Three-Dimensional Kinematics of Capuchin Monkey Bipedalism

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ABSTRACT   Capuchin monkeys are known to use bipedalism when transporting food items and tools. The bipedal gait of two capuchin monkeys in the laboratory was studied with three-dimensional kinematics. Capuchins progress bipedally with a bent-hip, bent-knee gait. The knee collapses into flexion during stance and the hip drops in height. The knee is also highly flexed during swing to allow the foot which is plantarflexed to clear the ground. The forefoot makes first contact at touchdown. Stride frequency is high, and stride length and limb excursion low. Hind limb retraction is limited, presumably to reduce the pitch moment of the forward-leaning trunk. Unlike human bipedalism, the bipedal gait of capuchins is not a vaulting gait, and energy recovery from pendulum-like exchanges is unlikely. It extends into speeds at which humans and other animals run, but without a human-like gait transition. In this respect it resembles avian bipedal gaits. It remains to be tested whether energy is recovered through cyclic elastic storage and release as in bipedal birds at higher speeds. Capuchin bipedalism has many features in common with the facultative bipedalism of other primates which is further evidence for restrictions on a fully upright striding gait in primates that transition to bipedalism. It differs from the facultative bipedalism of other primates in the lack of an extended double-support phase and short aerial phases at higher speeds that make it a run by kinematic definition. This demonstrates that facultative bipedalism of quadrupedal primates need not necessarily be a walking gait. Am J Phys Anthropol 145:147–155, 2011.   © 2011 Wiley-Liss, Inc.

Capuchin monkeys (genus *Cebus*) are quadrupeds, but on the ground they often use bipedal gaits in their natural habitats. This has been reported in particular for *Cebus libidinosus*, the bearded capuchin,[1] in the context of food and tool transport (Fragaszy et al., 2004; Wright, 2007; Ottoni and Izar, 2008; Liu et al., 2009). At the field site of Piauí in Brazil, bearded capuchins have been observed transporting palm nuts and hammer stones to anvil sites where they crack the nuts. Orthograde activity of *Cebus apella* has also been reported from other sites (Youlatos, 1998; Boinski et al., 2000). Because capuchins switch with ease from quadrupedal to bipedal postures they represent a good model species for studying what kind of bipedal gait a quadrupedal primate adopts—a topic of interest to anthropologists that study the evolution of human bipedalism.

While many species of primates opportunistically use bipedal gaits, precious few have been studied using quantitative methods of gait analysis. These are three species of apes (chimpanzees, bonobos, and gibbons) and the Old World monkeys *Macaca fuscata* and *Papio anubis* (Reynolds, 1987; Aerts et al., 2000; D'Août et al., 2001, 2002; Hirasaki et al., 2004; Vereecke et al., 2006a,b; Kimura and Yaguramaki, 2009; Berrillon et al., 2010; Ogihara et al., 2010). The capuchin monkey represents an interesting addition to this canon for two reasons: 1) It was a study on cebine hip musculature (Stern, 1971, 1975) that has let to a paradigmatic insight into bipedal gaits of nonhuman primates and the earliest hominin bipeds (Stern and Susman, 1981): With iliac blades facing posteriorly, rather than laterally, the lesser gluteal muscles aren't capable of balancing an adduction moment at an extended hip joint during unilateral stance, forcing nonhuman primates to walk bipedally with flexed limbs (so-called bent-hip, bent-knee or BHBK gait: Crompton et al., 1998). 2) Observational and preliminary data on capuchin monkeys suggest that they use what seems to be a bipedal *running* gait, rather than a walk (Demes and O'Neill, 2009). Studies on the mechanics of nonhuman primate bipedalism are almost exclusively focused on bipedal *walking* (but see Vereecke et al., 2006b), like most of the discussion of the earliest stages of hominid bipedalism is focused on walking and pendulum mechanics. Bipedal running is only invoked at the onset of the genus *Homo* and associated with erect postures, limb elongation, and pelvic reorientation (Carrier, 1984; Bramble and Lieberman, 2004; Lieberman et al., 2006; Sockol et al., 2007). Running has not been explored as an incipient bipedal gait.

I here present spatiotemporal parameters of capuchin bipedalism derived from 3D kinematics. A parallel study (Demes and O'Neill, 2009; in preparation) will focus on the *dynamics* of capuchin bipedalism. The following specific questions will be addressed:

1. What characterizes the bipedal gait of capuchin monkeys?

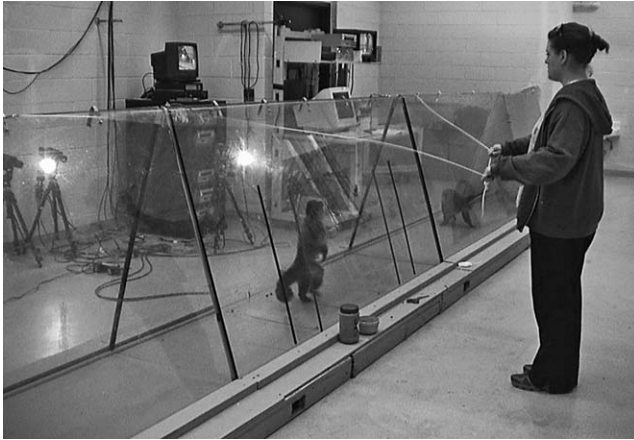[1]Until recently considered a subspecies of *C. apella* (Groves, 2001).

Fig. 1. Experimental setup. The animals moved on a runway enclosed by a Lexan tunnel. A food reward is offered to them suspended on a pulley system.

Fig. 2. Stick figure showing marker positions, segment orientations and angles.

2. How do bipedal capuchins modulate speed?
3. How does the bipedal gait of capuchins compare to their quadrupedal gait?
4. How does the bipedal gait of capuchins compare to other nonhuman primates' bipedal gaits and to human bipedalism?

METHODS

All procedures were approved by the Institutional Animal Care and Use Committee of Stony Brook University. Data were collected for two male capuchin monkeys of the species *Cebus apella,* ages 9 and 11 years and weighing 3 and 3.1 kg, respectively. They were coaxed to walk bipedally with food rewards offered at a height that forced them to move on their hind limbs alone (see Fig. 1). The animals adapted bipedal postures immediately and without any training in the experimental setup. Like capuchins in the wild, the captive subjects were observed using bipedal postures regularly in their home enclosures when carrying food items or toys.

Animals moved on a wooden runway enclosed in a clear Lexan tunnel 10.5-m long and 0.7-m wide (Polk, 2001). Prior to trials, animals were briefly anaesthetized, shaved, and outfitted with reflective tape markers over major joints. Postural data are reported here for the hind limb and trunk using the following joint markers (see Fig. 2): tip of acromion (shoulder), tip of greater trochanter (hip), lateral epicondyle (knee), lateral malleolus (ankle), and head of 5th metatarsal (metatarsophalangeal joint, MT5). Shoulder and hip markers defined the trunk segment, hip and knee markers the thigh, knee and ankle markers the leg, and ankle and MT5 markers the foot. Hind limb pro- and retraction angles were calculated as angles of a line connecting the hip with MT5 at touchdown and liftoff and vertical (see Fig. 2). MT5 was considered the appropriate reference point because the animals make first contact and lift off at the forefoot (see below). Hind limb excursion is the sum of pro- and retraction angles. Trunk pitch and tilt angles were determined relative to vertical in frontal and sagittal planes. See Table 1 for further variable definitions. Arm and forearm movement was recorded, but not quantified for this study.
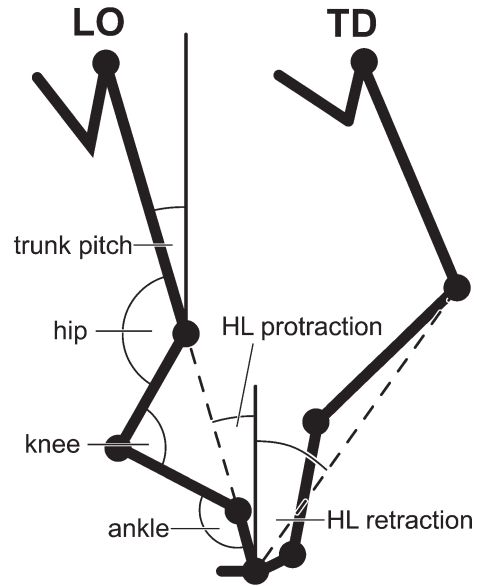
Animals were filmed with three video cameras at 60 Hz, positioned at angles of ~50° to each other to produce a lateral and two oblique views. Prior to recording onto VCRs, video signals from all four cameras were sent through a time code generator (GL-250, J.C. Labs, La Honda, CA) which superimposed a time stamp on each video field. This time stamp was used to synchronize videos. Selected video clips from the three cameras were imported into Peak Motus software v. 5.1.2. (Peak Performance Technologies, Englewood, CO, now Vicon, Los Angeles, CA) and markers digitized in three views. Prior to each trial, a calibration object with 35 control points with known coordinate distances to each other was placed on the runway and filmed. The control points were digitized in the three camera views in Motus, and the 3D coordinates calculated by the software produced 12 coefficients that were used in the direct linear transformation algorithm to reconstruct the 3D coordinates of the joint markers on the animals as they passed through the calibrated space. Positional data were not conditioned (filtered) with the exception of the trunk vertical tilt angle in the frontal plane which was fit to a binomial curve with a window of two prior to calculating the trunk tilt angle. This absolutely small angle had more digitizing noise associated with it than any of the other kinematic variables. The temporal and spatial variables calculated from the coordinate data over time are listed in Table 1.

SPSS 17 (IBM, Chicago, IL) was used for all statistical calculations. Standard descriptive statistics were calculated for postural variables at defined gait events, namely touchdown (TD), midsupport (MS), and liftoff (LO). Average angles over a stride were calculated for the trunk, hip, knee, and ankle angles and the thigh abduction angle. Relationships of selected gait variables with speed were explored using linear regressions. Variables that were found to be significantly correlated with speed were entered into standard multiple regressions and their importance for speed modulation assessed with semipartial correlation statistics. Stride duration was

TABLE 1. Variable definitions

Trunk pitch angle	Angle of shoulder—hip with vertical in sagittal plane
Trunk tilt angle	Angle of shoulder—hip with vertical in frontal plane
Hip angle	Vector angle between trunk and thigh
Hip abduction	Frontal plane angle between trunk and thigh
Knee angle	Vector angle between thigh and leg
Knee yield	Difference between knee angle at TD and MSUP
Ankle angle	Vector angle between leg and foot (>90 = plantarflexion, <90 = dorsiflexion)
Foot angle	Angle of ankle—MT5 with horizontal
Hip height	Vertical distance of hip above ground
Protraction at touchdown	Angle of hip—MT5 with vertical at TD
Retraction at lift off	Angle of hip—MT5 with vertical at LO
Hind limb angular excursion	Sum of pro- and retraction angles
Stride length	Distance between fore/aft coordinate of MT5 of two subsequent touchdowns
Stride frequency	Strides/second
Duty factor	Stance duration/stride duration
Froude number	$v^2/(9.81 \times$ hip height at midstance)

Angles are in degrees, distances in meters, and time in seconds.
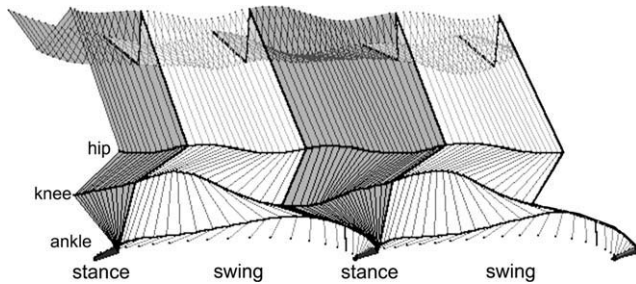Duty factor and Froude number are dimensionless.

Fig. 3. Stick figure representation of representative bipedal steps. The trajectories of the hip, knee and ankle are shown as bold lines. The stick figures at touchdown and liftoff are also in bold.

determined as the time of a complete stride from TD to TD of the same limb, stance duration as the time from TD to LO of the same limb. Stride frequency in Hz is 1/stride duration, and duty factor is stance duration/stride duration. Average speed was determined in the side view camera as the time it took the animal's nose to pass two markers placed one meter apart on the tunnel wall. Froude number was calculated as $F = v^2/gh$, with v = average speed, g = gravitational constant, and h = hip height at midsupport.

Differences between individuals were tested by introducing individual as a factor in linear regression analyses. No significant differences were found (results not reported) and data were subsequently pooled to yield a total sample of 30 strides with approximately equal numbers for the two subjects. The similarities between the two subjects suggest that the gait characteristics reported here might be representative for the species; however, the small number of subjects involved (not uncommon for primate gait studies) should be kept in mind.

RESULTS
Positional changes

Figure 3 illustrates representative bipedal steps in the form of a stick figure graph. Figures 4A–F show positional changes of landmarks, segments and joints superimposed over the course of 30 strides. Descriptive statistics are provided in Table 2. Bipedal capuchins walk

with a BHBK gait (see Fig. 3). The trunk is slightly pitched forward throughout the stride at an average angle with vertical of 23° (Table 2, Fig. 4A). It is held steady in the sagittal plane (see Fig. 3), with the pitch angle fluctuating no more than 10° over a stride (Table 2). The trunk is also not moving much from side to side. The maximum angular excursion of the trunk with vertical in the frontal plane (tilt angle) is 5° on average (Table 2). Note in the stick figure representation (see Fig. 3) that the forelimb is also held relatively steady (upper limb movements not quantified).

The hip is never fully extended; the average hip angle throughout a stride is 109° (Table 2), and maximum extension is about 130° at LO (Fig. 4B). The knee is flexed throughout stance, and even more so during the swing phase (Fig. 4C) to allow the long foot that is plantarflexed ("hanging down"), rather than dorsiflexed, to clear the ground (Figs. 3 and 4D). The minimum knee angle during swing is 55° (Table 2). The knee is moderately flexed at touchdown at an angle of 141°. The angle drops to 97° at midsupport, resulting in a yield angle of 44°. The knee stays flexed throughout the second half of stance, and at toe-off it is angled at 85° (Table 2). In other words, the knee yields early in stance, but never "recoils." Knee flexion late in stance is associated with lifting off the long foot (see Fig. 3). Foot contact at touchdown is at the forefoot, with the foot angled against the substrate (horizontal) at 29° (Fig. 4E, Table 2); the ankle is subsequently dorsiflexed, but the heel never contacts the ground during stance. The minimum angle of the foot with the ground is ~20° shortly after TD, and almost 70° at liftoff; i.e., liftoff is at the forefoot (Fig. 4E). The hind limbs move at moderate angles to sagittal planes. The average thigh abduction angle is 7° (Table 2). Maximum abduction occurs at the beginning of the swing phase, when the limb is swung forward and out (not shown).

The changes in hind limb joint angles over a stride result in fluctuations in height of the hip by about 2 cm (Figs. 3 and 4F, Table 2), with two oscillations per stride. The two minima in hip height occur around midsupport during stance and early in the swing phase, presumably at contralateral midsupport.

Angular excursions and stride length

Capuchins walk bipedally at a stride length of half a meter on average (Table 2). The hind limb is more
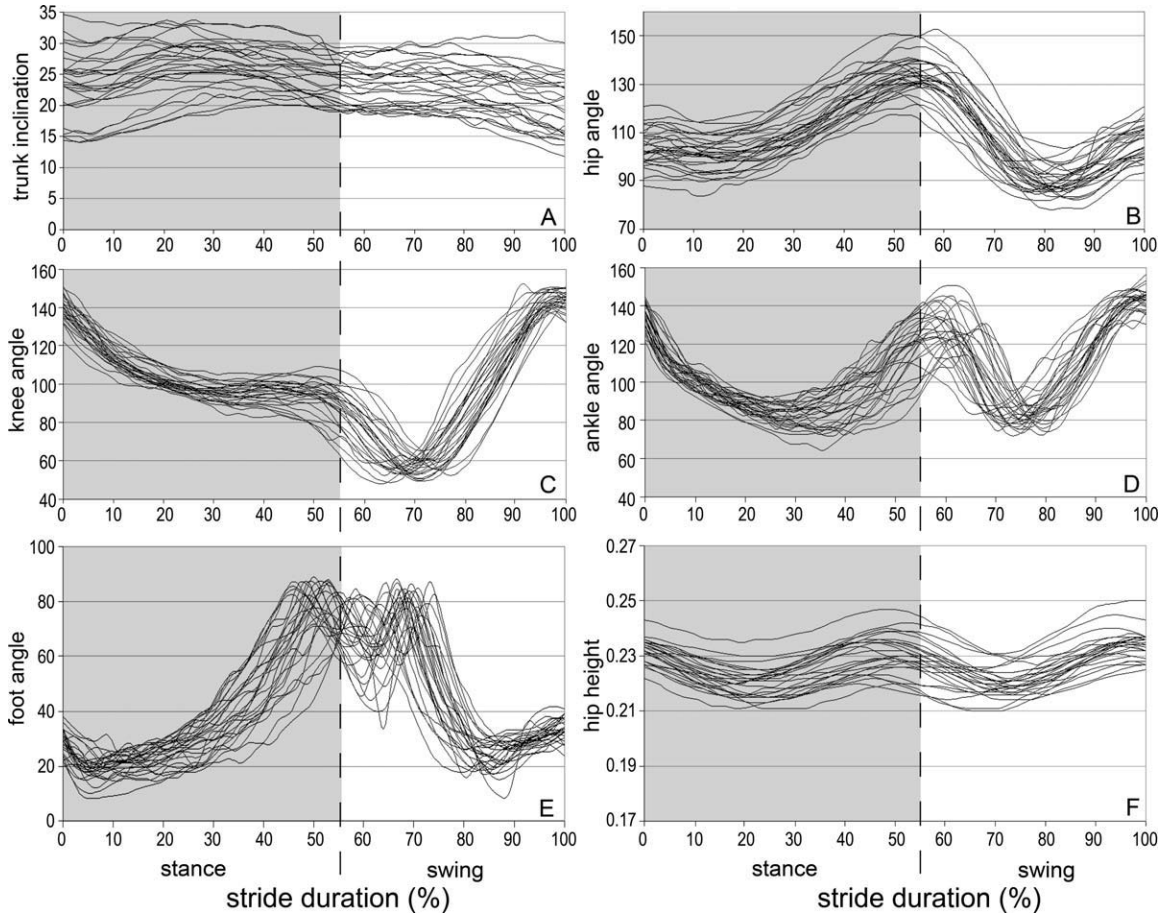
Fig. 4. Positional changes of landmarks, segments and joint angles. These graphs depict superimposed positional data of 30 complete strides, plotted on %stride duration. The stance phase (at an average of 55% of stride duration) is shown in gray. A: Trunk inclination with vertical. B: Hip angle. C: Knee angle. D: Ankle angle. E: Angle of the foot with the ground. F: Hip height. Angles are in degrees, hip height in meters.

TABLE 2. Descriptive statistics of gait variables

Variable	n	Mean	stdev	Min–max[a]
Average trunk pitch inclination stride (°)	30	23	4	17–27
Change in trunk pitch inclination stride (sway) (°)	30	10	4	4–18
Max trunk tilt excursion (sway) (°)	27	5	2	2–9
Average thigh abduction angle (°)	30	7	2	0–19
Average hip angle stride (°)	30	109	6	88–134
Average knee angle stride (°)	30	94	5	55–145
Knee angle at TD (°)	30	141	6	130–151
Knee angle at MSUP (°)	30	97	6	82–112
Knee angle at LO (°)	30	85	7	70–100
Knee yield TD—MSUP (°)	30	44	8	24–60
Average ankle angle stride (°)	30	105	4	77–146
Ankle angle at TD (°)	30	133	7	116–145
Ankle angle at LO (°)	30	126	10	107–142
Foot angle at TD (°)	30	29	4	20–38
Foot angle at LO (°)	30	69	9	43–87
Hip angular excursion (°)	30	28	7	18–44
HL excursion (°)	30	63	5	48–73
HL protraction at TD (°)	30	38	2	33–43
HL retraction at LO (°)	30	25	5	13–34
Hip height at MSUP (m)	30	0.22	0.01	0.20–0.24
Stride length (m)	30	0.54	0.05	0.47–0.67
Stride frequency (Hz)	30	1.71	0.16	1.22–1.94
Duty factor	30	0.55	0.05	0.44–0.65
Average speed (m s^{-1})	30	1.00	0.14	0.75–1.28
Froude number	30	0.47	0.14	0.25–0.82

[a] Minima and maxima of variables calculated over a time interval (stride) were extracted for each stride and averaged across all strides; for angles at defined events (e.g., TD) and the last six variables the ranges of the means are provided.

TABLE 3. Regressions on speed

	R^2	P-value	Constant	Coefficient
Stride length	0.49	0.001	0.30	0.24
Stride frequency	0.52	0.001	0.88	0.83
Duty factor	0.07	0.161		
Hip angular excursion	0.01	0.541		
Limb protraction	0.01	0.847		
Limb retraction	0.08	0.118		
Knee angle at TD	0.24	0.006	122	19.35
Knee angle at LO	0.05	0.234		

protracted at touchdown than retracted at lift off. The average protraction angle (hip to MT5) is 38°, whereas the average retraction angle is 25° (Table 2). Throughout 70% of stride duration, the limb is in a protracted position (not shown). Hip excursion angles are small in comparison to overall limb excursions, only 28° on average (Table 2), indicating that knee and ankle are major contributors to overall limb excursions. In fact, the thigh is never in a retracted position (see Fig. 3).

Temporal gait parameters

The voluntary bipedal walking speed of the capuchins is 1 m s^{-1} on average, with a narrow speed range (Table 2). The double-support phase is short, with duty factors of only 0.55 on average. The range of duty factors includes values below 0.5, indicating that some of the strides have a short aerial phase. The average Froude number, calculated with functional hip height at midstance, is 0.47 (Table 2).

Relationships with speed

Speed modulation is accomplished by changes in stride length as well as stride frequency. Both variables are significantly, albeit not highly, correlated with speed (Table 3). Strides become longer with increasing speed, and the frequency increases (see Fig. 5). A multiple regression with stride length and stride frequency as independent variables reveals that, in combination, these two variables explain about 3/4 of the variation in speed ($R^2 = 0.74$). Semipartial correlations of 0.47 for stride length and 0.50 for stride frequency are similar and indicate that both variables are equally important contributors to speed modulation. Only one of the postural variables tested was found to be significantly correlated with speed. The knee angle at TD is significantly and positively correlated with speed ($P = 0.006$, Table 3), indicating that the greater stride length at higher speeds is at least in part due to a more extended knee at touchdown. Note that the speed range was narrow, and this impedes identification of potential correlations. Visual inspection of postural variables plotted on speed revealed that none of them changes abruptly throughout the range of speeds; such a change would be indicative of a change in gait.

Comparison with capuchin quadrupedal gaits

Comparative data on capuchin quadrupedalism are available for knee angles, hind limb angular excursions, and temporal gait parameters. They have been collected for two different male individuals of comparable body size and are restricted to symmetrical gaits, with diagonal and lateral sequence strides pooled (Wallace and
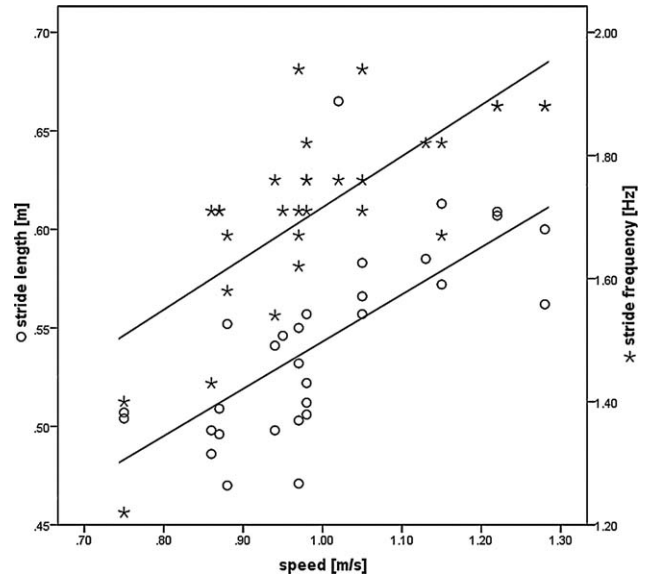

Fig. 5. Scatterplot of stride length (left axis, circles) and stride frequency (right axis, stars) on speed. Both variables increase and explain about [3/4] of speed modulation.

Demes, 2008; Carlson and Demes, 2010; Larson and Demes, 2011). The average speed for symmetrical quadrupedal gaits is over twice that in bipedalism (1.0 m s^{-1} BP vs. 2.0 and 2.5 m s^{-1} QP in two different studies: Wallace and Demes, 2008; Carlson and Demes, 2010). These are preferred speeds that the animals offer voluntarily for food rewards. Stride frequency is only slightly lower in bipedalism (1.7 Hz BP vs. 1.8 Hz QP; calculated for dataset in Wallace and Demes, 2008), so the major contributor to the greater speed in quadrupedalism must be greater stride length (no direct comparative data for QP stride length). At touchdown, the knee is more extended during quadrupedalism (151° QP vs. 141° BP). Like in bipedalism, the knee collapses into flexion during the first half of support (knee angle at midsupport: 109° QP vs. 97° BP), but unlike in bipedalism, it extends prior to liftoff (131° QP vs. 85° BP). This is probably related to the greater retraction angle in quadrupedalism. While hind limb protraction is greater than retraction in bipedalism, the opposite is the case for quadrupedalism (HL protraction 38° BP vs. 34° QP; HL retraction: 24° BP vs. 27° QP). The hind limb duty factor for quadrupedalism is lower than for bipedalism (~0.40 QP vs. 0.55 BP), and this is most likely related to the faster speed in quadrupedal progression.

DISCUSSION

Capuchin monkeys are adept bipeds in an experimental setting as well as in the wild. Bipedal postures and gaits of wild capuchin monkeys are often associated with terrestriality, food transport and manipulation, and tool use. They have been reported frequently for tufted capuchins (which include *C. apella*) in savannah-like environments, but not for populations inhabiting the South American rainforest (Fragaszy et al., 2004; Ottoni and Izar, 2008). These behaviors seem to open up a more terrestrial niche for an arboreal monkey, and allow it to access nutrition-rich, embedded foods (Ottoni and Izar, 2008).

Unlike humans, capuchin monkeys do not adopt a striding walk, but use a BHBK gait like other nonhuman primates. If hip height is taken as an indicator of center of mass (CoM) position, the CoM drops during the support phase whereas it rises in human walking as the body vaults over an extended hind limb (Cavagna and Margaria, 1966; Cavagna et al., 1977). Foot kinematics is also distinctly different from that of human bipedalism in that it lacks the dorsiflexion during swing phase that allows ground clearance without much flexion at the hip and ankle, as well as a heel strike at touchdown. In that respect capuchin bipedalism resembles human infant bipedalism that also lacks a heel strike (Hallemans et al., 2005). While human infants swing their limbs out to accomplish ground clearance, capuchins adopt a "high-stepping" gait. Capuchin bipedalism also lacks powerful plantarflexion at the end of stance and the foot is lifted off rather than pushes off—again more like in immature human gait (Hallemans et al., 2005).

The low duty factors suggest that the bipedal gait of capuchins is a running gait. If defined kinematically (Hildebrand, 1985; Reilly and Biknevicius, 2003) by the lack of a double support phase, the numerous steps with a duty factor below 0.5 are runs. Preliminary substrate reaction force data suggest that this gait also fulfills the dynamic criteria of a running gait with potential and kinetic energy fluctuating in phase (Demes and O'Neill, 2009, in preparation). The fluctuations in height of the hip (Fig. 4F) are unlike those in human walking (Alexander, 1992). The hip drop during stance is incompatible with pendulum-like movement of the CoM. If capuchin gait parameters are entered into the "compass gait" model by Usherwood et al. (2008), the bipedal gait of the capuchins falls near or on the outer boundaries of passive vaulting gaits that characterize humans and some bipedal birds at lower speeds. Calculated with average hind limb length at midstance and throughout the entire ranges of relative speeds (Froude "speeds": 0.50–0.91) and step angles (1/2 angular excursions: 24°–36.5°), the capuchin gait groups with bird gaits that are characterized by low pendulum energy recovery rates.

In human running, lowering the CoM during stance loads up the leg spring for elastic recoil (Cavagna and Kaneko, 1977; Cavagna et al., 1977). The knee joint kinematics in capuchin bipedalism is not suggestive of elastic mechanisms because the knee does not recoil in the second half of stance (Fig. 4C). However, the hip rises during the second half of stance, probably due to strong plantarflexion of the ankle, and such movements are compatible with elastic energy storage and release. Ultimately, though, kinetic and oxygen consumption data are needed to determine whether such mechanisms are at work.

The bipedal speed of the capuchin monkeys is equivalent to a fast walking speed of humans. At a Froude number of 0.47 (Table 2), the average for capuchin bipedalism, humans with a hip height of ~0.8 m would progress at a speed of 1.9 m s^{-1} or 6.8 km h^{-1}. This is very close to the speed of 2.0 m s^{-1} at which humans transition from a walk to a run (Hreljac, 1993). At a speed corresponding to the upper range of capuchin Froude numbers (0.82), humans would run at 2.5 m s^{-1}.

There is no evidence for a distinct gait transition in capuchin bipedalism. In many animals and humans there is transition from a walking gait to various bouncing gaits with an aerial phase at Froude numbers of around 0.5 (Alexander, 1989; Kram et al., 1997). Froude numbers of the capuchins are on average very close to this value, and the range (0.25–0.82, Table 2) extends into speeds at which animals and humans use bouncing gaits. The speed that corresponds to a Froude number of 0.5 for an animal of capuchin functional hip height is 1.04 m s^{-1}—which is within the speed range of the two capuchin monkeys (0.75–1.28 m s^{-1}; Table 2). A lack of a distinct gait transition is also found in avian bipeds that have a smooth transition from slower walks to faster runs (Gatesy and Biewener, 1991). Despite the lack of an abrupt gait transition, avian running is nevertheless a bouncing gait (Rubenson et al., 2004) and in this respect resembles human running (Cavagna and Kaneko, 1974; Cavagna et al., 1977). Bipedal gibbons also transition smoothly to a gait with in-phase fluctuations of the COM and the potential for elastic energy storage at higher speeds (Vereecke et al., 2006b). Duty factors also occasionally drop just below 0.5. It remains to be explored whether bipedal primates at faster speeds use bouncing mechanics with cyclical storage and release of energy by elastic elements.

Comparison with other nonhuman primate bipedal gaits

Although detailed comparisons are hampered by the lack of standardized data protocols, it is quite obvious that the general pattern of nonhuman primate bipedal gait is grossly similar across species studied so far. The following comparisons are mainly based on Hirasaki et al., (2004) and Ogihara et al., (2010) (Japanese macaques), Berrillon et al., (2010) (olive baboons), Vereecke et al. (2006a) (gibbons), Aerts et al., (2000), and D'Août et al. (2002) (bonobos), and Kimura and Yaguramaki (2009) (chimpanzees[2]). Additional studies add qualitative support to the trends described here (e.g., Prost, 1967; Jenkins, 1979; Okada, 1985).

Nonhuman primates all adopt a BHBK gait when walking bipedally, even after many years of training (Japanese Sarumawashi macaques; Hirasaki et al., 2004). Knee and ankle kinematics are similar in their general patterns across species (Table 4). Knee flexion during swing is usually pronounced to accommodate a plantarflexed ankle position. Only the apes seem to have a somewhat more dorsiflexed foot during swing phase (D'Août et al., 2002; Vereecke et al., 2006a). The smallest dorsiflexion angle in capuchins is over 20° larger than that of gibbons and bonobos (77° vs. 54.7° and 52.1°; Table 4). Not surprisingly, only bonobos (and maybe chimpanzees) start the stance phase with a heelstrike, whereas the monkeys and the lesser ape make initial contact with more distal elements of their feet (Okada, 1985; Schmitt and Larson, 1995; D'Août et al., 2001; Vereecke et al., 2005; Barden et al., 2010). The maximum degree of hip extension in the capuchins (143°) exceeds that of bonobos (137.0°; D'Août et al., 2002), but is less than that of gibbons (151.4°; Vereecke et al., 2006a). The higher degree of hip extension accomplished by gibbons is probably related to a very upright trunk posture. The average forward pitch in gibbons is only 15.32°, whereas it is 23° in the capuchins. Maximum knee extension of the capuchins (145°) is comparable to that of bipedal apes (bonobos: 143.9°, gibbons: 131.4°; Vereecke et al., 2006a), but the minimum knee angle of capuchins is smaller than that of both apes.

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[2]Data were extracted for adult chimpanzees only.

TABLE 4. Comparative data on nonhuman primate bipedalism

	Capuchin[a]	Macaque[b,c]	Baboon[d]	Gibbon[e]	Chimpanzee[f,g]	Bonobo[h,i]
Duty factor	0.55 ± 0.05; 0.44–0.65	0.60–0.70	0.69 ± 0.30	0.60 ± 0.07	0.75	0.64 ± 0.05; 0.55–0.75
Dimensionless "speed" (= √ Froude number)	0.68 ± 0.1; 0.50–0.91	0.44–0.78	0.64 ± 0.18	<0.7–>1.4	0.21 ± 0.03	0.67 ± 0.22; 0.23–1.04
Absolute speed (m s⁻¹)	1.00 ± 0.14; 0.75–1.28	0.83–1.39	0.79 ± 0.19	0.71–3.53	0.94	1.42 ± 0.50; 0.57–2.39
Stride frequency (Hz)	1.71 ± 0.16; 1.22–1.94	~1.2–2.4[j]	1.52 ± 0.32	1.66 ± 0.33		1.57 ± 0.38; 0.87–2.19
Average trunk pitch inclination (°)	23 ± 4; 14–30	~20[j]		15.32 ± 5.88	34.3 ± 4.5	14.7–28.3
Average hip angle stride (°)	109 ± 6; 88–143	~100[j]		100.8–151.4	max = 118.4	95.6–137.0
Average knee angle stride (°)	94 ± 5; 55–145	~90[j]		72.6–143.9		62.3–131.4
Average ankle angle stride (°)	105 ± 4; 77–146	~100[j]		54.7–119.2		52.1–88.1
HL angular excursion (°)	63 ± 5; 48–73			75.4	~65[k]	
HL protraction (°)	38 ± 2; 33–43			48.2 ± 4.0		
HL retraction (°)	24 ± 5; 18–39			27.2 ± 16.7		

Cells contain mean ± 1 standard deviation and ranges as available Data from:
a This study.
b,c Hirasaki et al., 2004 (untrained macaques) and Ogihara et al., 2010.
d Berillon et al., 2010.
e Vereecke et al., 2006a,b.
f,g Reynolds, 1987 and Kimura and Yaguramaki, 2009 (adult chimpanzees only).
h,i Aerts et al., 2000 and D'Août et al., 2002.
j Estimated from Figs. 2 and 3 in Hirasaki et al., 2004.
k Estimated from Fig. 6 in Reynolds, 1987.

In comparison to chimpanzees and bonobos, as well as two cercopithecine monkeys, capuchins progress bipedally with very low duty factors (Table 4). Only gibbons approach the capuchin condition. Their duty factors may at faster speeds drop just below 0.5 (Vereecke et al., 2006a), whereas those of the capuchins drop to 0.44. Duty factors for the other nonhuman primates are well above 0.5. Some of this variation in duty factors is almost certainly related to speed. The chimpanzees in particular walked slowly (Kimura and Yaguramaki, 2009). However, as the primates chose their speeds, the wide range of duty factors also reflects different movement strategies. Only gibbons and capuchins bipedalism enclose runs, but both lack the long aerial phases that characterize human running.

In comparison to chimpanzees and bonobos, capuchins walk bipedally with a trunk that is more upright. The average forward inclination (pitch) of the trunk in adult chimpanzees is 34.3° (Kimura and Yaguramaki, 2009) as compared to 23° in the capuchin monkeys (Table 4), that of bonobos ranges from 14.7° to 28.1° with vertical (D'Août et al., 2002). Spider monkeys seem to have an even more upright trunk when walking bipedally (Okada, 1985).

The bipedal gaits of most nonhuman primates are slow in comparison to their quadrupedal gaits, even if compared only in the range of symmetrical gaits (i.e., excluding gallops). The voluntary speed the capuchin monkeys offer in bipedal progression is only half that of their voluntary speed in quadrupedal progression (this study, Wallace and Demes, 2008; Carlson and Demes, 2010). The difference in speed is less pronounced in baboons (0.64 m s⁻¹ BP vs. 0.79 m s⁻¹ QP; Berrillon et al., 2010). Interestingly, the bonobos in the Aerts et al. (2000) sample walked slightly faster on two legs than on four (1.42 m s⁻¹ BP vs. 1.25 m s⁻¹ QP), even though their hips undergo smaller excursions in bipedalism and their strides are shorter (D'Aout et al., 2002; see below). The higher speed is due to the greater frequency in bipedal progression (Aerts et al., 2000). The chimpanzees in Reynolds' study, on the other hand are slower when walking bipedally (Reynolds, 1987). Overall, speed in BHBK bipedalism seems to be limited, and even though capuchins and to a certain extant gibbons use some kind of a bipedal run, no species offers a human-like run with long aerial phases. Adopting a bipedal gait as a quadrupedal primate is clearly not motivated by the need for fast progression, and evidence from labyrinthine morphology does not support rapid progression in the earliest hominids either (Spoor et al., 1994).

Although direct comparisons of hind limb excursions in bipedalism and quadrupedalism can only be made for a very limited number of species (capuchins: this study; chimpanzees and spider monkeys: Reynolds, 1987), it can be safely assumed that nonhuman primate bipedalism in general is characterized by small hind limb excursions. Hip excursion angles are available for additional species, and they also are clearly more limited in bipedalism than in quadrupedalism. Hip excursion angles in baboon bipedalism are almost 20° lower than in quadrupedalism (Berrillon et al., 2010), bonobos walk with about 12° smaller hip excursions when bipedal (D'Aout et al., 2002), and common chimpanzees with more than 20° smaller excursion (Reynolds, 1987). A spider monkey also reduced its hip excursion by more than 20° in bipedal walking as compared to quadrupedal walking (Reynolds, 1987). The shorter strides in bipedal as com-

pared to quadrupedal gaits are additional evidence for restricted hind limb excursions in nonhuman primate bipedal gaits and have been documented for spider monkeys, baboons, chimpanzees and bonobos (Reynolds, 1987; Aerts et al., 2000; Berrillon et al., 2010).

Quadrupedally, primates walk with large excursion angles in comparison to other mammals (Larson et al., 2001). Restricted limb excursions during bipedalism may be related to the need to balance the CoM over the small support base offered by a single foot in contact with the ground. Jenkins (1972), Vereecke et al. (2006a), and this study additionally demonstrate that small hind limb retraction angles in capuchin, gibbon, and chimpanzee bipedalism are primarily responsible for reduced hind limb excursions (Table 4). This is in contrast to the particularly large retraction angles during quadrupedalism (Larson et al., 2001). Vereecke et al. (2006a) relate the emphasis on protraction to the need to support and balance a CoM that is located anteriorly due to the forward-leaning trunk. The lack of retraction may also be related to hip extensors working in a suboptimal range of their length-tension curve due to the orthograde trunk. Neither the hind limb retraction angle nor overall hind limb excursion increase with increasing speed (Table 4).

While stride length and angular excursions are limited in bipedalism, the stride frequency of primate bipedal gaits is higher than that of quadrupedal walking and running gaits. This has been shown here not only for the capuchins, but also for bonobos (Aerts et al., 2000) and baboons (Berrillon et al., 2010), and suggests that it is the preferred way of producing at least moderately fast walking speeds. It also seems to play an important role in increasing speed of progression. The slopes of regression lines of frequency over speed are higher in capuchin bipedal gait (0.83, Table 3) than quadrupedal gait (0.35 based on the Wallace and Demes, 2008, data set). Interestingly, bipedal macaques that have been trained to walk bipedally over many years increase stride length with speed more than less experienced animals, whereas the less experienced macaques increase stride frequency more than the "professional" bipeds (Hirasaki et al., 2004). Speed increases primarily achieved by increased stride length is characteristic for habitual bipeds, human and avian (Nilsson et al., 1985; Gatesy and Biewener, 1991), but also for bipedal gibbons (Vereecke et al., 2006a) that have a very upright trunk and may therefore be able to balance their CoM throughout a greater range of excursion angles.

The variation in bipedal gaits in this sample of primates is not easily explained by predominant locomotor mode, predominant substrate use, body size or phylogeny. The sample discussed here includes a terrestrial monkey (baboon) that doesn't seem to differ in its bipedal gait from arboreal monkeys (capuchin, macaque), a suspensory, orthograde species (gibbon) that shares a lot of gait characteristics with the monkeys, in particular the capuchins, and great apes that do not stand out clearly from the lesser ape or the monkeys, except for having a more dorsiflexed ankle. The ubiquitous use of BHBK gait for all species strongly points to a mechanical constraint that prevents extended hind limb joint postures, and this is most likely the lack of an abductor mechanism at the hip (Stern, 1971; Ogihara et al., 2007). The ease with which all these nonhuman primates can be coaxed or trained to walk bipedally suggests that the transition to a BHBK bipedal gait is possible from a variety of primate postural and locomotor modalities.

In conclusion, capuchins and other quadrupedal and suspensory nonhuman primates are not striding bipedal walkers like humans. Capuchins progress bipedally with bent hips and bent knees, with a knee that collapses into flexion during early stance like in human running, with a high stepping gait, with fluctuations in trunk height that rule out pendulum-like gait mechanics, with a gait that resembles running more than walking and speeds that extend into the running range. The conventional view is that an incipient bipedal gait is a walking gait and that early hominids were bipedal walkers, rather than runners (e.g., Crompton et al., 1998; Bramble and Lieberman, 2004; Lieberman et al., 2006; Sockol et al., 2007). Capuchins demonstrate that bipedal running with short aerial phases is feasible for a primate quadruped, and, by analogy, such a gait should not be excluded from consideration as an incipient gait for the earliest hominin bipeds. The constraint in limb excursions, particularly limb retraction, that seems to be imposed by keeping a not completely orthograde trunk over a supporting foot limits speed modulation through stride length increases—one of two mechanisms by which humans increase walking speed (Nilsson et al., 1985). Instead, frequency increases and double-limb support decreases, bringing duty factors below 0.5 and turning the gait into a run. While the bipedal gait of capuchin monkeys is constrained by their quadrupedal anatomy and is comparatively slow and probably energetically costly, it allows them to access food resources that require bimanual transport and to use tools, and it opens up a savannah-like niche.

LITERATURE CITED

Aerts P, Van Damme R, Van Elsacker L, Duchene V. 2000. Spatio-temporal gait characteristics of the hind-limb cycles during voluntary bipedal and quadrupedal walking in bonobos (*Pan paniscus*). Am J Phys Anthropol 111:503–517.

Alexander RMCN. 1989. Optimization and gaits in the locomotion of vertebrates. Physiol Rev 69:1199–1227.

Alexander RMCN. 1992. The human machine. New York: Columbia University Press.

Barden MB, Wunderlich RE, Demes B. 2010. Plantar pressure during bipedalism and quadrupedalism in *Cebus*. Am J Phys Anthropol Suppl 50:61.

Berillon G, Daver G, D'Août K, Nicolas G, de la Villetanet B, Multon F, Digrandi G, Dubreuil G. 2010. Bipedal versus quadrupedal hind limb and foot kinematics in a captive sample of *Papio anubis*: setup and preliminary results. Int J Primatol 31:159–180.

Boinski S, Quatrone RP, Swartz H. 2000. Substrate and tool use by grown capuchins in Suriname: ecological contexts and cognitive bases. Am Anthropol 102:741–761.

Bramble DM, Lieberman DE. 2004. Endurance running and the evolution of *Homo*. Nature 424:345–352.

Carlson KJ, Demes B. 2010. Gait dynamics of *Cebus apella* during quadrupedalism on different substrates. Am J Phys Anthropol 142:273–286.

Carrier D. 1984. The energetic paradox of human running and hominid evolution. Curr Anthropol 25:483–495.

Cavagna GA, Heglund NC, Taylor CR. 1977. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am J Physiol 233:R243–R261.

Cavagna GA, Kaneko M. 1977. Mechanical work and efficiency in level walking and running. J Physiol 268:467–481.

Cavagna GA, Margaria A. 1966. Mechanics of walking. J Appl Physiol 21:271–278.

Crompton RH, Li Y, Wang W, Günther MM, Savage R. 1998. The mechanical effectiveness of erect and "bent-hip, bent-knee" bipedal walking in *Australopithecus afarensis*. J Hum Evol 35:55–74.

D'Août K, Aerts P, DeClerq D, De Meester K, Van Elsacker L. 2002. Segment and joint angles of hind limb during bipedal and quadrupedal walking of the bonobo (*Pan paniscus*). Am J Phys Anthropol 119:37–51.

D'Août K, Aerts P, DeClerq D, Schoonaert K, Vereecke EE, Van Elsacker L. 2001. Studying bonobo (*Pan paniscus*) locomotion using an integrated setup in a zoo environment: preliminary results. Primatologie 4:191–206.

Demes B, O'Neill M. 2009. Capuchin monkey bipedalism. Am J Phys Anthropol Suppl 48:117.

Fragaszy DM, Visalberghi E, Fedigan LM. 2004. The complete capuchin: the biology of the genus *Cebus*. Cambridge: Cambridge University Press.

Gatesy SM, Biewener AA. 1991. Bipedal locomotion: effects of speed, size and limb posture in birds and humans. J Zool Lond 224:127–147.

Groves CP. 2001. Primate taxonomy. Washington, DC: Smithsonian Institution Press.

Hallemans A, Aerts P, Otten B, DeDeyn PP, De Clercq D. 2005. Mechanical energy in toddler gait. J Exp Biol 207:2417–2431.

Hildebrand M. 1985. Walking and running. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, editors. Functional vertebrate morphology. Cambridge: Harvard University Press. p 38–57.

Hirasaki E, Ogihara N, Hamada Y, Kumakura H, Nakatsukasa M. 2004. Do highly trained monkeys walk like humans? A kinematic study of bipedal locomotion in bipedally trained Japanese macaques. J Hum Evol 46:739–750.

Hreljac A. 1993. Preferred and energetically optimal gait transition speeds in human locomotion. Med Sci Sports Exerc 25:1158–1162.

Jenkins FA Jr. 1972. Chimpanzee bipedalism: cineradiographic analysis and implications for the study of gait. Science 178:877–879.

Kimura T, Yaguramaki N. 2009. Development of bipedal walking in humans and chimpanzees: a comparative study. Folia Primatol 80:45–62.

Kram R, Domingo A, Ferris DP. 1997. Effect of reduced gravity on the preferred walk-run transition speed. J Exp Biol 200:821–826.

Larson SG, Demes B. 2011. Weight support distribution during quadrupedal walking in *Ateles* and *Cebus*. Am J Phys Anthropol. DOI: 10.1002/ajpa21460.

Larson SG, Schmitt D, Lemelin P, Hamrick M. 2001. Limb excursion during quadrupedal walking: how do primates compare to other mammals? J Zool Lond 255:353–365.

Lieberman DE, Raichlen DA, Pontzer H, Bramble DM, Cutright-Smith E. 2006. The human gluteus maximus and its role in running. J Exp Biol 209:2143–2155.

Liu Q, Simpson K, Izar P, Ottoni E, Visalberghi E, Fraganszy D. 2009. Kinematics and energetics of nut-cracking in wild capuchin monkeys (*Cebus libidinosus*) in Piauí, Brazil. Am J Phys Anthropol 138:210–220.

Nilsson J, Thorstensson A, Halbertsma J. 1985. Changes in leg movements and muscle activity with speed of locomotion and mode of progression in humans. Acta Physiol Scand 123:457–475.

Ogihara N, Hirasaki E, Kumakura H, Nakatsukasa M. 2007. Ground-reaction-force profiles of bipedal walking in bipedally trained Japanese monkeys. J Hum Evol 53:302–308.

Ogihara N, Makishima H, Nakatsukasa M. 2010. Three-dimensional musculoskeletal kinematics during bipedal locomotion in the Japanese macaque, reconstructed based on an anatomical model-matching method. J Hum Evol 58:252–261.

Okada M. 1985. Primate bipedal walking: comparative kinematics. In: Kono S, editor. Primate morphophysiology, locomotor analyses and human bipedalism. Tokyo: University of Tokyo Press. p 47–58.

Ottoni EB, Izar P. 2008. Capuchin monkey tool use: overview and implications. Evol Anthropol 17:171–178.

Polk JP. 2001. The influence of body size and body proportions on primate quadrupedal locomotion. Ph.D. Dissertation. Stony Brook University, Stony Brook, NY.

Prost JH. 1967. Bipedalism of man and gibbon compared using estimates of joint motion. Am J Phys Anthropol 26:135–148.

Reilly SM, Biknevicius AR. 2003. Integrating kinetic and kinematic approaches to the analysis of terrestrial locomotion. In: Bels VL, Gasc J-P, Casinos A, editors. Vertebrate biomechanics and evolution. Oxford: BIOS Scientific Publishers. p 243–265.

Reynolds TR. 1987. Stride length and its determinants in humans, early hominids, primates, and mammals. Am J Phys Anthropol 72:101–115.

Rubenson J, Heliams DB, Lloyd DG, Fournier PA. 2004. Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. Proc R Soc Lond B 271:1091–1099.

Schmitt D, Larson SG. 1995. Heel contact as a function of substrate type and speed in primates. Am J Phys Anthropol 96:39–50.

Sockol MD, Raichlen DA, Pontzer H. 2007. Chimpanzee locomotor energetics and the origin of human bipedalism. Proc Nat Acad Sci USA 134:12265–12269.

Spoor F, Wood B, Zonneveld F. 1994. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. Nature 369:645–648.

Stern JT Jr. 1971. Functional mycology of the hip and thigh of cebid monkeys and its implications of the evolution of erect posture. Bibliotheca Primatol 14:1–318.

Stern JT Jr. 1975. Before bipedality. Yearb Phys Anthropol 19:59–68.

Stern JT Jr., Susman RL. 1981. Electromyography of the gluteal muscles in *Hylobates*, *Pongo*, and *Pan*: implications for the evolution of hominid bipedality. Am J Phys Anthropol 55:153–166.

Usherwood JR, Szymanek KL, Daley MA. 2008. Compass gait mechanics account for top walking speeds in ducks and humans. J Exp Biol 211:3744–3749.

Vereecke EE, D'Août K, Aerts P. 2006a. Speed modulation in hylobatid bipedalism: a kinematic analysis. J Hum Evol 51:513–526.

Vereecke EE, D'Août K, Aerts P. 2006b. The dynamics of hylobatid bipedalism: evidence for an energy-saving mechanism? J Exp Biol 209:2829–2838.

Vereecke EE, D'Août K, Van Elsacker L, DeClerq D, Aerts P. 2005. Functional analysis of the gibbon foot during terrestrial bipedal walking: plantar pressure distributions and three-dimensional ground reaction forces. Am J Phys Anthropol 128:659–669.

Wallace IJ, Demes B. 2008. Symmetrical gaits of *Cebus apella*: implications for the functional significance of diagonal sequence gait in primates. J Hum Evol 54:783–794.

Wright KA. 2007. The relationship between locomotor behavior and limb morphology in brown (*Cebus apella*) and weeper (*Cebus olivaceus*) capuchins. Am J Primatol 69:736–756.

Youlatos D. 1998. Positional behavior of two sympatric guianan capuchins monkeys, the brown capuchin (*Cebus apella*) and the wedge-capped capuchin (*Cebus oliavceus*). Mammalia 62:351–365.