

# Ground Reaction Forces and Center of Mass Mechanics of Bipedal Capuchin Monkeys: Implications for the Evolution of Human Bipedalism

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**ABSTRACT** Tufted capuchin monkeys are known to use both quadrupedalism and bipedalism in their natural environments. Although previous studies have investigated limb kinematics and metabolic costs, their ground reaction forces (GRFs) and center of mass (CoM) mechanics during two and four-legged locomotion are unknown. Here, we determine the hind limb GRFs and CoM energy, work, and power during bipedalism and quadrupedalism over a range of speeds and gaits to investigate the effect of differential limb number on locomotor performance. Our results indicate that capuchin monkeys use a “grounded run” during bipedalism ( $0.83\text{--}1.43\text{ ms}^{-1}$ ) and primarily ambling and galloping gaits during quadrupedalism ( $0.91\text{--}6.0\text{ ms}^{-1}$ ). CoM energy recoveries are quite low during bipedalism (2–17%), and in general higher during quadrupedalism (4–72%). Consistent with this, hind limb vertical

GRFs as well as CoM work, power, and collisional losses are higher in bipedalism than quadrupedalism. The positive CoM work is  $2.04 \pm 0.40\text{ Jkg}^{-1}\text{ m}^{-1}$  (bipedalism) and  $0.70 \pm 0.29\text{ Jkg}^{-1}\text{ m}^{-1}$  (quadrupedalism), which is within the range of published values for two and four-legged terrestrial animals. The results of this study confirm that facultative bipedalism in capuchins and other nonhuman primates need not be restricted to a pendulum-like walking gait, but rather can include running, albeit without an aerial phase. Based on these results and similar studies of other facultative bipeds, we suggest that important transitions in the evolution of hominin locomotor performance were the emergences of an obligate, pendulum-like walking gait and a bouncy running gait that included a whole-body aerial phase. *Am J Phys Anthropol* 150:76–86, 2013. ©2012 Wiley Periodicals, Inc.

Habitual bipedal walking and running is an uncommon mode of locomotion among vertebrates, and practicing these gaits on extended lower limbs and with an upright trunk is unique to humans. Many nonhuman primates use bipedal gaits opportunistically, but they all move on flexed limbs, in a so-called bent-hip, bent-knee (BHBK) gait (reviewed in Demes, 2011). Understanding the mechanics of this gait is of considerable interest to anthropologists, since BHBK gait was likely the earliest form of bipedalism in the hominin lineage (Stern and Susman, 1981; Stern, 2000; but see Latimer and Lovejoy, 1989; Lovejoy, 2005).

The kinematics and kinetics of human bipedalism have been extensively studied. It is widely accepted that the mechanical principles that are applied in human locomotion are pendulum-like swings in walking and spring-like bounces in running (Cavagna et al., 1976; Cavagna and Kaneko, 1977). These two principles are not unique to bipedalism or humans, but are widespread across terrestrial animals (Cavagna et al., 1977; Heglund et al., 1982a; Farley et al., 1993; Dickinson et al., 2000; Biewener, 2003, 2006). Fluctuations in the height of the center of mass (CoM) are different for pendulum- and spring-like gaits, as are the fluctuations in potential and kinetic energy: out-of-phase for the former, in-phase for the latter. These fluctuations in height can be tracked from measured ground reaction forces and have been extensively documented for human locomotion (e.g., Cavagna and Margaria, 1966; Cavagna et al., 1976; Cavagna and Kaneko, 1977; Donelan et al., 2002a), and the quadrupedal gaits of many animals (e.g., Cavagna et al., 1977; review in Biewener, 2006), including three species of primates (Cavagna et al., 1977; Ogihara et al.,

2012; O'Neill and Schmitt, 2012). Additional studies have tracked CoM mechanics in bipedal birds (Muir et al., 1996; Rubenson et al., 2004; Usherwood et al., 2008), and few CoM data on the bipedal gaits of nonhuman primates have also been reported (Vereecke et al., 2006: gibbon; Ogihara et al., 2007, 2010: Japanese macaque; Kimura, 1996; Kimura and Yaguramaki, 2009: chimpanzee).

When humans walk bipedally, the CoM vaults over an extended hind limb like an inverted pendulum. Some hind limb muscles are active only early and late during the stance phase to initiate and decelerate the passive swing and to modulate the transition into the next step (Knutson and Soderberg, 1995). Walking with flexed joints, on the other hand, requires prolonged activity of the antigravity muscles, which prevent the partially flexed joints from collapsing into full flexion during stance phase (Ishida et al., 1985). As muscle contractions consume metabolic energy, BHBK gait is, therefore, likely to be less economical than bipedalism on extended

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limbs (Crompton et al., 1998). And, indeed, it has been demonstrated that chimpanzee BHBK walking is energetically more costly than human bipedal walking on extended lower limbs (Sockol et al., 2007), and that human BHBK gait is more costly than erect bipedalism (Waters and Lundsford, 1985; Duffy et al., 1997; Carey and Crompton, 2005).

Although comparisons between erect and flexed bipedal gaits can offer insights into selective advantages of the unique form of bipedalism practiced by humans, a comparison of nonhuman primate quadrupedal and bipedal gaits can offer insights into adaptive scenarios driving the transition in the hominin lineage. Economy of transport is considered an important selection pressure on locomotor modes in many species (Alexander, 1989, 2003), and a number of studies on the adaptive value of human bipedalism have focused on the metabolic cost per distance (i.e., net cost of transport [CoT]; Rodman and McHenry, 1980; Carrier, 1984; Leonard and Robertson, 1997; Sockol et al., 2007; Pontzer et al., 2009). Few studies have been performed on the metabolic CoT of primate gaits that could inform such a comparison, and they are not conclusive. The classic study by Taylor and Rowntree (1973) on capuchin monkeys and chimpanzees found that the CoT is not different for their bipedal and quadrupedal gaits. More recently, Sockol et al. (2007) determined CoT for five chimpanzees, and, on average, confirmed the results by Taylor and Rowntree (1973), but when compared individually they found 10% higher costs for bipedal gaits in three of the five animals. The increase in walking CoT from quadrupedalism to bipedalism for Japanese macaques was found to be 30% (Nakatsukasa et al., 2004, 2006).

The relationships between CoM mechanics and metabolic costs are quite complex (e.g., Heglund et al., 1982a,b; Taylor, 1994). CoM mechanics can provide a measure of the minimal mechanical work required during the support phase of a stride, and, by extension, provide some insight into the demands placed on the muscles that rely on metabolic energy gained from aerobic oxidation. Numerous studies have indicated that the metabolic cost of transport (CoT) are set by the mechanical demands of the support phase of a stride (e.g., Farley and McMahon, 1992; Taylor, 1994; Donelan et al., 2002a,b; Griffin et al., 2003; Pontzer, 2007; Soo and Donelan, 2010), with limb swing accounting for a much smaller fraction of metabolic cost (Marsh et al., 2004; Rubenson and Marsh, 2009; Umberger, 2010). The use of a pendulum-like walking gait and a bouncing running gait appears to reduce the mechanical demands on the CoM during stance (Srinivasan and Ruina, 2006; Srinivasan, 2011), and this should also decrease CoT. However, the exact relationship between mechanics and energetics remains elusive. Note that the use of “bouncing” mechanics does not necessarily imply elastic storage and subsequent release of passive energy in tendons and connective tissue, but, as per definition by Srinivasan and Ruina (2006), includes the shortening and lengthening of “pseudo-elastic” leg springs.

CoM mechanical energy fluctuations for the bipedal gaits of nonhuman primates have been shown to be much more in-phase than for human walking, and, consequently, recovery of mechanical energy (i.e., the exchange between these two forms of mechanical energy) is lower. For gibbons, Vereecke et al. (2006) reported recovery rates of less than 25% for the majority of bipedal strides collected, but including a few slow strides that have peak recoveries of 60 to 70%, similar to those found for human

walking. Kimura (1996) and Kimura and Yaguramaki (2009) found highly variable recovery rates for chimpanzees, infants through adults. The lowest values are below 10%, the highest over 60%. Adult chimpanzees averaged 30%. Japanese macaques were reported to have vertical displacements of the CoM that differ from those of humans (Ogihara et al., 2007), and in-phase hip height (CoM proxy) fluctuations (Hirasaki et al., 2004). In a more recent paper, Ogihara et al. (2010) reported highly variable percent recoveries for bipedal Japanese macaques, ranging from 5.5 to 61.8%. Low recovery rates of 27% were found for human BHBK walking (Wang et al., 2003). CoM data for primate quadrupedal gaits are rare (Cavagna et al., 1977; Ogihara et al., 2012; O'Neill and Schmitt, 2012). They are not directly comparable to the bipedal data as species and/or methods differ.

We here add ground reaction force data collected for bipedal and quadrupedal gaits of tufted capuchin monkeys and evaluate whether their CoM mechanics is fundamentally different. Capuchin monkeys are arboreal quadrupeds, but in more open habitats tufted capuchins come to the ground frequently, and terrestrially they adopt bipedal gaits in the context of transport and tool use (Fragaszy et al., 2004; Ottoni and Izar, 2008; Liu et al., 2009). Because of this facultative use of bipedalism in their natural environments, they are an interesting species to study. In addition, they are one of only three nonhuman primate species for which CoT data for both quadrupedal and bipedal gaits are available (Taylor and Rowntree, 1973), thus allowing a comparison of CoM work and CoT across speed and gaits. Capuchin monkeys can also be easily enticed to walk on two legs (Demes, 2011), and their bipedal as well as quadrupedal locomotor kinematics have been documented (Wallace and Demes, 2008; Carlson and Demes, 2010; Demes, 2011).

In addition to the classic CoM calculations pioneered by Cavagna (1975), we also explore CoM mechanics using a more contemporary approach based on collision mechanics (Ruina et al., 2005; Lee et al., 2011; O'Neill and Schmitt, 2012). The mechanical work performed on the CoM includes the work required to redirect its path over the course of a stride. The amount of work depends on the angle between the CoM velocity and the GRF vectors. Large discrepancies from orthogonality increase the amount of work lost per stride. Gaits using pendulum-like mechanics tend to have smaller angular discrepancies than faster spring-like gaits, although these spring-like gaits could benefit from larger collision forces for tensing springs and storing passive elastic energy. Like the classic Cavagna approach, collision calculations only address the mechanical CoT. Mathematical models have shown that increasing the number of limbs in contact with the ground in a stride smoothes the down-to-up transition by decreasing the collisional angle of each limb contact (Smith and Berkemeyer, 1997; Ruina et al., 2005). It is expected then, based on collisional accounting alone, that the mechanical CoT would be lower in quadrupedalism than in bipedalism at similar speeds.

Ground reaction forces for bipedal and quadrupedal gaits were recorded to test the following hypotheses:

1. Peak vertical GRF magnitudes are different for capuchin bipedalism and quadrupedalism.
2. Hind limb vertical GRF curves are different for capuchin and human bipedalism.
3. CoM mechanics are different for capuchin bipedalism and quadrupedalism.

4. CoM mechanics are different for capuchin and human bipedalism.
5. The lack of a difference in CoT between capuchin bipedalism and quadrupedalism (Taylor and Rowntree, 1973) is reflected in CoM work per distance for these two locomotor modes.

Testing these hypotheses contributes to an understanding of the mechanical challenges of transitioning from a quadrupedal to a bipedal gait and possible energetic consequences of such a transition. Our study is the first that documents CoM mechanics for primate bipedalism and quadrupedalism using the same subjects and applying identical methods.

## METHODS

### Animals and data collection

Ground reaction forces (GRFs) were recorded for three adult tufted capuchin monkeys (*Cebus apella*), ages 8–11 and weighing  $3.1 \pm 0.09$  kg. Not all individuals contributed equally to the data set; the majority of data came from the two older animals, ages 9 and 11. Forces of 40 bipedal and 73 quadrupedal strides (touchdown to touchdown of the same limb) were collected and CoM mechanics calculated for these complete strides. Additionally, peak GRFs were extracted for the bipedal strides, and compared with previously published peak hind limb forces for capuchin quadrupedalism (Wallace and Demes, 2008; Carlson and Demes, 2010). Many of the quadrupedal strides did not lend themselves to the extraction of single limb forces because the force plates in this study were set up to maximize the collection of forces for complete strides rather than single limb contacts. Duty factors (the ratio of stance duration to stride duration) were calculated for the bipedal strides and quadrupedal strides excluding gallops, for which the video recording frequency of 60 Hz was insufficient.

The animals moved on a 10.5 m long wooden runway with two sequential AMTI force plates (Advanced Mechanical Technology, Watertown, MA) integrated into its center. The runway was enclosed in a translucent Lexan tunnel, which contained the animals and allowed monitoring activity with a lateral view video camera (Peak Performance Technologies, Englewood, CO). The animals were enticed to move back and forth on the runway with food rewards. To elicit bipedal gait, food items were offered to them at a height that forced them onto their hind limbs (see Demes, 2011, for more details).

GRFs were amplified and recorded digitally at a sampling rate of 1020 Hz using a Labview virtual instrument (National Instruments, Austin, TX). Traces representing the vertical, fore-aft, and mediolateral force channels were displayed on a computer monitor that simulated an oscilloscope and digitally stored. The computer images were then converted to a standard video signal and superimposed onto video recordings of the animals crossing the force plates using a special effects generator (WJ 45P, Panasonic, Secaucus, NJ, USA). Using taped records of the superimposed video, strides were selected for analysis and associated force files were identified. The nose was used as the anatomical landmark for determining speed as it passed between two markers 1 m apart on the runway. Change in speed was evaluated by dividing the net horizontal impulse over a stride by body weight (Farley and Ko, 1997). Mean change in speed of the bipedal strides was  $7.0 \pm 6.1\%$  of average speed and for the quadrupedal strides  $10.5 \pm 9.3\%$  of average speed. Three

bipedal strides included in the analysis exceeded our threshold value of 25% of the average speed.

### CoM classical calculations

CoM mechanics were calculated from the vertical (v), fore-aft (f-a), and mediolateral (m-l) GRFs following Cavagna (1975). Briefly, three-dimensional linear accelerations, velocities, and positions were calculated for the CoM assuming a periodic gait (e.g., Cavagna, 1975; Heglund et al., 1982a). The CoM velocities in the vertical and mediolateral directions, as well as the 3D positions, were assumed to oscillate around zero, while the average forward velocities were set equal to the average forward speed over the stride. The instantaneous kinetic (KE) and gravitational potential energies (PE) were derived from these values as:

$$\text{KE} = \frac{1}{2}M_b(v_v^2 + v_{f-a}^2 + v_{m-l}^2)$$

$$\text{PE} = M_bgs_v$$

where  $M_b$  = body mass (kg),  $g = 9.81$  ( $\text{ms}^{-2}$ ), and  $v_v$ ,  $v_{f-a}$ , and  $v_{m-l}$  = vertical and horizontal velocity components ( $\text{ms}^{-1}$ ), and  $s_v$  = vertical change in height of the CoM (m). The pendulum-like nature of the bipedal and quadrupedal strides was evaluated using the interchange of kinetic and gravitational potential energy of the CoM over a stride. The percent of CoM energy recovered ( $R$ ) throughout a stride was calculated as

$$R = \frac{\Sigma\text{KE}_{f-a} + \Sigma\text{PE} - \Sigma(\text{KE} + \text{PE})}{\Sigma\text{KE} + \Sigma\text{PE}}$$

where the sums refer to the sum of all positive incremental changes over the course of the stride.

The CoM mechanical work ( $J$ ) and power ( $W$ ) were determined for each bipedal and quadrupedal stride. The positive CoM work was calculated as the sum of the positive incremental changes in the KE + PE curve, whereas the negative CoM work summed the negative increments. The CoM power was calculated as the rate of CoM work in either the positive or negative direction. The CoM work per distance ( $\text{Jkg}^{-1} \text{m}^{-1}$ ) was calculated as the CoM power divided by the average overground speed. The overall CoM work and power over a stride is the sum of the positive and the absolute of the negative values (e.g., Cavagna, 1975; Heglund et al., 1982a). In a steady-state stride, the overall CoM work and power should be about twice the positive work and power.

To evaluate the relative contributions of CoM energy phasing to the measured percent CoM energy recoveries, we determined the phase relationship (i.e., congruity) of PE and KE, following Ahn et al. (2004). Congruity is positive when PE and KE change in the same direction (in phase) and negative when they change in opposite directions (out of phase). As a summary value, we use percent congruity, defined as the percentage of the stride in which congruity is positive. A high percent congruity means that PE and KE fluctuate largely in phase, whereas a low percent congruity means that PE and KE fluctuate largely out of phase.

### CoM collisional calculations

Following Lee et al. (2011) and others (e.g., Adamczyk et al., 2006; Adamczyk and Kuo, 2009), we also calculated the CoM collisional mechanics. Several studies



TABLE 1. Speed, duty factors, and peak vertical hind limb forces for bipedal strides and two comparative samples of quadrupedal strides

		<i>N</i>	Speed (m/s)	Duty factor	Peak vertical force (bw)
Bipedal	Mean ± sd	40	1.13 ± 0.15	0.57 ± 0.06	1.29 ± 0.11
	Range		0.86–1.43		
Quadrupedal ambles hind limb	Mean ± sd	60	1.51 ± 0.33	0.46 ± 0.05	–
	Range		0.91–2.50		
Quadrupedal ambles forelimb	Mean ± sd	60	1.51 ± 0.33	0.39 ± 0.05	–
	Range		0.91–2.50		
Quadrupedal gallops	Mean ± sd	13	4.39 ± 0.66	–	–
	Range		3.75–6.00		
Quadrupedal symmetrical <sup>a</sup>	Mean ± sd	49	2.01 ± 0.46	–	1.23 ± 0.17
	Range		1.28–3.33		
Quadrupedal gallops <sup>a</sup>	Mean ± sd	8	2.73 ± 0.59	–	1.41 ± 0.16
	Range		2.00–3.75		
Quadrupedal symmetrical <sup>b</sup>	Mean ± sd	65/85 <sup>c</sup>	2.04 ± 0.51	0.39 ± 0.04	1.20 ± 0.12
	Range		1.20–3.53		

<sup>a</sup> Hind limb data from Carlson and Demes, 2010.

<sup>b</sup> Hind limb data from Wallace and Demes, 2008.

<sup>c</sup> For duty factors and peak forces, respectively.

have argued that the fundamental reason CoM work and power are needed in steady, terrestrial locomotion is to replace the kinetic energy losses that occur when the CoM and limbs collide with the ground (e.g., Ruina et al., 2005; Bertram and Gutmann, 2009; Lee et al., 2011). Further, recent studies have shown the CoM work and power measured per stride are directly proportional to the geometry of these collisions (Lee et al., 2011; O’Neill and Schmitt, 2012). Given the CoM forces ( $f_v$ ,  $f_{f-a}$ , and  $f_{m-1}$ ) and velocities ( $v_v$ ,  $v_{f-a}$ , and  $v_{m-1}$ ), the instantaneous 3D orientation of the resultant GRF is calculated with respect to vertical and the orientation of the CoM velocity is calculated with respect to horizontal (fore-aft) as (Lee et al., 2011):

$$\theta_{\text{GRF}} = \cos^{-1} \left[ \frac{|f_v|}{\sqrt{f_v^2 + f_{f-a}^2 + f_{m-1}^2}} \right]$$

$$\lambda_{\text{vel}} = \cos^{-1} \left[ \frac{|v_{f-a}|}{\sqrt{v_v^2 + v_{f-a}^2 + v_{m-1}^2}} \right]$$

The instantaneous angle between the resultant GRF and velocity vectors is, therefore, given as:

$$\phi_{\text{col}} = \sin^{-1} \left[ \frac{|f_v \cdot v_v + f_{f-a} \cdot v_{f-a} + f_{m-1} \cdot v_{m-1}|}{\sqrt{f_v^2 + f_{f-a}^2 + f_{m-1}^2} \cdot \sqrt{v_v^2 + v_{f-a}^2 + v_{m-1}^2}} \right]$$

When the CoM force and velocity vectors are orthogonal, the kinetic energy lost in that instant is zero, and (in principle) no mechanical work or power is needed to keep the CoM moving. As such, we examined the difference in  $\lambda$ ,  $\theta$ , and  $\phi$  between bipedalism and quadrupedalism. The weighted averages of each of these parameters over a stride were calculated following Lee et al. (2011) for comparative purposes. Finally, the collisional fraction was calculated as a weighted sum of the instantaneous values (O’Neill and Schmitt, 2012). This fraction ranges from 0 (no collision) to 1 (high collision). A low collision fraction indicates small collisional losses and less work to redirect the path of the CoM.

## Statistical analyses

Descriptive statistics (mean, standard deviation and range) are reported for speed, duty factor, and peak vertical GRFs for 40 bipedal steps that match the sample for which CoM parameters were calculated, plus two comparative samples representing quadrupedal gaits (Wallace and Demes, 2008; Carlson and Demes, 2010). As the two peak force values and duty factors that can be extracted per stride are closely correlated, we only report the values for the first step in a stride to avoid sample inflation. We tested for significance of correlations of peak vertical GRFs, CoM work and power, and collision fraction with speed, as well as the correlation of % CoM energy recovery with % congruity. We report Pearson product-moment coefficients for variables that were found to be normally distributed (insignificant Shapiro-Wilk statistic for samples <50 or Kolmogorov-Smirnov for samples >50) or the nonparametric Spearman’s rho for variables that were not distributed normally (significant Shapiro-Wilk or Kolmogorov-Smirnov statistics).

Least-squares regressions were used to determine the changes of peak vertical GRFs, CoM work and power, and collisional fraction with overground speed. The equality of bipedal and quadrupedal regression slopes was tested using an analysis of covariance in which CoM mechanics, speed and locomotor mode (i.e., bipedal, quadrupedal) and speed × mode were factors. Note that these analyses included some variables that were not normally distributed, thereby violating an assumption of analysis of variance. The error due to non-normality is considered not serious (Sokal and Rohlf, 2012) and is unlikely to affect the drastic slope differences between bipedalism and quadrupedalism. All statistical tests were performed in SPSS 16 (IBM, Chicago, IL).

## RESULTS

### Kinematic gait characteristics

The capuchins volunteered bipedalism in a narrow speed range of 0.86 to 1.43 ms<sup>-1</sup> (Table 1). During quadrupedalism, overground speeds ranged from 0.91 to 6.00 ms<sup>-1</sup>. Voluntary speeds in two comparative quadrupedal samples collected previously for two animals of comparable sizes and ages (Wallace and Demes, 2008; Carlson

and Demes, 2010) were also higher than the bipedal speeds represented in the current sample, and speed ranges greater (Table 1). Duty factors for the bipedal strides are  $0.57 \pm 0.06$ , and range from 0.71 to 0.42. Values below 0.5 suggest that a short aerial phase occurs between individual limb touchdowns. Kinematically, three strides in the sample of 40 are bipedal runs with duty factors below 0.5. These three strides with speeds of  $1.05\text{--}1.25\text{ ms}^{-1}$  are not the fastest in the sample.

Most intermediate-speed quadrupedal strides of the capuchin monkeys are grounded runs or ambles (*sensu* Muybridge, 1887; Schmitt et al., 2006; see also Wallace and Demes, 2008), with duty factors below 0.5 (Table 1), but no whole-body aerial phase. Thirteen intermediate-speed strides have duty factors above 0.5 for the hind limbs (and one of them also for the forelimbs); i.e., the footfall timing of at least one pair of limbs conforms to a kinematic walk. With speeds of  $0.91\text{--}1.43\text{ ms}^{-1}$  these “walk/ambles” are in the lower range of quadrupedal speeds. We will refer to the intermediate-speed strides in the following collectively as ambles. Hind limb duty factors from a previously published quadrupedal sample (symmetrical gaits in a speed range of  $1.2\text{--}3.5\text{ ms}^{-1}$ ; Wallace and Demes, 2008) also almost all fell below 0.5 (Table 1). The fast quadrupedal strides of the capuchin monkeys will be referred to as gallops, although they may include canters (“grounded gallops”).

The vast majority of bipedal and quadrupedal strides are in the speed range of intermediate and fast-speed gaits, rather than walking gaits. Mammalian quadrupeds and bipeds transition from walking to intermediate-speed gaits (e.g., runs, trots, canters) at a Froude number of about 0.5 (Alexander and Jayes, 1983; Kram et al., 1997; O'Neill and Schmitt, 2012), with some studies reporting lower values (e.g., Griffin et al. 2004; Usherwood et al. 2008). The average mid-stance hip height

for our capuchins is  $0.22 \pm 0.01\text{ m}$  in bipedalism (Demes, 2011), and  $0.23 \pm 0.01\text{ m}$  in quadrupedalism (unpublished data from previous kinematic studies on the same individuals). Thus, the predicted bipedal gait transition speed was  $\sim 1\text{ ms}^{-1}$  (with  $v = \sqrt{Fgh}$ ,  $F$  = Froude number (0.5),  $g = 9.81\text{ ms}^{-2}$ ,  $h$  = hip height; vertical line in Fig. 3). In general, the bipedal strides were found to be in close vicinity to the predicted walk-run transition speed, and almost all of the quadrupedal strides are faster than the predicted highest walking speed.

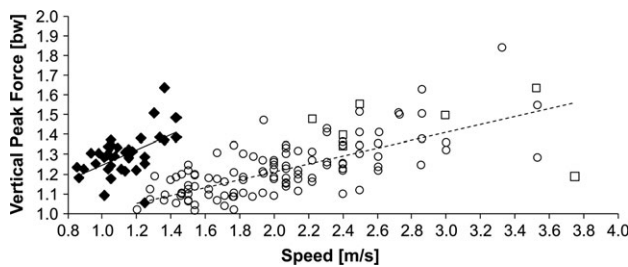
### Hind limb vertical GRFs

The hind limb peak vertical GRFs for bipedalism are shown in Figure 1, with descriptive statistics reported in Table 1. Comparative hind limb forces for quadrupedal gaits collected previously (Wallace and Demes, 2008; Carlson and Demes, 2010) were added to Table 1. Not surprisingly, hind limb peak forces are higher for bipedalism than quadrupedalism at comparable speeds ( $1.2\text{--}1.5\text{ ms}^{-1}$ ; Fig. 1). Only the faster quadrupedal steps have force magnitudes overlapping those recorded for bipedalism at moderate speeds (Fig. 1). Correlations with speed are low, but significant (bipedal steps: Spearman's  $\rho = 0.56$ ,  $P < 0.01$ ; quadrupedal steps: Spearman's  $\rho = 0.44$ ,  $P < 0.01$ ; Table 2). The increase of peak force magnitudes with speed does not differ between bipedalism and quadrupedalism ( $P = 0.10$  for mode  $\times$  speed interaction).

Unlike for human walking, almost all of the vertical force traces for capuchin monkey bipedalism have one peak (Fig. 2). Only few, for slow steps, have an incipient second hump (see insert in Fig. 2). The traces also lack the impact spike that is characteristic of human walking and running with a prominent heel strike (Nigg, 1988; Lieberman et al., 2009).

### CoM mechanics

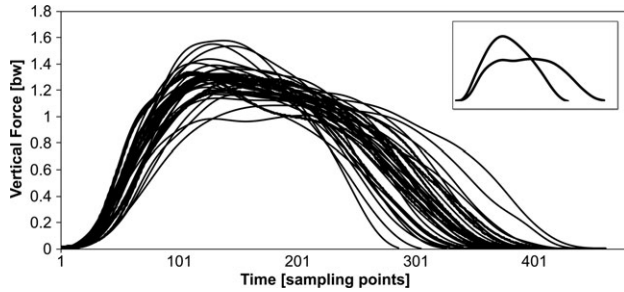
CoM energy recoveries are low for capuchin bipedalism and, on average, much lower than for quadrupedalism at comparable speeds (Fig. 3). The bipedal values range from 2 to 17%, with CoM recoveries generally decreasing with speed (Pearson  $r = -0.49$ ,  $P = 0.01$ ; Table 2). In contrast, the CoM energy recoveries for capuchin quadrupedalism range from 4 to 72%. Although most of this substantial variation is unrelated to speed, a slight, albeit significant, decrease in CoM energy recovery with speed is evident (Pearson  $r = -0.32$ ,  $P = 0.01$ ; Table 2), mostly driven by the lower recovery rates of the gallops. The three bipedal runs with duty factors below 0.5 are nested within the majority of bipedal walking strides by kinematic definition (see above), with recoveries of 5.5%, 6.1%, and 12.1%. The 13 quadrupedal strides with hind limb duty factors above 0.5 range in re-



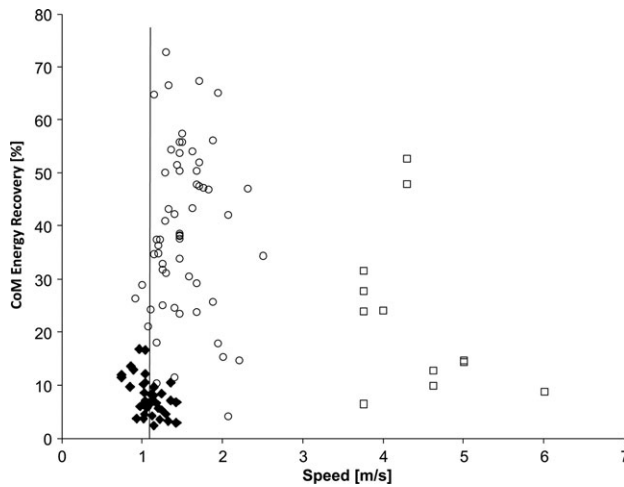
**Fig. 1.** Peak vertical hind limb GRFs for bipedalism (closed diamonds) and quadrupedalism (open circles and squares) as a function of speed. Open circles = ambles (from Wallace and Demes, 2008; Carlson and Demes, 2010); open squares = gallops (from Carlson and Demes, 2010). Trend lines are least-squares regressions for bipedalism (solid) and quadrupedalism (dashed) across the measured speed range.

TABLE 2. Least squares regression statistics of variables on speed

	Bipedalism				Quadrupedalism			
	Intercept	Slope	s.e.	$R^2$	Intercept	Slope	s.e.	$R^2$
Peak vertical GRF	0.86	0.38	0.10	0.29	0.81	0.20	0.04	0.47
CoM energy recovery	19.56	-10.56	3.06	0.24	46.04	-4.75	1.56	0.12
CoM total work	-0.41	3.85	0.65	0.48	0.26	1.04	0.08	0.69
CoM positive work	-0.21	1.93	0.33	0.48	0.13	0.52	0.04	0.69
CoM total power	-6.71	15.95	1.76	0.68	-0.77	3.83	0.28	0.74
CoM positive power	-6.30	12.10	1.27	0.70	-1.03	2.79	0.20	0.74
Collisional fraction	0.38	0.35	0.07	0.41	0.47	-0.01	0.10	0.02



**Fig. 2.** Superimposed vertical GRFs for 40 bipedal steps as a function of time (sampling points). Each sampling point = 0.0167s. The inset shows example GRFs for a single slow and a fast bipedal step. Note that the slow step includes an incipient double-humped curve, as has been observed in some other facultative bipeds during walking (Kimura et al., 1977; Ogiwara et al., 2010), whereas the fast step is single-humped, consistent with a bipedal running gait.

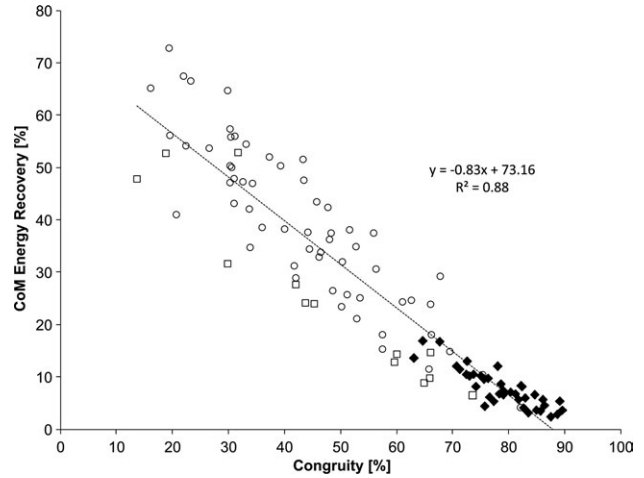


**Fig. 3.** CoM percent energy recovered during bipedal (closed diamonds) and quadrupedal strides (open circles = ambles, open squares = gallops) across the measured speed range. The vertical line indicates the predicted walk-to-run gait transition, based on studies of quadrupeds and bipeds (Alexander and Jayes, 1983; Froude number of 0.5). Based on the mass and hip height of a capuchin, a Froude number of 0.5 corresponds to a speed of about  $1 \text{ ms}^{-1}$ .

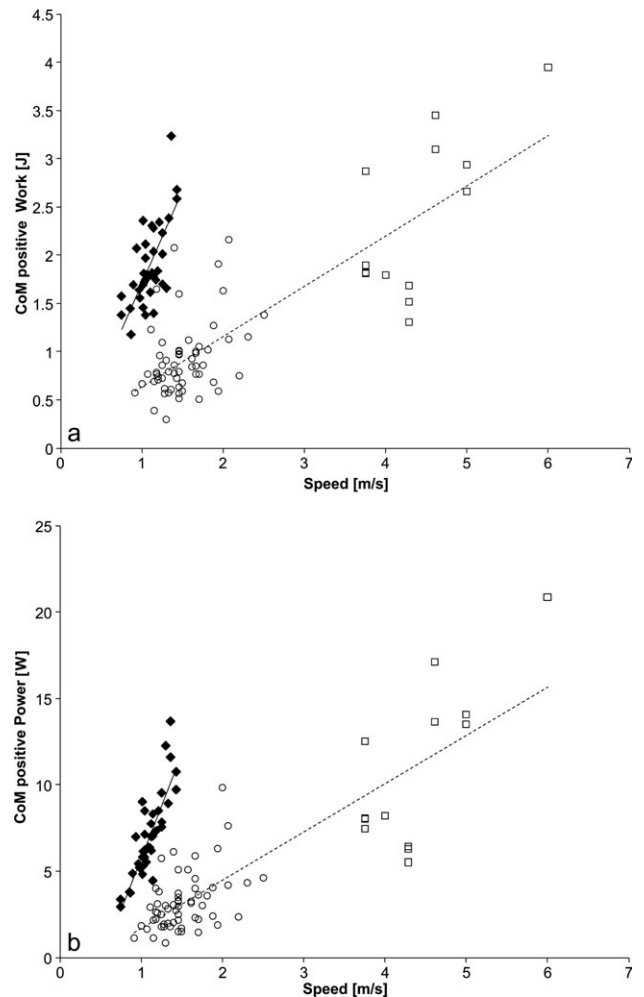
covery rates from 11.4 to 64.7%; i.e., they span almost the entire range of quadrupedal recovery rates. It is notable that most of the variation in CoM energy during quadrupedalism was found at speeds comparable to those of bipedalism.

As has been observed in other animals (e.g., Bishop et al., 2008; O'Neill and Schmitt, 2012), CoM energy recoveries are strongly correlated with the congruity of KE and PE fluctuations (Fig. 4, all gaits: Spearman's  $\rho = -0.95$ ,  $P < 0.01$ ). Congruity is lowest for bipedalism, and so is CoM energy recovery. Clearly, the lack of energy fluctuations out of synchrony does not allow for much energy exchange.

The CoM work ( $J$ ) and power ( $W$ ) are significantly higher in bipedalism than in quadrupedalism (Fig. 5). Total and positive CoM work are fit moderately well by linear regressions (bipedal: Spearman's  $\rho = 0.63$  for both total and positive work; quadrupedal: Spearman's

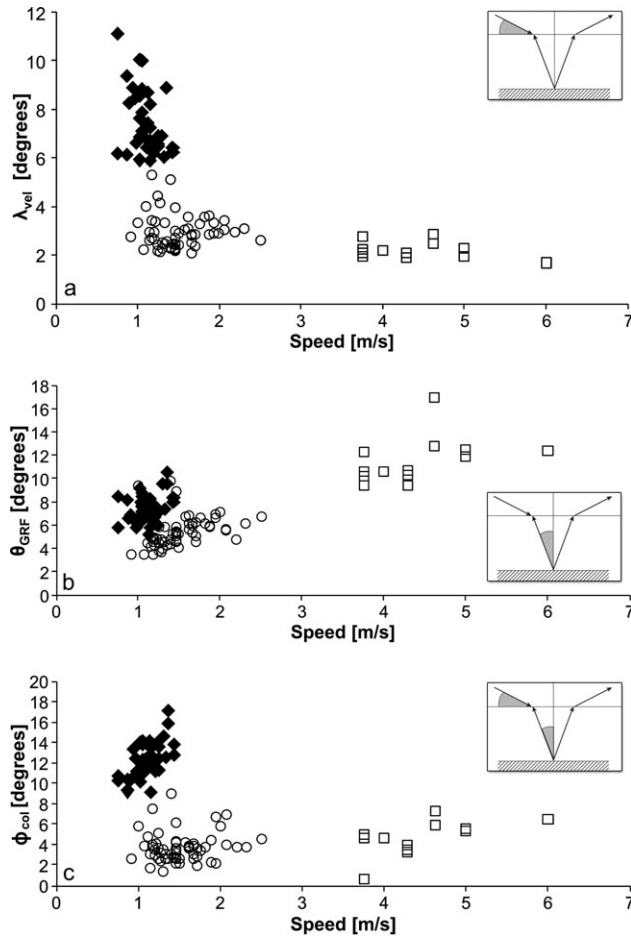


**Fig. 4.** CoM percent energy recovery vs. congruity. Differences in CoM percent energy recovery between bipedalism and quadrupedalism are largely explained ( $R^2 = 0.88$ ) by the phase relationship of PE and KE. Symbols as in Figure 3. The trend line is a least-squares regression line.



**Fig. 5.** Positive CoM work (a) and power (b) for bipedalism and quadrupedalism across speed and gaits. Symbols as in Figure 3. Trend lines are least-squares regressions for the bipedalism (solid) and quadrupedalism (dashed).

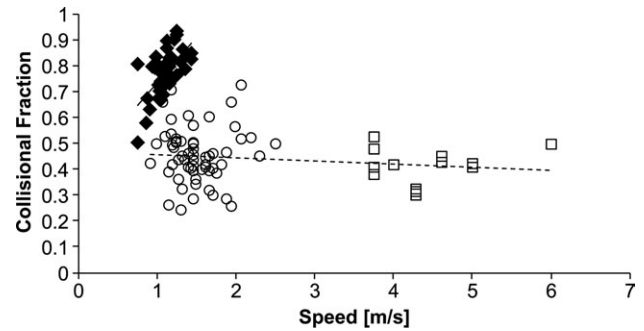




**Fig. 6.** CoM collisional angles in bipedalism and quadrupedalism across speed and gaits. The angles that the CoM velocity vector forms with the horizontal (a), the resultant GRF forms with vertical (b), and the collision angle between the CoM velocity and resultant GRF with respect to orthogonal axes (c) are each shown. Symbols as in Figure 3.

$\rho = 0.63$  for both total and positive work; Table 2), but with a significantly steeper slope in bipedalism than quadrupedalism ( $P < 0.01$  for mode  $\times$  speed interactions for both total and positive work). Per mass and distance, the total and positive CoM work ( $\text{Jkg}^{-1} \text{m}^{-1}$ ) is  $3.18 \pm 0.50$  and  $2.04 \pm 0.40$  for bipedalism, and  $1.08 \pm 0.41$  and  $0.70 \pm 0.29$  for quadrupedalism. The total and positive CoM power is fit moderately well by linear regressions (bipedal: Pearson  $r = 0.84$  and  $0.83$ ; quadrupedal: Spearman's  $\rho = 0.69$  and  $0.67$ ; Table 2), but with significantly steeper slopes for bipedalism than quadrupedalism ( $P < 0.01$  for mode  $\times$  speed interactions for both positive power and total power). Across the full speed range, the maximum positive CoM power outputs measured are  $13.7 \text{ W}$  in bipedalism and  $20.9 \text{ W}$  in quadrupedalism.

CoM collisional calculations complement the findings from classical CoM calculations, and further indicate important differences between bipedal and quadrupedal locomotor mechanics. The mean CoM velocity vector ( $\lambda_{\text{vel}}$ ) forms larger angles with the ground in bipedalism than in quadrupedalism, with almost no overlap between them (Fig. 6a). In contrast, mean GRF angles ( $\theta_{\text{GRF}}$ ) are more similar for the two locomotor modes, with only slightly



**Fig. 7.** The instantaneous collisional fraction for bipedalism and quadrupedalism as a function of speed and gaits. Symbols as in Figure 3. The average collisional fraction is  $0.77 \pm 0.09$  for bipedalism and  $0.44 \pm 0.10$  for quadrupedalism.

higher angles for bipedal strides (Fig. 6b). Taken together, bipedal strides have larger mean CoM collisional angles ( $\phi_{\text{col}}$ ; Fig. 6c), indicating larger collisional losses than in quadrupedalism. The collision angle is on average  $12.4 \pm 1.7^\circ$  in bipedalism and  $3.9 \pm 1.5^\circ$  in quadrupedalism. As noted in Lee et al. (2011) and O'Neill and Schmitt (2012), the mechanical CoT is directly proportional to  $\phi_{\text{col}}$ .

The collisional fractions—calculated as a weighted average of the instantaneous ratio of  $\phi$  to  $(\lambda + \theta)$ —are  $0.77 \pm 0.09$  for bipedalism and  $0.44 \pm 0.10$  for quadrupedalism (Fig. 7). Interestingly, the instantaneous collisional fraction is significantly correlated with speed across the bipedal strides (Pearson  $r = 0.64$ ,  $P = 0.01$ ) but not the quadrupedal strides (Pearson  $r = -0.15$ ,  $P = 0.21$ ; Table 2).

## DISCUSSION

The data and analyses presented here provide clear answers to all hypotheses tested: Capuchin monkey bipedalism is different from quadrupedalism in its peak vertical GRFs and CoM mechanics. CoM energy recoveries are lower, the CoM work and power output are higher, and so is the collisional fraction, indicating that more work is needed to redirect the velocity vector of the CoM in bipedalism. Increases of work, power, and collisional fraction with speed are steeper in bipedalism than in quadrupedalism, suggesting that speed increase on two legs comes at a higher mechanical price. The peak GRF generated and sustained by the hind limbs are higher. Over the measured speed range, capuchin monkey bipedalism differs distinctly from human bipedal walking in that it is not governed by pendulum mechanics with out-of-phase energy fluctuation and high recovery rates. Vertical GRF profiles also differ, having one maximum, rather than two distinct peaks like in human walking. Finally, the distinct difference in CoM work between capuchin bipedalism and quadrupedalism is not reflected in the CoT which Taylor and Rowntree (1973) found to be the same. The details and implications of these results will be discussed in greater detail in the following.

### CoM energy, work, and power

The bipedal gait of capuchin monkeys lacks the out-of-phase fluctuations of kinetic and potential energies of the CoM that allow converting one into the other. Recovery of mechanical energy is therefore low, and positive mechanical work required to accelerate the CoM is high.

These results are consistent with results of previous studies on the percent recoveries of bipedal macaques (Ogihara et al., 2010), gibbons (Vereecke et al., 2006), and chimpanzees (Kimura and Yaguramaki, 2009), which have reported quite low percent recoveries, especially at higher speeds. Energy recoveries at lower speeds were somewhat higher. We cannot exclude higher energy recoveries at lower speeds for our capuchin monkeys. However, if there is a more pendulum-like, slow bipedal gait in capuchin monkeys, it is not within the speed range they volunteer. Bipedal speeds recorded for tufted capuchin monkeys in the field are comparably high (Fragaszy, pers. comm.).

It has been suggested that CoM mechanics, rather than kinematic variables (e.g., duty factors and speed), is a more reliable measure for differentiating walking from running strides (Biknevicius and Reilly, 2006; Bertram and Gutmann, 2009). This is because CoM mechanics is more directly tied to the functioning of the musculoskeletal system than duty factor or speed parameters, which can fail to detect significant shifts in gait mechanics (e.g., McMahan et al., 1987; Muir et al., 1996; Parchman et al., 2003; Rubenson et al., 2004). This is evident in the bipedal strides of the capuchins. While the duty factors and nondimensional speeds (Froude numbers) suggest a mix of walking and running strides, the CoM mechanics of capuchin bipedalism all indicate a mass-spring-like running gait. This is consistent with recent measures of hind limb kinematics, which indicate a down-to-up (i.e., spring-like) path of the hip joint during the second half of stance phase (Demes, 2011).

Whether or not passive elastic tissues are involved in powering the spring-like bipedal gait of capuchin monkeys is unknown. CoM fluctuations in height and angular kinematics of the hind limb (Demes, 2011) are compatible with the loading and release of energy in elastic elements, with the knee extensors and ankle flexors being stretched out in the first half of the stance phase when knee and ankle collapse into flexion and dorsiflexion, respectively. The knee joint, however, is not extended in the second half of stance (Demes, 2011). Whether the ankle plantarflexion observed in the second half of support involves elastic element recoil is not clear. To confirm spring action, more direct measurements of muscle-tendon function are needed (i.e., Roberts et al., 1997; Fukunaga et al., 2001). It should also be noted that nonhuman primate hind limb muscles tend to have long fibers and short tendons (Alexander et al., 1981; Payne et al., 2006), which is the opposite of what is found in muscle-tendon units capable of significant strain energy storage (Alexander, 1988; Roberts, 2002). For these reasons, it is unlikely that elastic energy storage and recoil in the free tendons at the ankle play a significant role in the active work generation in capuchin monkey bipedalism.

The high collisional fraction found for the bipedal strides of the capuchin monkeys is mostly a result of the steeper angles that the CoM velocity vector forms with the horizontal (Fig. 6a). As a result, the vertical displacements of the CoM are relatively high, with average values of  $2.78 \pm 0.77$  cm. That almost doubles the vertical CoM displacements of quadrupedal strides at similar speed (ambles:  $1.55 \pm 0.59$  cm) and, on average, is much more comparable to galloping ( $2.78 \pm 0.41$  cm). Although capuchin monkey bipedalism is a compliant gait (Demes, 2011), its CoM fluctuations are quite pronounced.

Neither on two legs nor on four legs did the capuchin monkeys use distinct gaits in the slow to intermediate

speed range, and, related to that, there was no abrupt gait change. In humans, at the walk-to-run transition, dynamics change abruptly from pendulum to spring (Cavagna et al., 1976). In fact, capuchin monkeys seem to lack a true running gait like that of human bipeds. Neither enticing them nor chasing them elicited higher bipedal speeds and a run with an extended whole-body aerial phase. The lack of a distinct gait change seems to characterize nonhuman primate gaits in general, quadrupedal (Schmitt et al., 2006; O'Neill and Schmitt, 2012) as well as bipedal (Vereecke et al., 2006; Ogihara, 2010, 2012). Primates, however, are not unique in that respect. Many quadrupedal animals also change gradually from walking to running gaits (Alexander and Jayes, 1983; Biknevicius and Reilly, 2006; Hutchinson et al., 2003, 2006), and so do bipedal birds (Gatesy and Biewener, 1991; Rubenson et al., 2004; Usherwood et al., 2008). Despite the lack of a distinct gait change, bouncing mechanics is generally adopted in the running range in these species (Hutchinson et al., 2003; Biknevicius and Reilly, 2006). The gaits of nonhuman primates may be selected for by demands other than locomotor economy, like moving safely on compliant arboreal supports (e.g., Demes et al., 1990; Schmitt, 1999; O'Neill and Schmitt, 2012).

Our study, considered in combination with an earlier study of locomotor costs in capuchin monkeys (Taylor and Rowntree, 1973), suggests that CoM work per distance and net CoT are not tightly correlated when assuming a constant efficiency (Hill, 1950). That is, between quadrupedal and bipedal strides, we observed a 2.9 times increase, on average, in positive CoM work per distance, whereas Taylor and Rowntree (1973) found only a slight (1.15 times), nonsignificant difference between the net CoT of capuchin monkey bipedalism ( $6.43 \text{ Jkg}^{-1} \text{ m}^{-1}$ ) and quadrupedalism ( $5.63 \text{ Jkg}^{-1} \text{ m}^{-1}$ ) for speeds that overlapped with the speeds used by our subjects. Combining their locomotor cost data with our positive CoM work values, the positive CoM efficiencies ( $[\text{positive CoM work per distance/CoT}] \times 100$ ) for capuchins can be estimated as 31.7% for bipedalism and 12.4% for quadrupedalism (across ambling and galloping gaits). These values should hold even if our quadrupedal data are restricted to the narrower speed range measured by Taylor and Rowntree (1973), since no significant difference was found in the positive CoM work per distance between ambling and galloping in our animals.

### Limitations of this study

Measures of CoM mechanics, including estimates of mechanical work, will be underestimates when compared with individual-limb mechanics when individual-limb forces overlap in a single stride (e.g., Donelan et al., 2002a; Ren et al., 2010; O'Neill and Schmitt, 2012). This is the case for all the quadrupedal strides. This confounding factor limits our ability to interpret the differences in bipedal and quadrupedal CoM work, power, and efficiencies with respect to the actual limb, joint or active muscle work performed over a stride (Sasaki et al., 2009). It is likely that there is more overlap in individual limb forces, and therefore greater underestimation of mechanical work, in quadrupedalism than in bipedalism at the same speed in capuchins. However, previous studies of CoM work and power have reported no significant difference between bipeds and quadrupeds (Heglund et al., 1982a). Nevertheless, more studies are needed to



evaluate whether the differences in CoM mechanics between bipedalism and quadrupedalism found here translate into measureable differences in limb, joint, and active muscle work.

In addition to the “internal” mechanical work done when individual limbs work against each other, the mechanics of limb swing in capuchin bipedalism and quadrupedalism were not measured in this study. As such, the total mechanical work and power required in a stride will be underestimated by our CoM measurements. This is especially the case for fast speed locomotion, as the mechanical power required for limb swing appears to increase exponentially with speed (Fedak et al., 1982; Rubenson and Marsh, 2009).

### Implications for the evolution of human bipedalism

Our data demonstrate that capuchin monkeys are capable of adopting a spring-like bipedal gait at intermediate and fast speeds, but without a whole-body aerial phase. This is consistent with previous kinematic measurements (Demes, 2011), as well as the CoM mechanics of bipedalism in gibbons (Vereecke et al., 2006). This has also been observed in the overground locomotion of birds (Muir et al., 1996; Rubenson et al., 2004; Hancock et al., 2007) and is in marked contrast to the running abilities of modern humans. Capuchin monkeys also do not use a pendulum-like walking gait like modern humans, at least not in the speed range they volunteer. Although more data are needed, current evidence clearly suggests that facultative bipedalism of nonhuman primates is not restricted to pendulum-like walking, but rather includes “grounded running.” We suggest that the emergence of an obligate pendulum-like walking gait and a spring-like running gait with elastic recoil (Lichtwark et al., 2007) and a whole-body aerial phase represent important transitions in the evolution of hominin bipedalism.

Reducing the number of supports from four to two and, consequently, having intervals of single-limb support in a stride, is a destabilizing factor when engaged in facultative bipedalism. Adoption of a BHBK posture allows side-to-side stabilization at the hip (Stern and Susman, 1981), and at the same time brings the support leg forward to accommodate a CoM that is more anterior than in humans walking with an upright trunk (Lovejoy, 2005). Flexed limb postures also make a gait compliant and attenuate GRFs generated and sustained by the limbs (Schmitt, 1999, 2003), which is advantageous with a decrease in number of support limbs and accompanied increase in ground forces (Fig. 1). Indeed, the knee at midstance is about 13° more flexed in bipedalism than in quadrupedalism (Carlson and Demes, 2010; Demes, 2011). If analogies can be drawn to the earliest hominid bipeds, studies of nonhuman primate bipedal gait, including the present one, suggest that they did not use fully upright postures, but rather walked with bent hips and bent knees. The transition to habitual upright posture and locomotion presented a mechanical challenge that involved sustaining higher forces on the hind limbs and reduced stability due to fewer limb-ground supports.

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