercept values for quadrupedal trials below. Finally, we analyzed VO₂ values using a general linear model (JMP®) that accounted for the effects of speed (continuous variable), and gait and individual (categorical variables).

Kinematic measurements

Movements of the limbs and trunk were recorded using high-speed (125 fields s⁻¹) digital video (Redlake®) during a set of treadmill trials. We note that the inverse-dynamics modeling in our previous studies (Sockol et al., 2007; Pontzer et al., 2009) used kinematics measurements from force-plate trials. Non-toxic, water-based white paint was used to mark the skin overlying the distal fifth metatarsal, calcaneal tuberosity, lateral malleolus, lateral femoral condyle, greater trochanter, humeral head, lateral humeral condyle, ulnar styloid, and distal fifth metacarpal. The camera was positioned approximately 5 m from the treadmill and perpendicular to the direction of travel (i.e., facing the sagittal plane). Subjects walked or ran, bipedally or quadrupedally, at a range of speeds. In each trial, a minimum of three strides was captured. One complete stride was defined as the time from one left foot strike to the subsequent left foot strike.

Afterward, the digital video recordings were played back frame by frame in a custom-written Matlab® routine, and a mouse driven

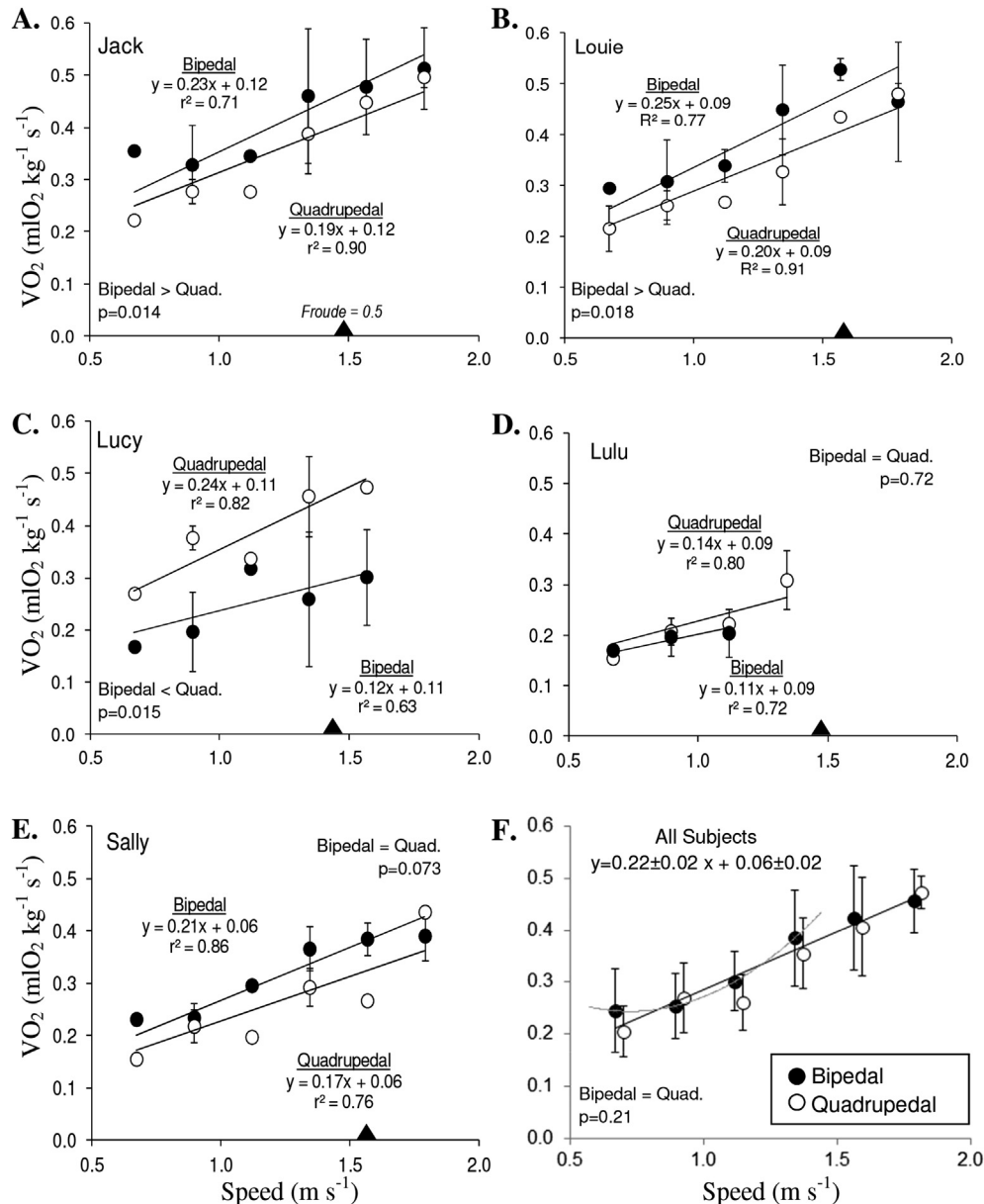


Figure 1. Mass-specific metabolic rate, VO_2 , versus travel speed. For individual subjects (A–E), bipedal and quadrupedal least-squares regressions are given separately. Black triangle on x-axis indicates speed at which Froude = 0.5. For the All Subjects plot (F), the least-squares regression line (\pm standard error) combines bipedal and quadrupedal measurements.

cursor was used to identify and record the x,y coordinates of each skin marker in each frame. Pixel coordinates were converted to real distances (cm) using a scale attached to the treadmill, visible in each frame. These coordinates were used to calculate limb segment and joint angles, as well as effective limb length at touch-down (Pontzer, 2007). The times of hind limb touch-down, toe-off, hand-strike, and hand-off were also recorded from the digital video. Limb excursion, retraction angles, and effective limb lengths, as well as stride frequencies (strides/s), periods (stride duration, s), and lengths (m, calculated as speed \times duration), contact times (stance duration, the period between touch-down and take-off of a limb), and hind limb duty factors (stance duration/stride period) were calculated for three strides, and the means of these values for each trial were used for subsequent analyses.

Froude number [$\text{speed}^2 / (L g)$] was calculated for each trial to facilitate comparisons across speeds and subjects. Effective limb

length, the length of the limb as a strut (Pontzer, 2007) was calculated as the straight-line distance from the hip marker to the foot marker at hind limb touch-down. Mean effective limb lengths, used for calculations of Froude number, are shown in Table 1. Limb length was calculated in this way because crouching by the chimpanzees while standing, and limb compliance during stance phase, precluded accurate measurement of effective limb length while standing or at midstance.

Limb phase was calculated as the percentage of stride duration that the forelimb touches down following touch-down of the ipsilateral hind limb. Definitions for gait categories follow Cartmill et al. (2002). Limb phases from 0.00 to 0.25 are defined as Lateral Sequence Lateral Couplets (LSLC), 0.25 to 0.50 are defined as Lateral Sequence Diagonal Couplets (LSDC), 0.50 to 0.75 are defined as Diagonal Sequence Diagonal Couplets (DSDC), and 0.75 to 1.00 are defined as Diagonal Sequence Lateral Couplets (DSLCL).

The fore- and hind limb data reported are all for the same (left) side. To smooth the data and present ‘average’ joint and segment angles for all of the chimpanzees, lowess regressions were plotted for both individuals and for the group data, using the *lowess* function in R ($f = 0.2$, $iter = 5$). Definitions and conventions of joint and segment angles are shown in Fig. 2.

Kinematics were also recorded during force-plate trials (see below), using a similar approach and angle definitions as in the treadmill trials. These analyses are limited by the narrow range of speeds (range: 0.57 – 1.50 m s⁻¹) and limited number of subjects ($n = 3$) and steps examined in force-plate trials. Further, only stance-phase angles (not swing phase) were digitized and analyzed. Nonetheless, while these trials cannot be considered ad libitum, as the subjects were instructed to walk along the force-plate trackway, they provide a limited comparison of treadmill and overground locomotion.

Force-plate measurements

Three subjects (Jack, Louie, and Sally) participated in a set of force-plate trials to record walking kinetics. In these trials, the subject walked (quadrupedally or bipedally) along an elevated (3 cm high) wooden trackway (approximately 0.5 m wide \times 6.0 m long). A portable forceplate (Kistler®) was positioned at the midpoint of the trackway, its surface flush with the walking surface of the trackway. As with the kinematic trials, non-toxic water-based white paint was used to mark joint centers and anatomical landmarks. Kinematic data (two-dimensional, lateral view; Redlake®, 125 f s⁻¹) and kinetic data (1000 Hz) were recorded simultaneously as the subject walked over the forceplate. Trials in which only one limb (hand or foot) contacted the forceplate were used for subsequent analyses if 1) the limb was from the side of the subject facing the camera, and 2) the entire hand or foot was on the plate during stance phase. For quadrupedal trials, a thin (~ 6 mm) rigid steel plate was used to cover a portion of the forceplate, preventing multiple limbs (e.g., a hand and a foot) from contacting the forceplate. Care was taken to ensure that this steel plate did not contact the forceplate. We did not distinguish between quadrupedal steps in which the foot landed laterally, versus medially, to the hand.

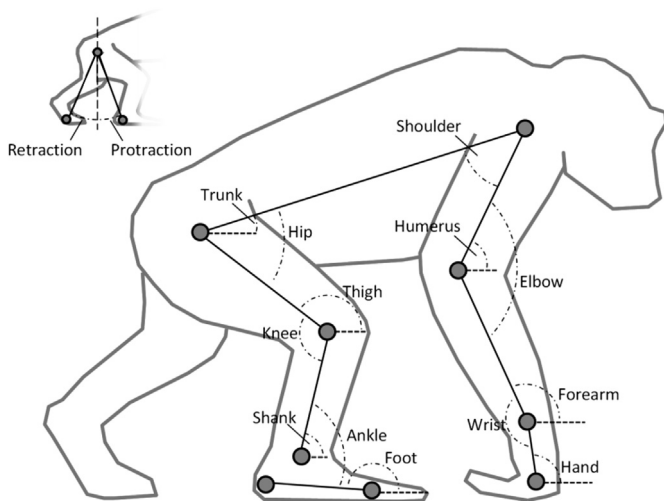


Figure 2. Definitions and conventions for joint and segment angles. Segment angles were measured relative to global horizontal. For the ankle, joint angle was measured between the foot segment (foot–metatarsal head) and shank (knee–lateral malleolus). Protraction and retraction conventions are also shown (inset).

Two previous studies examined joint moments and effective mechanical advantage in detail for these chimpanzees (Sockol et al., 2007; Pontzer et al., 2009). Here, we review these results and focus on the shape of the GRF curves and implications for gait mechanics. GRF force traces were passed through a 4th order zero-lag low-pass Butterworth filter with a frequency cut-off of 200 Hz. To provide an average for the vertical, anterior–posterior, and mediolateral traces, data from individual traces were combined and plotted against percent stance duration, and a lowess regression was calculated using the *lowess* function in R ($f = 0.1$, $iter = 3$).

Results

Metabolic data

Chimpanzee VO₂ and COT The relative metabolic cost of bipedal and quadrupedal locomotion varied among subjects, but there was no consistent difference between these locomotor modes. A two-way repeated measures ANOVA found no significant effect of posture (bipedal versus quadrupedal: $F[1,4] = 0.44$, $p = 0.54$), a significant effect of speed ($F[2,8] = 15.78$, $p = 0.002$), and no significant interaction between posture and speed ($F[2,8] = 3.61$, $p = 0.08$). We note that there is a great deal of variation within this sample, and we therefore examined individual data separately to explore variation in bipedal and quadrupedal costs that are attributed to individual differences in locomotor mechanics or anatomy (e.g., Sockol et al., 2007). The two males (Louie and Jack) had bipedal costs $\sim 20\%$ greater than quadrupedal costs at similar speeds ($p < 0.02$, paired *t*-tests; Fig. 1). A third subject, Sally, had bipedal costs that were greater, but the statistical significance was marginal ($p = 0.07$ in a two-tailed test, or $p = 0.04$ in a one-tailed test). Among the two older females, Lulu showed no difference in cost between modes ($p = 0.72$), and Lucy had $\sim 55\%$ greater quadrupedal costs ($p = 0.015$). When all data are pooled, a paired *t*-test revealed no difference between bipedal and quadrupedal cost ($n = 52$ (26 pairs), $p = 0.37$). These results are consistent with Taylor and Rowntree's (1973) comparison of bipedal and quadrupedal cost in chimpanzees and *Cebus* monkeys, and with our initial analysis of this dataset, which included only walking speeds (Sockol et al., 2007). Metabolic data are shown in Fig. 1 and Table 1.

Fig. 1 shows each subject's mean VO₂ and COT (i.e., the slope of the VO₂:speed trendline) for bipedal and quadrupedal trials. With VO₂ for all subjects combined, a linear trendline fit the data well, with oxygen consumption increasing with speed as $y = 0.21 \pm 0.02x + 0.08 \pm 0.03$ for bipedal locomotion and $y = 0.24 \pm 0.03x + 0.04 \pm 0.03$ for quadrupedal locomotion. A general linear model with speed and locomotor mode (bipedal versus quadrupedal) revealed a significant effect of speed ($p < 0.0001$) but no effect of locomotor mode ($p = 0.21$), and gave a combined VO₂:speed trendline of $y = 0.22 \pm 0.02x + 0.06 \pm 0.02$ ($r^2 = 0.95$). This relationship is shown in Fig. 1.

These species mean COT values (i.e., the VO₂:speed trendline slopes; bipedal: 0.21 ± 0.02 , quadrupedal: 0.24 ± 0.03 , combined: 0.22 ± 0.02) are somewhat greater than means calculated from individual COT values. Calculating a species mean from individual COT values gives a mean (\pm standard deviation) of 0.18 ± 0.06 mlO₂ kg⁻¹ m⁻¹ and 0.19 ± 0.04 mlO₂ kg⁻¹ m⁻¹ for bipedal and quadrupedal locomotion, respectively; these values are not significantly different ($p = 0.91$). The discrepancy in species COT values arises from differential weighting of subjects. Taking the mean of individual COT values weights each *subject* equally, while calculating COT from mean VO₂ values weights each VO₂ *measurement* equally, and therefore weights subjects with more VO₂

measurements more heavily. While either approach is reasonable, the latter is likely preferable here since it lends greater statistical power to subjects for which we have more data and therefore greater confidence. We favor the combined approach (Fig. 1) for this reason.

Another approach for calculating the relationship between speed and VO_2 , and thus COT, is to calculate the effect of speed on VO_2 in a general linear model controlling for locomotor mode (bipedal or quadrupedal) and subject. This analysis revealed a significant effect of speed ($p < 0.0001$) and significant differences among subjects ($p < 0.0001$), but no effect of locomotor mode ($p = 0.30$) on VO_2 . The estimate for the effect of speed (estimate: 0.20, standard error ± 0.02) was similar to other methods for calculating COT.

Effects of speed and gait As noted above and shown in Fig. 1, the rate of oxygen consumption, VO_2 , generally increased linearly with speed for all subjects, with no clear break or discontinuity over the range of speeds examined ($0.67\text{--}1.79\text{ m s}^{-1}$). Similarly, there was no discrete kinematic change over this range of speeds, even though the range of Froude numbers ($0.09\text{--}0.73$) included in metabolic trials strongly suggests chimpanzees were using walking mechanics at the slowest speeds and mass-spring running mechanics at the fastest speeds (see below). The pattern of linearly increasing VO_2 , and the similarity in walking and running COT it implies contrasts with the pronounced change between walking and running in humans (Rubenson et al., 2007), but is similar to that seen in many (perhaps most) other species (e.g., Taylor et al., 1982) and consistent with Taylor and Rowntree's (1973) study of juvenile chimpanzees. Note that chimpanzees used symmetrical gaits for all metabolic trials. The range of speeds included in VO_2 measurements did not elicit galloping.

There is limited evidence of a curvilinear VO_2 :speed relationship for bipedal locomotion at slower speeds, below $\text{Fr} = 0.5$, but this curvature is not apparent in every subject (Fig. 1), and is not as pronounced as the curvature evident in human walking. Indeed, we previously stated, based on the variability of the relationship and the lack of apparent curvature in the quadrupedal VO_2 :speed relationship, that such curvature was not present in chimpanzee locomotor cost (Pontzer et al., 2009), and we note here that a linear trendline fits the data with a high degree of determination ($r^2 = 0.96$ for combined bipedal data). Nonetheless, a polynomial equation does fit the combined bipedal data for walking speeds quite well ($\text{VO}_2 = 0.37\text{speed}^2 - 0.54\text{speed} + 0.44$, $r^2 > 0.99$, Fig. 1), providing a minimum COT for bipedal walking of $0.19\text{ mlO}_2\text{ kg}^{-1}\text{ m}^{-1}$ at 1.03 m s^{-1} , or Froude = 0.23. A curved VO_2 :speed relationship is expected for pendular-mechanics walking gaits (Pontzer, 2005), and thus might indicate at least some exchange of potential and kinetic energy during the stride cycle for at least some chimpanzees. Additionally, this minimum COT occurs at a Froude number quite close to the preferred speed of movement for humans and other mammals ($\text{Fr} = 0.25$; Minetti, 2001).

Interspecific comparison Chimpanzee locomotor cost is greater than expected for a mammal of their size, based on allometric relationships reported previously (Taylor et al., 1982; Rubenson et al., 2007; Fig. 3). Mean postural cost ($\text{mlO}_2\text{ kg}^{-1}\text{ s}^{-1}$) calculated for the chimpanzees in our sample (mean: 0.094; Table 1) was similar to that predicted allometrically (0.088, eq. (7) in Taylor et al., 1982). However, chimpanzee COT was greater than expected allometrically. Of the 63 mammals included in the Taylor et al. (1982) dataset, only three (*Panthera leo*, *Dipodomys merriami*, and *Galago senegalensis*) have a positive residual from the All Mammals trendline equal or greater than that of the chimpanzees in this study. Chimpanzee COT is similar to that of

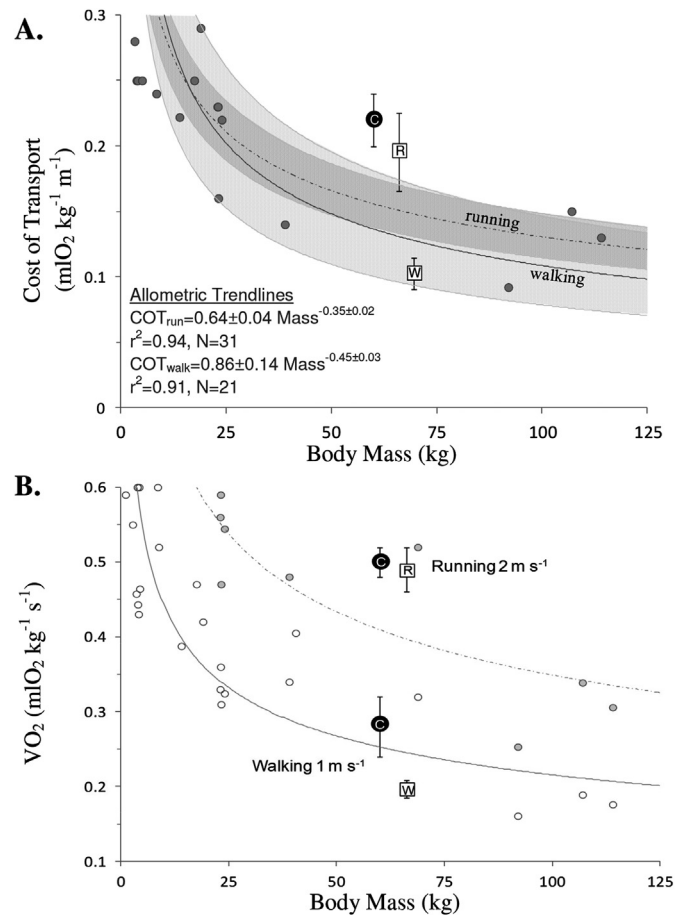


Figure 3. Locomotor cost versus body mass for chimpanzees, humans, and other mammals. A. Mean (\pm st.dev.) cost of transport, COT, for chimpanzees (C, bipedal and quadrupedal combined) compared with running (R) and walking (W) COT for humans (from Rubenson et al., 2007) and other mammals (gray circles; from Taylor et al., 1982). Error bars for chimpanzees denote std. error of COT regression (Fig. 1), error bars for humans denote std. dev. of populations means. Dashed line and dark gray region denotes trendline (\pm std. error) for running COT. Solid line and light gray region denotes trendline (\pm std. error) for walking COT for terrestrial mammals (Rubenson et al., 2007). B. Mass-specific metabolic rate, VO_2 , calculated for traveling at 1.0 m s^{-1} and 2.0 m s^{-1} . Includes the postural cost of locomotion. Lines indicate trendlines for comparative data (Taylor et al., 1982); solid: 1.0 m s^{-1} , dashed: 2.0 m s^{-1} .

human running (0.20 , standard deviation ± 0.03) but approximately twice that of human walking (0.10 ± 0.01) reported in a recent meta-analysis of human locomotor COT (Rubenson et al., 2007).

The pattern of results is similar when VO_2 , which includes postural cost, is calculated for walking at 1.0 m s^{-1} and running at 2.0 m s^{-1} (Fig. 3).

Kinematics

Spatiotemporal results Limb phases for symmetrical gaits for most subjects centered around ~ 0.50 (mean 0.50 ± 0.06); symmetrical gaits were classified as either DSDC (12/27 bouts) or LSDC (15/27). The sole exception to this pattern was Lucy, who used LSLC gaits (mean limb phase 0.19 ± 0.03) for all but her slowest trial (limb phase 0.38). Limb phase values were generally lower (0.32 ± 0.01) for asymmetrical, galloping gaits (see below). A general linear model including Froude number, gait (symmetrical or asymmetrical) and subject found that limb phase increased with Froude number ($p = 0.036$) and differed between subjects and gaits

($p < 0.0001$). For the four subjects using DC gaits, the least-squares regression for limb phase against duty factor indicates that most chimpanzees transitioned from LSDC to DSDC gaits at $Fr \sim 0.5$. Limb phases are plotted against duty factor and Froude number in Fig. 4.

Spatiotemporal characteristics were broadly similar for bipedal and quadrupedal locomotion (Fig. 5; Table 2). Due to similarities in hind limb length among chimpanzees in this sample, Froude number was highly correlated with absolute speed in this dataset as $Fr = 0.22\text{speed}^{1.97}$ ($r^2 = 0.99$), where speed is in m s^{-1} . Therefore, spatiotemporal data are plotted against speed, as limb-length correction does not provide much additional explanatory power in our dataset. Chimpanzees tended to use higher stride

frequencies and shorter strides during bipedal locomotion (Fig. 5). Duty factor (stance-phase duration/stride period) tended to be greater during bipedal trials. Nonetheless, because stride periods were somewhat shorter bipedally, contact times (i.e., the duration of stance phase) were quite similar for bipedal and quadrupedal locomotion. When the inverse of contact time, t_c^{-1} (a predictor of locomotor cost; Kram and Taylor, 1990) was plotted against speed, slightly lower values are evident for quadrupedal trials ($F(64) = 6.34$, $p = 0.01$, ANCOVA), but this difference was small. At 1.5 m s^{-1} , the average difference in t_c^{-1} was less than 7%, and across speeds t_c^{-1} values overlapped considerably (Fig. 5).

Chimpanzees increased speed by increasing both stride frequency and stride length (Fig. 5). Stride lengths increased with speed in both bipedal (stride length = $0.34\text{speed} + 0.59$, $r^2 = 0.86$, $p < 0.001$) and quadrupedal (stride length = $0.32\text{speed} + 0.85$, $r^2 = 0.59$, $p < 0.001$) trials, and were longer when walking quadrupedally ($F(67) = 28.64$, $p < 0.001$). Hind limb excursion angles increased with speed in both locomotor modes. This increase was driven primarily by the strong relationship between retraction angle and speed (bipedal: retraction = $20.38\ln(\text{speed}) + 6.29$, $r^2 = 0.73$, $p < 0.001$; quad: retraction = $17.59\ln(\text{speed}) + 19.20$, $r^2 = 0.57$, $p < 0.001$). Hind limb protraction was more variable and essentially independent of speed (bipedal: $r^2 = 0.02$ with $\ln(\text{speed})$, mean = $28.5 \pm 2.7^\circ$; quadrupedal: $r^2 = 0.12$, mean = $22.7 \pm 3.9^\circ$). Forelimb excursion angles also increased with speed in quadrupedal walking as well (forelimb excursion = $14.62\ln(\text{speed}) + 37.23$, $r^2 = 0.40$, $p < 0.01$), but this increase was driven more strongly by the change in protraction (protraction = $7.93\ln(\text{speed}) + 12.78$, $r^2 = 0.60$, $p < 0.01$) than retraction (retraction = $6.32\ln(\text{speed}) + 24.57$, $r^2 = 0.18$, $p = 0.01$).

While chimpanzees tended to switch from LS to DS gaits at $Fr \sim 0.5$ (Fig. 4), they showed no discrete kinematic transition between walking and moderate ($Fr > 0.5$) running speeds. However, most (two out of three) did transition to asymmetrical galloping gaits at faster ($Fr > 1.0$) running speeds. We were not able to determine the mechanical transition from pendular walking to mass-spring running, as we did not collect force-plate measurements at sufficiently high speeds. However, most terrestrial species transition from pendular walking gaits to mass-spring running or trotting gaits at a Froude number of ~ 0.5 or lower (Griffin et al., 2004; Usherwood, 2005; Vereecke et al., 2006a,b; Rubenson et al., 2007). For example, gibbons display mass-spring mechanics at Froude numbers above 0.5 (Vereecke et al., 2006a). For chimpanzees in our sample, spatiotemporal variables did not show any abrupt change even as speeds approached $Fr = 1.0$, the theoretical maximum for pendular walking gaits (Usherwood, 2005). Hind limb duty factors decreased with speed but remained above 50% even when Froude number exceeded 0.5 (equivalent to $1.4\text{--}1.6 \text{ m s}^{-1}$), indicating that chimpanzees in our sample transitioned fluidly into quadrupedal ambling and bipedal running walks. This kinematic pattern is consistent with the ambling and running walks observed in other primates (Schmitt et al., 2006; Demes and O'Neill, 2013).

Only at speeds in excess of $Fr > 1.0$ did gait cycles consistently include an aerial phase (Fig. 5); note that $Fr = 1.0$ is equivalent to $2.1\text{--}2.3 \text{ m s}^{-1}$ for the subjects (Jack, Louie, and Sally) that were able to achieve these higher speeds. At these faster running speeds (2.24 , 2.68 , and 3.58 m s^{-1}), Jack and Louie adopted an asymmetrical galloping gait, while Sally maintained a symmetrical diagonal sequence, diagonal couplet gait. At 1.79 m s^{-1} , Jack and Louie began the trial with a slow gallop as the treadmill belt came up to speed, but settled into a symmetrical diagonal sequence, diagonal couplet gait soon afterward. Choice of gait was self-directed; no guidance was given by the trainer. This suggests the amble-gallop transition for many chimpanzees may be near $Fr = 1.0$, and could suggest that

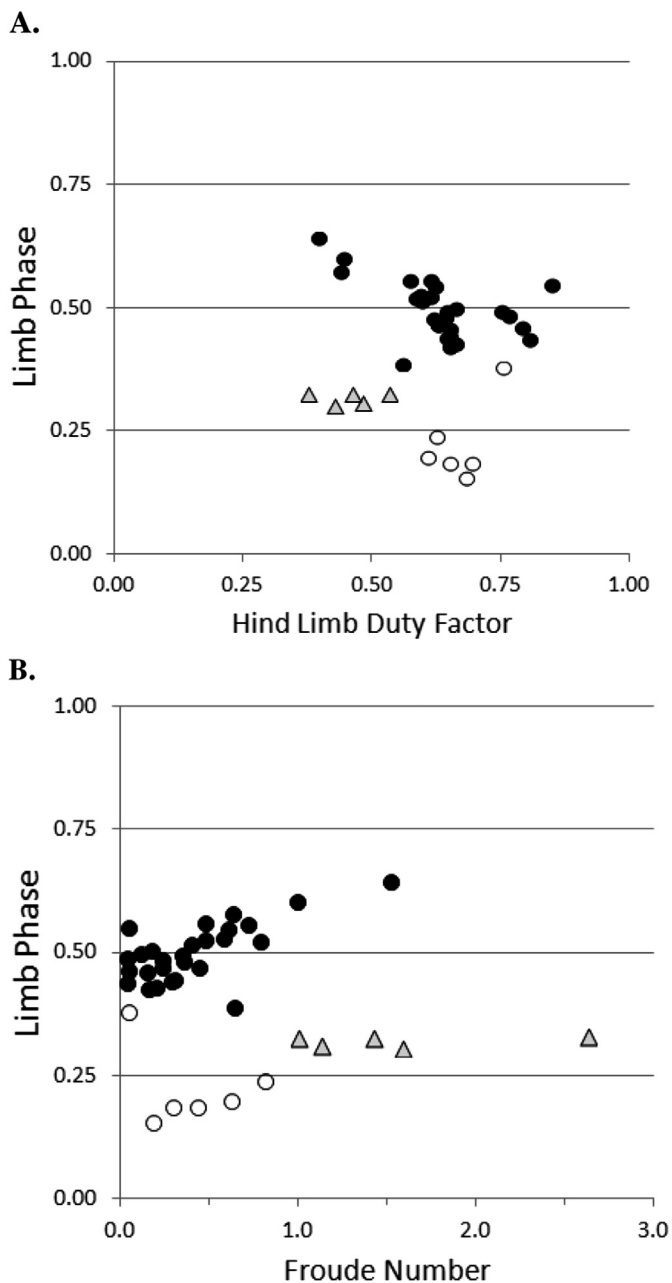


Figure 4. Limb phase for treadmill trials plotted against (A) hind limb duty factor, and (B) Froude number. Filled circles: symmetrical gaits for Jack, Louie, Lulu, and Sally. Open circles: symmetrical gaits for Lucy. Gray triangles: asymmetrical (gallop) gaits for Jack and Louie.

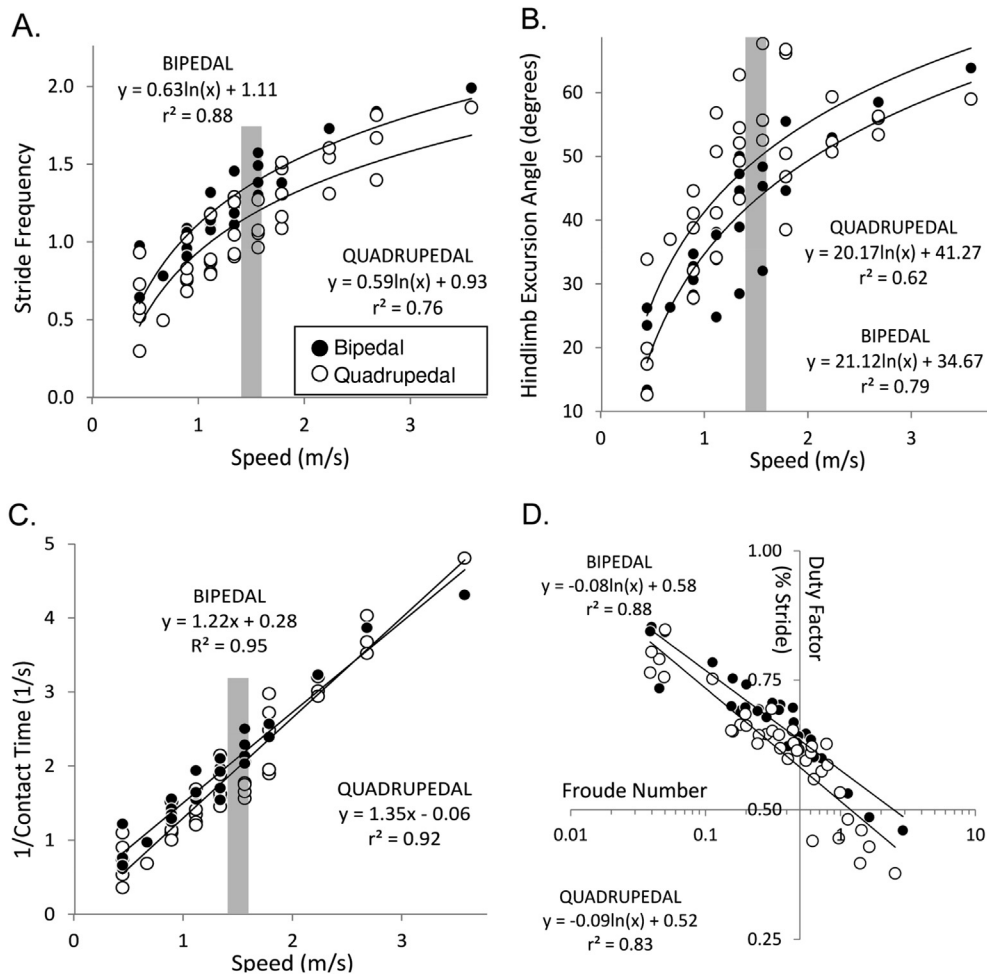


Figure 5. Spatiotemporal characteristics of quadrupedal and bipedal locomotion. Chimpanzees tended to use higher stride frequencies (A) and shorter hind limb excursions (B) when walking and running bipedally. Despite these differences, hind limb contact times were similar between gaits for a given speed. The inverse of contact time increased linearly with speed in both quadrupedal and bipedal locomotion (C), mirroring the increase in COL with speed (Fig. 1). Gray regions in A–C indicate Froude ~ 0.5 . Because contact times were similar and stride frequencies were shorter in bipedal locomotion, hind limb duty factors used bipedally tended to exceed those used quadrupedally (D). In D, the y-axis crosses at $Fr = 0.5$; chimpanzees maintained duty factors above 0.5 for some speeds exceeding $Fr = 0.5$ (see text).

ambling is constrained to speeds below $Fr \sim 1.0$. The full spatiotemporal dataset is given in the [SOM Table S1](#).

Hind limb kinematics Joint and segment angles for the torso and hind limb during treadmill trials are shown in [Figs. 6 and 7](#) and [Table 3](#), and additional figures showing results for individual chimpanzees and for additional speeds are available in [SOM Figs. S1–S7](#). As expected, the hip was more extended and the trunk held more vertically during bipedal locomotion ([Figs. 6 and 7](#)). The knee also tended to be more flexed, and the thigh held more horizontally during bipedal trials ([Figs. 6 and 7](#)). The angles of the shank and foot segments were very similar during quadrupedal and bipedal locomotion, with the ankle being slightly more dorsiflexed in quadrupedalism. As noted previously ([Sokol et al., 2007](#)), there was some between-subject variability in hind limb kinematics. This variability was generally greater during bipedal trials ([SOM Figs. S1–S7](#)).

Forelimb kinematics Forelimb joint and segment angles during treadmill trials are shown in [Fig. 8](#) for 0.89 m s^{-1} quadrupedal walking. The range of motion in the elbow and wrist are quite limited, approximately 10° over the course of a stride ([Fig. 8](#)). Most of the forelimb movement occurs at the shoulder. For four of the five chimpanzees, forelimb touch-down tended to occur later in the hind limb stride cycle with increasing speed: at 45%

($\pm 4\%$) of the hind limb cycle at 0.89 m s^{-1} , 49% ($\pm 3\%$) at 1.34 m s^{-1} , and 51% ($\pm 8\%$) at 1.79 m s^{-1} . Take-off of the forelimb (the end of forelimb stance phase) tended to occur earlier with increasing speed: at 111% ($\pm 2\%$) at 0.89 m s^{-1} , 105% ($\pm 8\%$) at 1.34 m s^{-1} , and 104% ($\pm 14\%$) at 1.79 m s^{-1} . This timing of forelimb contact is out-of-phase with the ipsilateral hind limb (see [Fig. 6](#)). These means exclude Lucy, the only chimpanzee with forelimb contact times in phase with the ipsilateral hind limb (forelimb touch-down at 18%, 22%, and 24%, take-off at 79%, 78%, and 77% of the hind limb cycle, at 0.89 , 1.34 , and 1.79 m s^{-1} , respectively). See [Fig. 6](#).

Overground versus treadmill locomotion data from force-plate trials (below) provided an opportunity to compare overground and treadmill kinematics. Force-plate trials include only three subjects (Jack, Louie, and Sally) and cover a limited range of speeds (bipedal: $0.92 \pm 0.21 \text{ m s}^{-1}$, quadrupedal: $1.20 \pm 0.19 \text{ m s}^{-1}$). Further, because shoulder position was not recorded for hind limb trials, only knee and ankle angles can be calculated. These limitations notwithstanding, comparisons with treadmill measurements indicate that chimpanzees used more flexed hind limbs during overground walking. When compared to 0.89 m s^{-1} bipedal treadmill trials, the knee was 14.1° more flexed at midstance during bipedal force-plate trials and the ankle was 12.4° more flexed.

Table 2
Spatiotemporal characteristics for bipedal and quadrupedal treadmill trials.

Speed (m s ⁻¹)	Mode	n	Froude Number (speed ² /(Lg))		Stride Frequency (strides/s)		Hind Limb Duty Factor (% stride)		Hind Limb					Forelimb						
									Contact Time (s)	Protraction (°)	Retraction (°)			Contact Time (s)	Protraction (°)	Retraction (°)				
0.45	B	4	0.04	0.01	0.69	0.19	79%	4%	1.32	0.36	25.7	1.6	−5.5	7.3						
	Q	5	0.04	0.01	0.61	0.24	82%	6%	1.60	0.75	18.8	1.8	2.2	9.3	1.71	0.66	3.8	2.9	16.2	7.8
0.89	B	5	0.18	0.02	0.98	0.09	72%	3%	0.73	0.06	29.0	3.0	1.8	1.2						
	Q	5	0.18	0.02	0.81	0.13	66%	1%	0.85	0.13	21.9	1.8	15.0	8.0	0.84	0.15	12.6	3.5	24.0	7.4
1.12	B	5	0.28	0.03	1.17	0.09	69%	1%	0.60	0.05	28.9	2.5	4.7	6.0						
	Q	5	0.28	0.03	0.91	0.16	65%	3%	0.74	0.09	21.8	3.9	21.6	9.1	0.72	0.12	14.2	3.7	28.0	8.4
1.34	B	5	0.40	0.05	1.25	0.13	68%	3%	0.55	0.07	29.7	2.6	12.2	8.4						
	Q	5	0.40	0.05	1.08	0.18	63%	2%	0.59	0.09	22.3	3.3	30.1	5.3	0.54	0.13	16.8	2.7	26.9	9.1
1.56	B	4	0.53	0.06	1.44	0.12	64%	1%	0.45	0.04	30.6	1.9	11.3	7.6						
	Q	5	0.55	0.06	1.09	0.11	61%	1%	0.57	0.06	26.7	2.4	31.1	6.4	0.51	0.08	17.1	2.2	26.6	8.1
1.79	B	2	0.68	0.06	1.44	0.08	56%	7%	0.40	0.02	28.6	2.6	21.5	10.3						
	Q	5	0.72	0.08	1.31	0.19	60%	0%	0.43	0.09	25.6	4.5	28.1	12.1	0.42	0.08	16.8	3.7	30.4	10.4
2.24	B	1	1.14	—	1.73	—	53%	—	0.31	—	26.2	—	26.7	—						
	Q ^a	3	1.03	0.09	1.49	0.16	49%	4%	0.33	0.01	24.0	4.6	30.1	7.7	0.31	0.05	21.6	5.3	28.4	2.8
2.68	B	1	1.64	—	1.84	—	49%	—	0.26	—	24.5	—	34.0	—						
	Q ^a	3	1.49	0.13	1.63	0.21	43%	3%	0.27	0.02	22.2	5.9	33.0	7.2	0.23	0.03	18.1	1.2	27.4	2.3
3.58	B	1	2.91	—	1.99	—	46%	—	0.23	—	27.2	—	36.7	—						
	Q ^a	1	2.55	—	1.86	—	38%	—	0.21	—	19.1	—	39.8	—	0.16	—	16.8	—	31.1	—

Means and standard deviations are shown. Modes B and Q denote bipedal and quadrupedal trials, respectively. Froude number calculated using effective hind limb length, L (Table 1). Duty factor calculated for the hind limb. Number of chimpanzees measured, n , is given for each speed.

^a For speeds above 1.79, Jack and Louie (but not Sally) used an asymmetrical gait (gallop). See Table S1 for additional data.

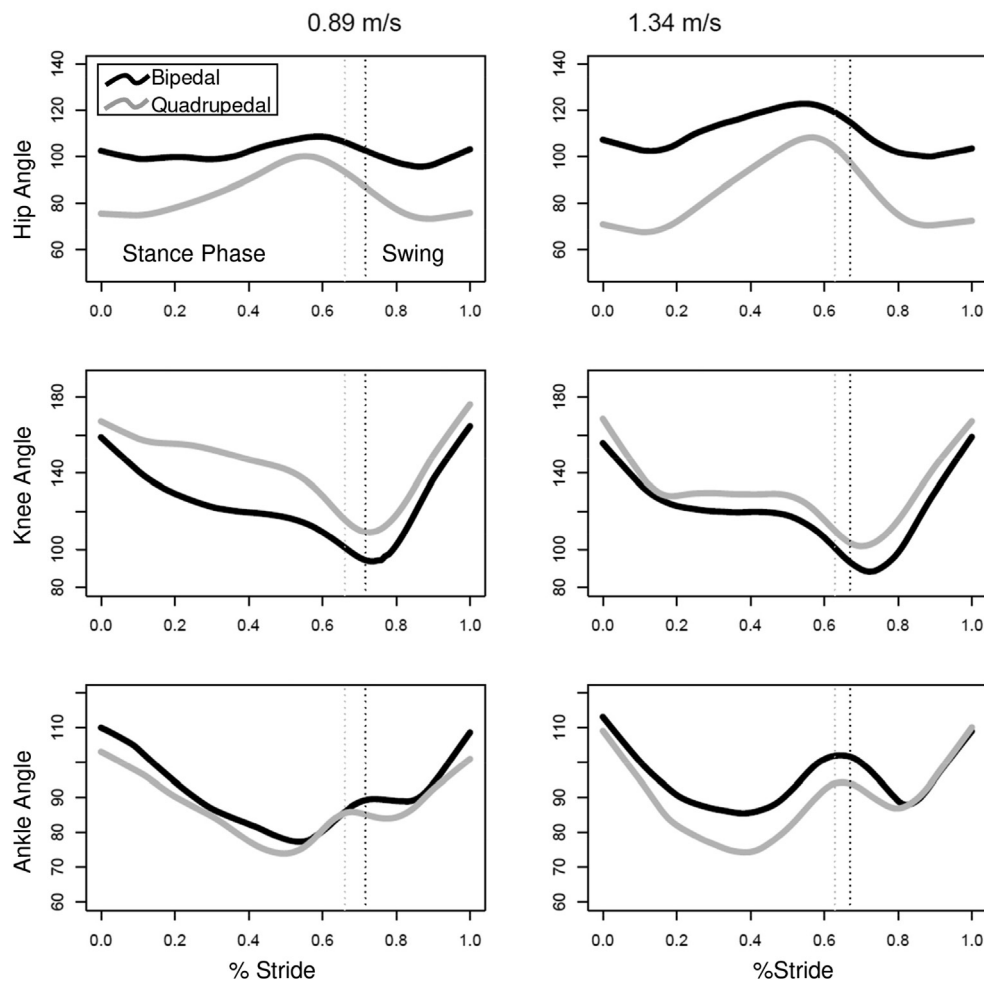


Figure 6. Average hind limb joint angles during bipedal (black) and quadrupedal (gray) locomotion at 0.89 m s⁻¹ and 1.34 m s⁻¹. Plots begin at touch-down (0% stride); dashed vertical lines indicate toe-off (black: bipedal, gray: quadrupedal).

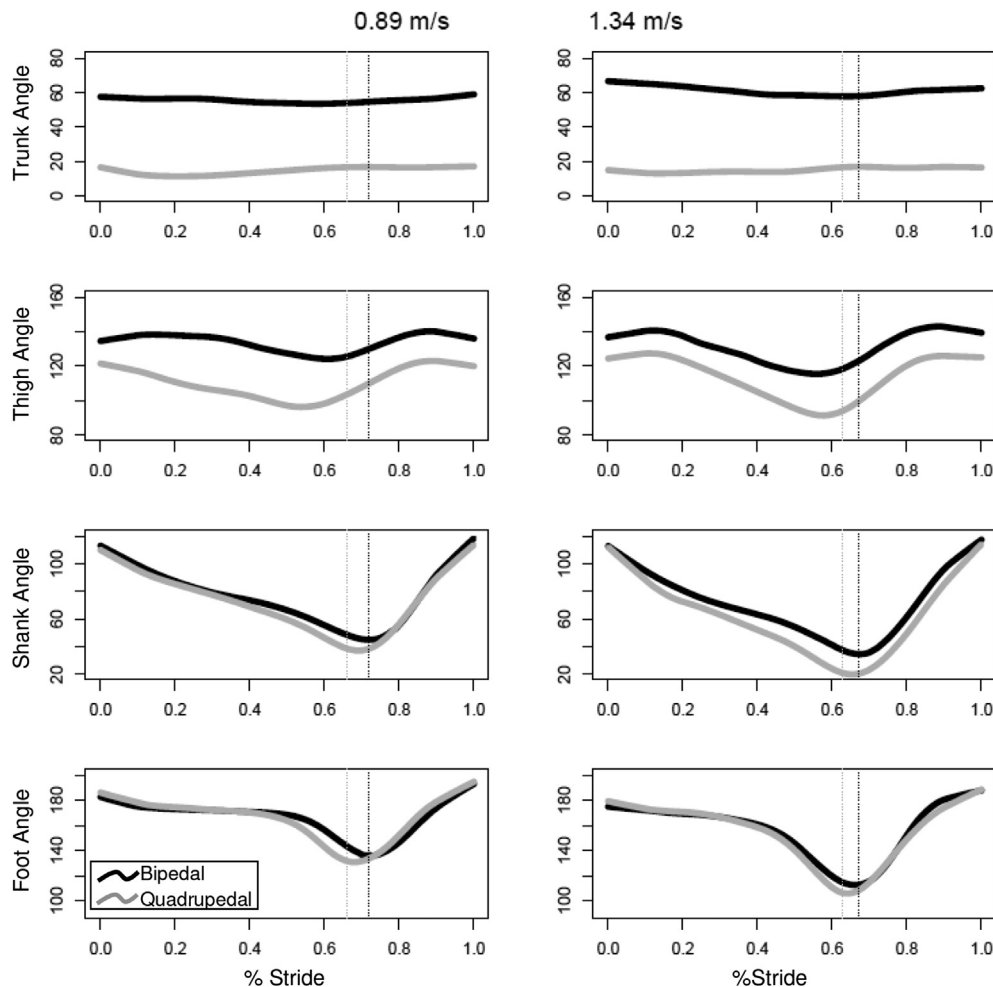


Figure 7. Segment angles during bipedal (black lines) and quadrupedal (gray lines) locomotion. Dashed vertical lines indicate toe-off.

Similarly, when compared to 1.34 m s^{-1} quadrupedal treadmill trials, the knee was 18.8° more flexed at midstance during quadrupedal force-plate trials while the ankle was 10.7° more flexed.

In order to compare spatiotemporal characteristics of overground and treadmill locomotion, power-law regressions were fit to plots of contact time versus walking speed (Fig. 9). For the range of bipedal overground speeds recorded, there was no difference in contact time between overground and treadmill trials. For the range of quadrupedal overground speeds recorded, contact times were approximately 10% shorter during overground trials compared with treadmill trials. Swing phase kinematics were not recorded for overground trials.

Kinetics

Ground reaction forces Individual and averaged GRF traces are shown in Fig. 10. All force-plate trials are from walking speeds, and many (but not all) show a two-peak vertical trace typical of human walking. Variation in the presence of one- or two-peak vertical GRF traces is largely explained by individual differences among subjects. Sally displayed two-peak vertical GRF traces in all but one of her recordings (four out of five bipedal steps, five out of five quadrupedal). Jack displayed single peaks in all of his recordings (four out of four bipedal, two out of two quadrupedal), and Louie displayed two-peaked traces in approximately half of his

recordings (two out of three bipedal, zero out of two quadrupedal). Speeds (mean \pm st.dev., m s^{-1}) were similar among subjects (bipedal: Sally 0.86 ± 0.13 , Louie 1.22 ± 0.39 , Jack 0.99 ± 0.04 ; quadrupedal: Sally 1.14 ± 0.20 , Louie 1.13 ± 0.07 , Jack 1.35 ± 0.14), and thus differences in GRF traces among subjects do not appear to be due to variation in speed. Jack and Louie displayed foot-strike transients in all bipedal recordings, but Sally did not. Foot-strike transients were rare, and small when present, in quadrupedal trials. As with the number of vertical GRF peaks, the presence of a foot-strike transient appears to be a function of individual bipedal mechanics rather than speed. Exemplar GRF traces are shown in SOM Fig. S7.

Even in GRF traces with two peaks, the amplitude of these peaks is small (i.e., the vertical GRF trace is relatively flat) relative to that seen in humans. This pattern is consistent with vertical GRF traces reported in previous studies of chimpanzee kinetics (Kimura, 1991; Kimura and Yaguramaki, 2009), and suggests some minimal transfer of kinetic and potential energy through the stride cycle in both bipedal and quadrupedal walking. Vertical force traces were greater earlier in stance during bipedal trials. In some bipedal trials a foot-strike transient is also evident, something not seen in quadrupedal trials. Braking and propulsive (AP) impulses were of similar magnitude in bipedal trials, but the propulsive impulse was relatively greater in quadrupedal trials. This difference reflects the hind limb's net propulsive role in quadrupedal walking; the forelimb provides a net braking impulse. Mediolateral (ML) forces were

Table 3
Hind limb segment and joint angles at three different treadmill speeds.

Speed:		0.89 m s ⁻¹				1.34 m s ⁻¹				1.79 m s ⁻¹			
Mode:		B		Q		B		Q		B (n = 2)		Q	
Trunk	max	66.5		38.9		75.5		31.8		72.6		36.2	
	min	40.5		1.2		44.3		−3.2		15.0		−2.1	
	TD	56.0	8.9	18.2	7.9	63.3	9.3	15.3	5.8	75.6	30.9	20.1	8.0
	MS	55.1	8.0	12.8	7.6	61.6	3.8	14.5	8.2	66.0	24.9	15.1	7.7
	TO	54.9	6.4	17.3	5.3	57.5	5.2	16.8	8.2	63.4	27.3	14.2	6.4
Thigh	max	156.5		143.3		155.4		143.8		152.9		146.0	
	min	108.5		74.6		93.5		65.4		83.8		61.6	
	TD	135.3	5.6	122.7	7.3	137.0	4.7	124.3	6.0	132.0	4.8	129.5	5.5
	MS	135.8	6.8	107.7	8.4	127.8	12.6	111.4	14.1	130.9	8.5	118.2	12.3
	TO	129.5	10.9	100.7	9.2	123.3	12.5	92.4	11.9	110.7	17.2	94.3	13.1
Shank	max	117.8		118.5		119.4		121.2		121.9		124.0	
	min	34.5		27.9		20.4		5.3		12.5		6.6	
	TD	111.4	4.0	109.8	2.6	107.6	12.6	108.6	8.5	114.4	1.2	110.7	7.8
	MS	74.8	3.8	75.3	4.9	66.8	7.3	62.5	10.1	66.4	9.1	59.5	6.2
	TO	41.6	4.1	36.8	4.5	39.6	18.2	18.2	6.1	19.1	3.2	23.2	13.2
Foot	max	199.7		202.9		202.9		204.0		198.0		198.0	
	min	115.4		106.4		85.5		91.1		84.8		76.1	
	TD	186.0	4.7	192.8	5.3	177.1	8.7	183.0	9.1	175.7	1.9	178.8	8.9
	MS	171.1	3.6	172.2	3.8	161.9	14.4	166.0	5.4	160.5	4.0	156.1	8.3
	TO	130.0	7.1	130.5	12.8	118.2	24.2	100.1	5.5	95.5	6.5	97.1	18.0
Hip	max	133.0		118.1		149.7		123.1		162.3		122.9	
	min	64.4		58.7		83.6		53.5		54.1		52.0	
	TD	100.7	13.0	75.5	2.5	106.3	10.9	71.0	4.8	125.8	75.5	71.3	4.3
	MS	98.2	14.3	84.3	6.7	114.4	14.1	83.1	8.6	124.8	63.3	76.8	7.6
	TO	102.6	17.3	94.9	7.0	114.9	15.8	104.4	8.4	148.7	82.9	99.9	9.8
Knee	max	167.7		181.9		172.9		187.9		176.8		180.6	
	min	76.0		92.2		73.1		76.8		64.2		73.1	
	TD	156.6	3.5	166.7	8.4	155.2	6.9	165.7	12.6	162.3	3.9	161.2	8.1
	MS	119.0	5.9	147.6	9.8	119.1	6.4	132.5	24.9	115.5	9.5	121.3	17.1
	TO	92.1	12.2	116.1	9.0	96.3	14.6	109.1	14.7	88.5	17.3	108.9	21.4
Ankle	max	122.4		126.3		138.5		123.0		122.6		128.4	
	min	67.2		59.1		60.4		64.1		70.0		65.7	
	TD	105.2	5.4	97.7	3.6	110.5	13.2	102.8	6.6	118.6	3.0	110.9	5.7
	MS	84.1	5.9	83.2	7.0	84.9	12.0	76.2	4.8	85.8	11.6	83.5	10.0
	TO	92.9	6.8	86.2	10.1	101.3	16.8	96.2	3.7	103.7	5.2	105.5	10.1

Data are means for five chimpanzees except for 1.79 m s⁻¹ bipedal trials (n = 2). For the 1.79 m s⁻¹ trials, individual trunk and hip angles are shown for each chimpanzee (Jack, Louie) rather than a mean due to the large difference in angles. For all other touch-down (TD), midstance (MS) and take-off (TO) angles, means and *standard deviations* are shown.

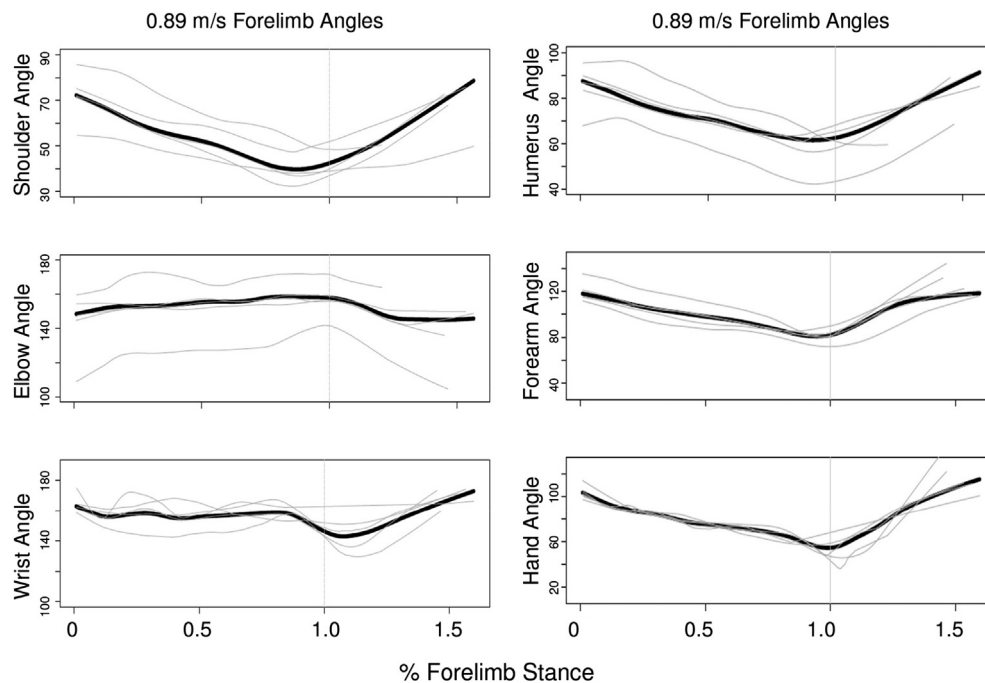


Figure 8. Forelimb joint and segment angles at 0.89 m s⁻¹ plotted against forelimb stance phase. Black line is the average of the individual traces (gray) using a lowess regression. Gray lines indicate lowess regressions for individuals. Vertical line indicates take-off of the hand.

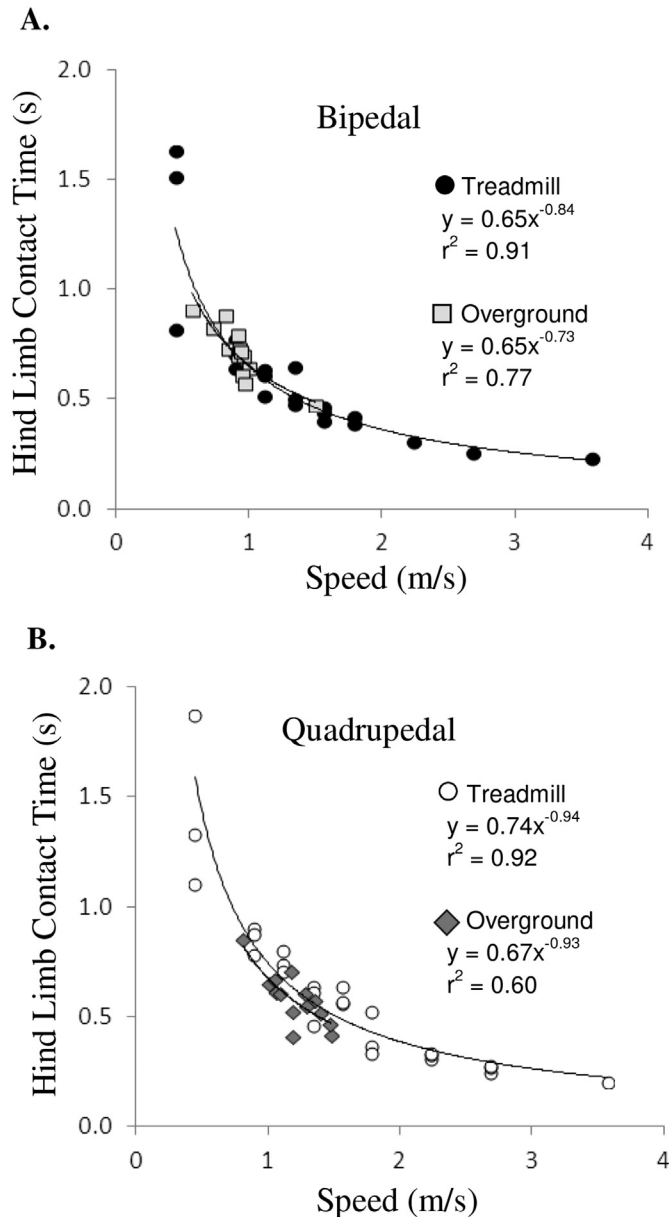


Figure 9. Hind limb contact times plotted against speed for overground and treadmill trials. A shows bipedal trials, B shows quadrupedal.

small (~10% of body weight in bipedal trials, and ~5% in quadrupedal trials) but markedly greater during bipedal walking.

Discussion

Previous chimpanzee studies

Kinematic, kinetic, and metabolic measurements of chimpanzees in this sample are consistent with previous work on chimpanzee locomotion. Chimpanzees in this study used a compliant 'bent-knee, bent-hip' gait during both bipedal and quadrupedal locomotion. The double-peaked vertical GRF traces are consistent with a small degree of transfer between potential and kinetic energy at low speeds, similar to that reported previously for chimpanzees (Kimura, 1991; Kimura and Yaguramaki, 2009) but much less than that of human walking. While we did not measure mediolateral movement (i.e., kinematics in the coronal plane), our

observations of chimpanzee walking, and the ML GRF force recordings (Fig. 10), indicate that the chimpanzees' center of mass moved from side-to-side with each step during bipedal walking, as reported in seminal work by Elftman (1944) and Jenkins (1972).

Our data also confirm the relatively high cost of locomotion for chimpanzees. For chimpanzees in this study, walking and running required 41% more energy than expected for a mammal of similar body mass (Fig. 3). This difference is consistent with that reported previously (Taylor et al., 1982) for juvenile chimpanzees (36%). Chimpanzee locomotor cost is similar to that of human running, but considerably more costly than human walking (Fig. 3). Our previous work has shown that this variation in cost among gaits and between species is well explained by differences in locomotor mechanics (Sockol et al., 2007; Pontzer et al., 2009). Kinematic differences also explain variation in cost within our chimpanzee sample. As described in our initial analysis of this sample (Sockol et al., 2007), the greater quadrupedal cost evident in Lucy (previously identified as C4) is related to her use of more crouched postures and relatively short contact times during quadrupedal trials.

Chimpanzees in this study differ from those in previous experimental studies in their training history, age, and body mass. It is unclear what effect, if any, the subjects' training for entertainment work as juveniles and adolescents had on their gait. It is possible that this training made them more comfortable or accustomed to walking bipedally, but it should be noted that chimpanzees at this facility spent the large majority of their time, even as juveniles, socially housed in large outdoor enclosures, without a trainer present. Even on data-collection days, the trainer limited the participation time of any individual chimpanzee to less than 2 h. Most of the chimpanzees in this sample are also considerably older than those in previous experimental locomotion studies, which tend to focus on juveniles. In this respect, our sample is more representative of adult chimpanzees than are previous studies. Average body mass for this sample (60.0 ± 18.5 kg) is considerably heavier than those of wild chimpanzees but is similar to that of healthy, captive, adult chimpanzees elsewhere (61.8 ± 18.7 kg, $n = 4$, Lincoln Park Zoo, Chicago; 53.9 ± 10.2 kg, $n = 6$, Tchimpounga Sanctuary, Congo; Pontzer, Unpublished data). The consistency in kinematic, spatiotemporal, and metabolic variables across the range of body mass in our sample suggests that standard approaches for accounting for size differences (e.g., Froude number, mass-specific COT) are effective here as well, and that body mass per se is not biasing the pattern of results. Still, the potential effect of body mass should be considered when comparing or extrapolating results from this study to other populations.

Quadrupedal versus bipedal locomotion

Bipedal and quadrupedal locomotion require similar metabolic energy expenditure in chimpanzees, consistent with our previous analyses of walking costs for these subjects (Sockol et al., 2007) and early work on locomotor cost in chimpanzees and *Cebus* monkeys (Taylor and Rowntree, 1973). That the cost of locomotion is unrelated to the number of limbs used is consistent with comparative studies showing that arthropods (six or eight limbs), mammals and reptiles (four limbs) and birds (two legs) all have similar walking and running costs for their body mass and limb length (Full and Tu, 1991; Pontzer, 2007). To our knowledge, the only animals for which bipedal locomotion has been shown to be more costly than quadrupedalism are Japanese macaques (Nakatsukasa et al., 2004, 2006). While the mechanics of bipedal and quadrupedal walking in these macaques have not been reported, we hypothesize that their greater bipedal costs are related to their gait mechanics rather than the number of limbs employed.

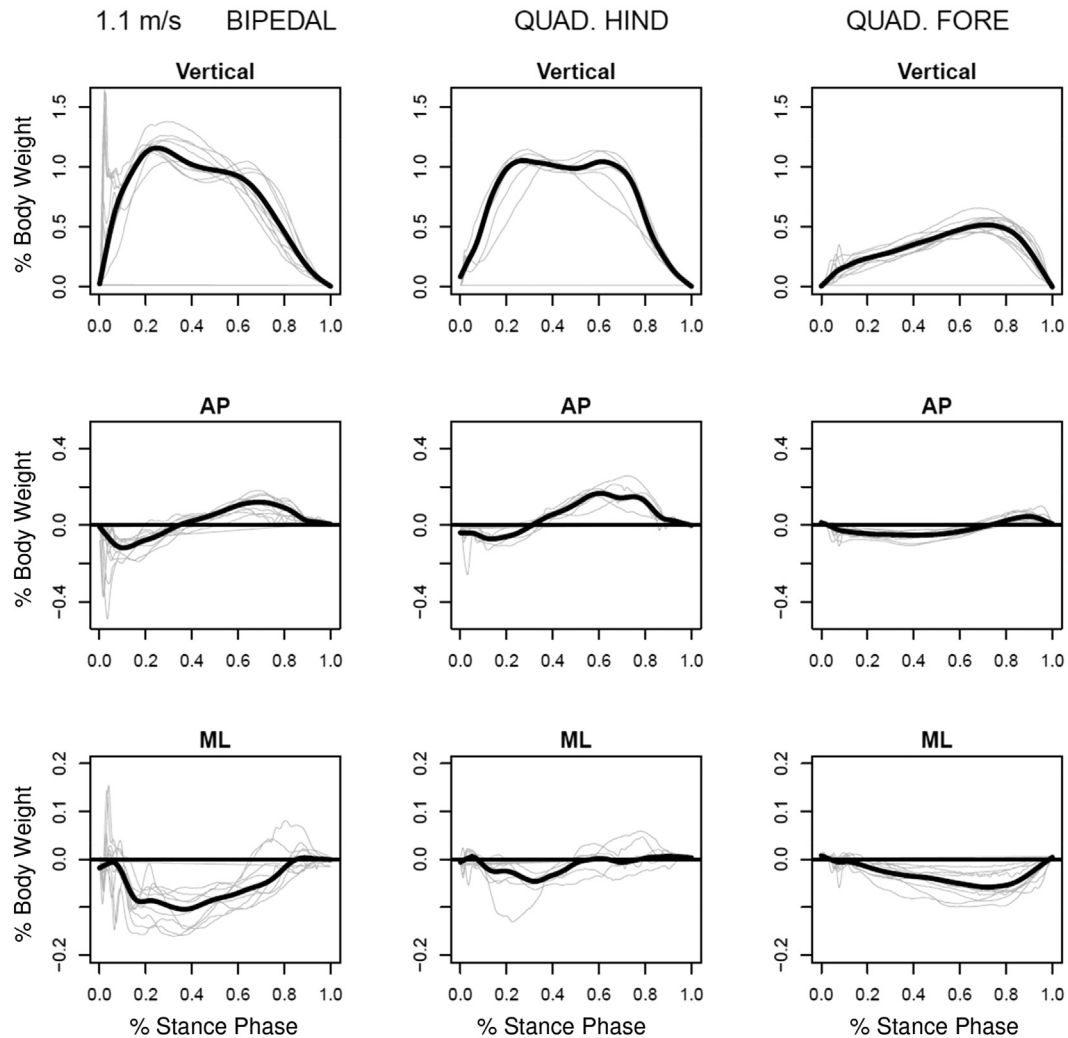


Figure 10. Ground reaction force, GRF, traces for bipedal and quadrupedal force-plate trials. Black line is the average of the individual traces (gray) using a lowest regression. For anterior–posterior (AP) traces, negative forces indicate braking (i.e., deceleration). For mediolateral (ML) traces, negative forces indicate medially directed GRF (i.e., limb adduction).

The similarity in quadrupedal and bipedal costs in our chimpanzee sample reflects the broad similarities in spatiotemporal and kinematic variables between locomotor modes. Shorter contact times and more crouched postures have been shown to increase locomotor cost by increasing the muscle force required to support body weight (Kram and Taylor, 1990; Pontzer et al., 2009). Chimpanzees not only tended to use shorter, faster strides when bipedal, but also maintained longer duty factors. The combined result was that contact time was similar for bipedal and quadrupedal gaits (Fig. 5). The hip and knee tended to be more flexed in bipedal trials (Figs. 6 and 7), which is consistent with the marginally greater bipedal costs for Louie, Sally, and Jack (Fig. 1). However, these angular differences were not large, and were sufficiently variable both among speeds (Figs. 6 and 7) and between subjects (SOM Figs. S1–S7) that no consistent difference in cost was discernible for the group (Fig. 1).

One consistent difference between locomotor modes was the greater ML GRF impulse evident in bipedal walking (Fig. 10). The increased ML ground force seen in bipedal trials reflects the biomechanical challenge of maintaining mediolateral balance with only one limb in support. Lacking the lateral placement of the lesser gluteals present in humans, chimpanzees must exert these ML ground forces by using the trunk musculature, resulting in large

side-to-side excursions of the upper body over the stance limb with each step (Jenkins, 1972; Shapiro and Jungers, 1994). While this biomechanical strategy is undoubtedly less efficient than that of humans, the similarity in locomotor cost between bipedal and quadrupedal walking indicates that its effect on the total cost of locomotion must be quite small.

Comparisons with bonobos

Quadrupedal and bipedal kinematics were broadly similar between the chimpanzees and bonobos, reflecting the similarity in their musculoskeletal anatomy. Nonetheless, there were some differences that warrant discussion. Chimpanzees in this study showed significant differences in bipedal and quadrupedal stride frequency (and length), but the differences among bonobos described by Aerts et al. and D'Août et al. tend to be larger (Fig. 11). Conversely, bipedal and quadrupedal duty factors were more similar in bonobos than among chimpanzees (Aerts et al., 2000; D'Août et al., 2002, 2004). As a result, there is a larger difference between bipedal and quadrupedal contact times for bonobos (Fig. 11). The difference in contact time holds implications for locomotor cost, because the inverse of contact time, t_c^{-1} , affects the muscle force needed to support body weight and is strongly

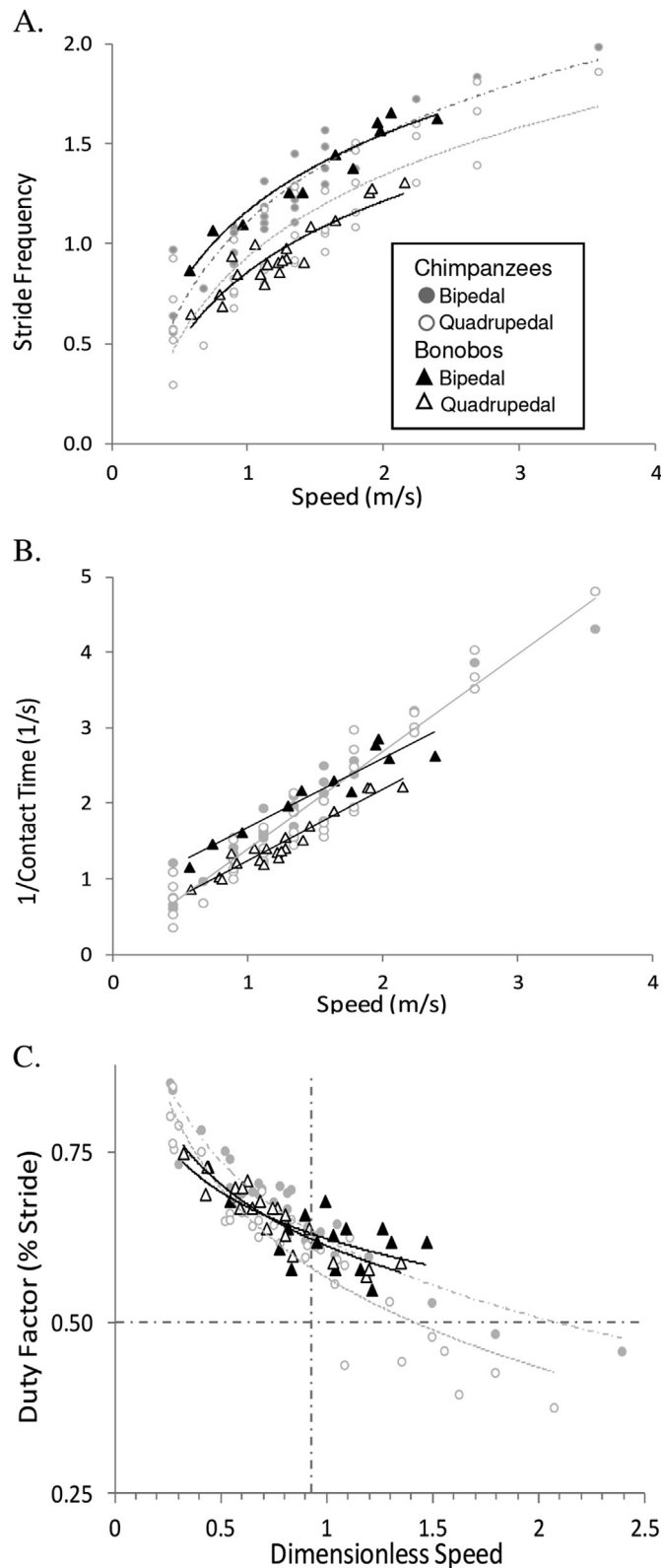


Figure 11. Comparison of spatiotemporal variables between bonobos and chimpanzees. Bonobo data calculated from data in Aerts et al. (2000). Gray circles: chimpanzees (filled: bipedal, open: quadrupedal), black triangles: bonobos (filled: bipedal, open: quadrupedal). A and B exclude the two year old juvenile in the Aerts et al. (2000) dataset (subject I). Vertical dashed line in C indicates a dimensionless velocity equal to a Froude number of 0.5.

correlated with locomotor cost (Kram and Taylor, 1990; Pontzer et al., 2009). While the difference between bipedal and quadrupedal t_c^{-1} was only 7% among chimpanzees, in bonobos, t_c^{-1} was approximately 30% greater for bipedal locomotion for the midrange of observed speeds (Fig. 11), suggesting that bipedal locomotion might have been relatively costly for the bonobos in that sample (Aerts et al., 2000; D'Août et al., 2002, 2004).

Hind limb joint angles also suggest differences in locomotor economy. Both species used similar hip excursions, but bonobos used a more flexed knee and dorsiflexed ankle than chimpanzees (Fig. 12). These differences were considerable: bonobo knee flexion was $\sim 20^\circ$ more acute, and their ankle was $\sim 20\text{--}30^\circ$ more dorsiflexed, outside the range seen in the chimpanzee sample at a comparable speed (SOM Fig. S2). More crouched postures generally

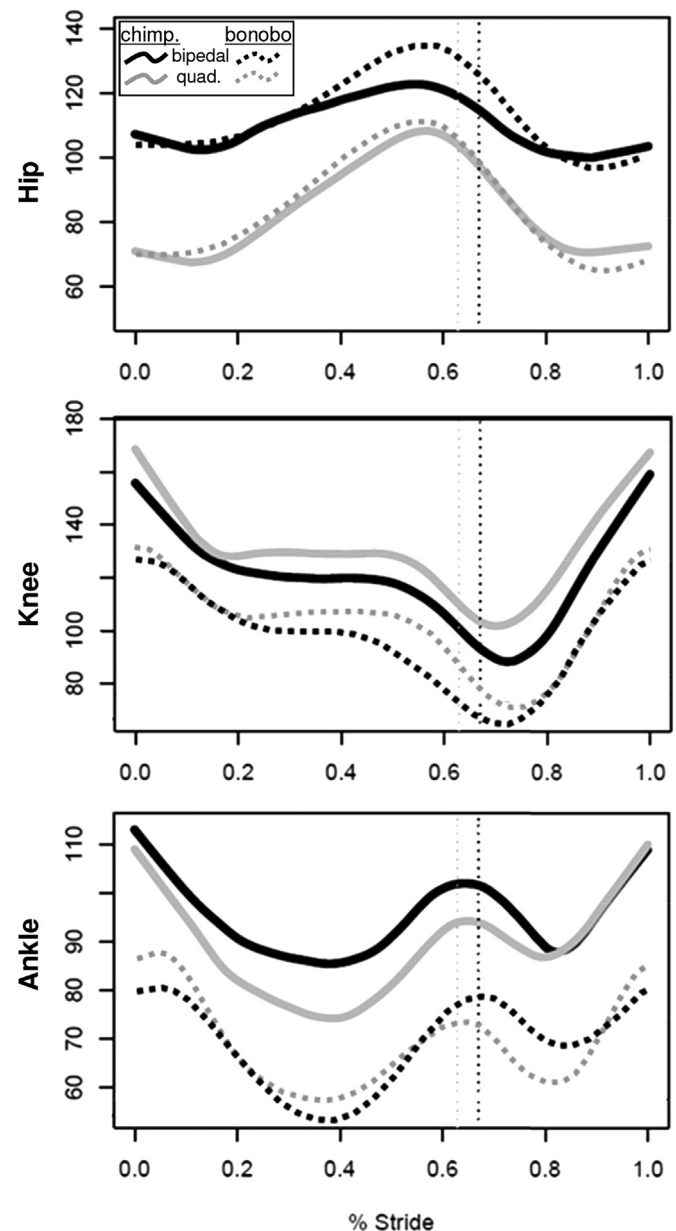


Figure 12. Hip, knee, and ankle angles during bipedal (black) and quadrupedal (gray) walking at 1.3 m s^{-1} in chimpanzees (solid lines) and bonobos (dashed lines) over the course of a stride cycle. Vertical dashed lines indicate toe-off for chimpanzees. Toe-off occurred at $\sim 65\%$ in the bonobo sample. Bonobo angles redrawn from D'Août et al. (2004).

diminish the effective mechanical advantage of the limb in supporting body weight (Biewener, 1989), which in turn tends to increase locomotor cost (Pontzer et al., 2009).

Differences in hind limb angles may reflect a larger difference in gait mechanics. Vertical GRF traces recorded in our chimpanzee sample (Jack, Louie, and Sally) were often double-peaked (Fig. 10), possibly indicating some exchange of potential and kinetic energy each step. There is also some evidence of a curved VO_2 :speed relationship for bipedal (but not quadrupedal) walking speeds (Fig. 1), which is expected for pendular gaits (Pontzer, 2005). In contrast, GRF recordings reported for bonobos (D'Août et al., 2004) are single-peaked, suggesting kinetic and potential energy were in phase, unlike pendular gaits.

These kinetic and kinematic differences might reflect differences in study design or subject history. The chimpanzees in this study were engaged in entertainment during their juvenile years, and likely engaged more frequently in bipedal walking during that period of development. Also, our measurements were collected during treadmill (kinematics) walking and running, or while walking over a novel trackway (kinetics), whereas the bonobos were measured during ad libitum overground locomotion in their normal enclosure. Our kinematic comparisons of force-plate and treadmill trials suggest that at least some of the difference in hind limb flexion between chimpanzees and bonobos may be due to differences in treadmill versus overground walking.

Comparisons with other non-human primates

Chimpanzees in this sample often used Lateral Sequence (LS) gaits, particularly at speeds below $\text{Fr} = 0.5$ (Fig. 4). Lucy used LS gaits exclusively. While the use of LS gaits has been documented previously for some primates (e.g., Cartmill et al., 2002; Raichlen, 2005a; Wallace and Demes, 2008; Young, 2012), their use is relatively rare among primates, and limb phases among chimpanzees here are in the low end of the primate range (see Cartmill et al., 2002). The preference for LS gaits and low (~ 0.50) limb phases may be partly a function of study design: Wallace and Demes (2008) reported that capuchin monkeys use LS gaits more frequently when walking on flat ground, similar to the chimpanzees here, than they do when walking on a pole. Whether the limb phases used by chimpanzees reflect an evolutionarily adaptive response to their mixed locomotor ecology as argued for other primates (e.g., Cartmill et al., 2002) or are emergent properties of their anatomy and limb proportions (e.g., Shapiro and Raichlen, 2005; Raichlen and Shapiro, 2007; Raichlen et al., 2009; Young, 2012) will require further study, ideally of arboreal and terrestrial locomotion in more natural settings.

Other aspects of chimpanzee kinematics and kinetics were similar to those of other non-human primates, including capuchins, gibbons, macaques, and bonobos (see Demes, 2011). As in other primates, chimpanzees used compliant, bent-hip bent-knee gaits during both bipedal and quadrupedal walking. Moreover, the chimpanzees in this study used shorter steps (i.e., smaller hind limb excursions) and higher stride frequencies (Fig. 5; Table 2) when walking bipedally, which is typical for non-human primates (e.g., Reynolds, 1987; Schmitt, 2003; Demes, 2011). While hind limb excursions were smaller during bipedal walking, protraction angles were larger, and retraction angles smaller, when compared with quadrupedal trials at the same speed ($p < 0.005$ both comparisons, paired t -test; Table 2). Increased protraction and decreased retraction of the hind limb during bipedalism likely reflects the need to place the support foot underneath the body's center of mass in the absence of forelimb support.

Trunk inclination in the chimpanzees here (touch-down: $59.7 \pm 9.1^\circ$, midstance: $58.4 \pm 5.9^\circ$, take-off: $56.2 \pm 5.8^\circ$) was

similar to that reported for chimpanzees previously (55.7° , Kimura and Yaguramaki, 2009) and at the low end of the range reported for other primates (61.7 – 75.3° ; Demes, 2011). Knee extension during bipedal walking (midstance: $117.9 \pm 7.3^\circ$) was greater in chimpanzees here than reported for other primates (average knee angle over a stride cycle: 72.6 – 94.0° ; Demes, 2011). Greater knee extension may be related to increased trunk pitch, which will place the body's center of mass farther forward and thus require more anterior foot placement at touch-down. As Demes (2011: 154) notes, the “variation in bipedal gaits [among species]... is not easily explained by predominant locomotor mode, predominant substrate use, body size or phylogeny” of the species examined. Instead, it appears that a broad range of primate species is capable of broadly similar, compliant, bipedal locomotion. More work is needed to examine how and whether differences in anatomy among primates are reflected in their gait.

Implications for hominin evolution

The bipedal performance of non-human primates provides important context for reconstructions of early hominin bipedalism. Biomechanical models linking locomotor performance to anatomy have the potential to reveal robust form–function relationships, but only if these models are shown to be accurate and reliable across a range of species and anatomies. From this perspective, chimpanzee locomotion is important not because *Pan* is a perfect model for the earliest hominins but because it enables us to test biomechanical models of locomotor performance in a large-bodied semi-arboreal primate. To the extent that the locomotor performance of chimpanzees and other species can be shown to fit biomechanical predictions, we can confidently extrapolate these models to the anatomy and locomotor performance of early hominins and to fossil primates in general.

Our measurements of locomotor cost in chimpanzees indicate that bipedalism is no more economical (nor costly) than quadrupedalism. This is consistent with both biomechanical models and experimental studies showing that the number of limbs used for walking and running has no effect on cost (Taylor and Rowntree, 1973; Taylor et al., 1982; Full and Tu, 1991; Sockol et al., 2007; Pontzer et al., 2009). These findings indicate that bipedalism per se would have had no effect on locomotor cost in early hominins. Instead, the *mechanics* of early hominin gait would have determined its cost; crouched postures and shorter hind limbs would increase cost, while more extended postures and longer hind limbs would tend to decrease cost (see Sockol et al., 2007; Pontzer et al., 2009).

The inefficient, crouched gait of chimpanzees appears to be common among extant hominoids (e.g., D'Août et al., 2002, 2004; Vereecke et al., 2006a,b), suggesting that Miocene hominoids, including the *Pan-Homo* last common ancestor, would have had locomotor costs similar to chimpanzees. We lack sufficient fossil material to reconstruct posture or hind limb length in the earliest putative hominins, *Sahelanthropus* and *Orrorin*, with any confidence, but the relevant features are preserved for later species. The ischium of *Ardipithecus ramidus* has been reconstructed as projecting caudally, similar to that of chimpanzees (Lovejoy et al., 2009). An ape-like ischial orientation provides a substantial moment arm for the hip flexors (hamstrings) when the hip is flexed, but limits the effectiveness of the hip flexors when the hip is extended (Robinson, 1972; Foster et al., 2013), and may therefore indicate that *Ardipithecus* walked with a flexed hip and a crouched gait (but see Lovejoy and McCollum, 2010). In contrast, the derived, dorsal projection of the ischium in *Australopithecus* (Robinson, 1972; Lovejoy et al., 2009) suggests an extended-hip gait. Recent analyses have indicated that *Ardipithecus* and *Australopithecus* also

differed in hind limb length. Relative to body mass, hind limb length in *Ardipithecus* appears to have been short, similar to extant African apes, while hind limbs in *Australopithecus* were longer, similar to the genus *Homo* (Holliday, 2012; Pontzer, 2012). Together, these traits suggest that walking and running in *Ardipithecus* would have been relatively inefficient, like that of chimpanzees, with a crouched gait and short contact times contributing to greater cost. Conversely, the extended hip and longer hind limbs in *Australopithecus* suggest improved efficiency in these hominins (see Pontzer et al., 2009; Pontzer, 2012).

Kinematic measurements of chimpanzees and other non-human primates suggest early hominin bipedalism would not require major changes in anatomy; joint excursions are similar between bipedal and quadrupedal walking (Figs. 5–7). The largest changes might be expected in the torso and hip, since the most dramatic differences between bipedal and quadrupedal walking are seen in the torso and hip joint (Figs. 6 and 7). Ground reaction force traces also identify mediolateral balance as a unique challenge for bipedal walking (Fig. 10), as noted in early studies of chimpanzee walking (Elftman, 1944; Jenkins, 1972). While this mechanical challenge does not appear to affect cost (i.e., bipedalism is no more costly than quadrupedalism), it may well have led to selection for improved reliability and efficiency of anatomical mechanisms to maintain balance, namely the medial gluteal muscles. Together, these data suggest the foci of selection in early hominin bipedalism would have been the lumbar spine, pelvis, and hip joint. This is consistent with the anatomy evident in *A. ramidus*, which has a heavily modified pelvis with lateral placement of the lesser gluteals but an ape-like grasping foot (Lovejoy et al., 2009), and is also consistent with analyses showing evolutionary dis-integration of the human pelvis (Grabowski et al., 2011).

Comparison with human locomotor cost suggests that evolved changes in locomotor anatomy and gait – specifically, our longer and more extended hind limbs – have reduced walking costs in the human lineage while running costs remained largely unchanged (Fig. 3). The relative inefficiency of human running is well explained by reduced mechanical advantage of the limb during running, as the mass-spring mechanics of running require a more flexed and compliant hind limb (Biewener et al., 2004; Pontzer et al., 2009). By contrast, humans use an extended, stiff hind limb while walking, which is critical for the efficient exchange of potential and kinetic energy of the body's center of mass through the stride cycle. The double-peaked vertical GRF and evidence for a curved VO_2 :speed relationship among the chimpanzees in this study suggest the potential for efficient, human-like, pendular walking mechanics may be latent in living apes.

The goal of this study was to test the relationships between locomotor anatomy, mechanics, and cost in chimpanzees (Sockol et al., 2007; Pontzer et al., 2009; Raichlen et al., 2009). Our results have provided a predictive model linking locomotor anatomy and cost for terrestrial animals (Pontzer et al., 2009), as well as a detailed examination of limb mechanics, kinematics, and cost in chimpanzees, but additional questions remain. For example, our analyses do not account for variation in foot anatomy at the species or individual level. Given the importance of foot anatomy for arboreal locomotion, its effects on locomotor cost in humans (e.g., Raichlen et al., 2011), and its complex evolutionary history in the hominin lineage (e.g., Harcourt-Smith and Aiello, 2004; DeSilva et al., 2013), more detailed analyses of form–function relationships in chimpanzees and other primates will no doubt yield important insights. Investigations of chimpanzee locomotion in more natural settings, across a broader range of ecologically relevant substrates, promise to shed additional light on the locomotor ecology and evolution of extant apes and fossil hominins.

Acknowledgments

Michael D. Sockol collected the oxygen consumption data as part of his doctoral research. We thank him for his immense effort. His work was supported by an NSF Doctoral Dissertation Improvement Grant (P.S.R. was the PI). Kinematic and kinetic data collection was led by D.A.R. and H.P. and supported by a L.S.B. Leakey Foundation grant. Daniel Lieberman and Andrew Biewener generously contributed equipment for data collection. Jeremy DeSilva and three anonymous reviewers provided helpful comments that improved this paper.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2013.10.002>.

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