



Contents lists available at SciVerse ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Kinematics of bipedal locomotion while carrying a load in the arms in bearded capuchin monkeys (*Sapajus libidinosus*)

Marcos Duarte ^a, Jandy Hanna ^b, Evandro Sanches ^a, Qing Liu ^c, Dorothy Fragaszy ^{c,*}^a Biomedical Engineering Program, Federal University of ABC, Santo Andre, Brazil^b West Virginia School of Osteopathic Medicine, United States^c Department of Psychology, University of Georgia, Athens, GA 30602, United States

ARTICLE INFO

Article history:

Received 28 March 2011

Accepted 9 October 2012

Available online xxx

Keywords:

Locomotor evolution

Biomechanics

Ankle excursion

New World monkey

ABSTRACT

Understanding the selective pressures that drove the evolution of bipedalism in the human lineage may help inform researchers about the locomotor mode(s) of pre-hominin ancestors. Several selective pressures have been hypothesized, including the need to carry food, tools, or infants. Bearded capuchin monkeys are an excellent primate in which to examine the hypothesis that carrying supported the evolution of bipedalism because they are morphologically generalized and in some ways similar to Miocene hominoids, from which the transitional biped evolved. Additionally, bearded capuchins regularly move bipedally while carrying tools that represent a significant portion of their body mass. Here, we examined the spatio-temporal and kinematic gait parameters in a wild setting of *Sapajus libidinosus* moving bipedally while carrying a stone tool, as well as unloaded bipedal tufted capuchins in the lab. Results indicate that compared with humans, the monkeys move with a more bent-hip, bent-knee posture during both types of bipedalism, as expected. Few differences exist in spatio-temporal or kinematic parameters within species across load-carrying and unloaded bipedalism. The capuchin ankle, however, during load-carrying goes through a greater range of motion in relatively less time than both humans and unloaded capuchins. Data from this study provide the first quantitative data on bipedalism during load-carrying by wild primates in a natural setting. As such, they are a useful comparative reference for understanding bipedalism, particularly during load-carrying.

© 2012 Elsevier Ltd. All rights reserved.

Introduction

Extended posture and habitual bipedal locomotion are key traits in humans and their appearance in ancestral hominins is the focus of much interest and debate. One of these debates is how the earliest obligate biped walked. This particular debate is often fueled by discussions about the locomotor repertoire of the last common ancestor (LCA) of hominins (e.g., arboreal biped [Thorpe et al., 2007; Crompton et al., 2008], terrestrial knuckle-walking [Richmond et al., 2001], and climbing [Fleagle et al., 1981; Lovejoy et al., 2009]). It is well accepted that understanding hominin origins is bolstered by a deeper understanding of the Miocene hominoids (Benefit and McCrossin, 1995; Begun et al., 1997; Nakatsukasa, 2004; Andrews and Harrison, 2005; Crompton et al., 2008). Early hominoids were generalized arboreal quadrupeds (Begun, 2007), and their morphological flexibility permitted the evolution of several different types of locomotion seen in later

hominoids including knuckle-walking, suspensory locomotion, bipedalism, etc. (Harrison, 1993; Rose, 1993; Begun et al., 1997; Ward, 1997). Such hominoids were the foundation for the transition to obligate bipedalism.

In order to understand the transition to obligate bipedalism that some of these hominoids eventually made, it is worth understanding the primitive condition of quadrupedal primates moving bipedally. There are some data about facultative bipedalism in quadrupedal primates currently available. Mainly, although the degree of joint flexion varies (see Crompton et al., 2010 for review), we know that all extant non-human primates that exhibit facultative bipedalism do so with greater bent-hip–bent-knee (hereafter BHBK) kinematics than humans (although see Thorpe et al., 2007). All of the quantitative data on this issue reflects analyses from individuals observed in laboratory settings but descriptions of individuals in field settings appear to corroborate this general picture as well. Very few quantitative data are available, however, about the manner in which primates move bipedally in the wild. Such data are important for understanding the environment in which bipedalism evolved (Schmitt, 2003; Crompton et al., 2008; Berillon et al., 2011; Carvalho et al., 2012).

* Corresponding author.

E-mail addresses: Dfragaszy@gmail.com, doree@uga.edu (D. Fragaszy).

Bearded capuchin monkeys (*Sapajus libidinosus*, formerly *Cebus libidinosus*¹) provide a unique opportunity to examine the use of regular, though not obligate, bipedal locomotion during transport of objects by a non-human primate in its natural setting. Bearded capuchin monkeys at Fazenda Boa Vista (Brazil) locomote bipedally for equivalent proportions of locomotor samples (1.2% of locomotor samples for adults and juveniles [Biondi, 2010]) as reported by Doran (1992, 1993, 1997) for adult African apes (1.5%, averaged across gorillas, bonobos, and chimpanzees, that did not differ substantively on this measure). Biondi (2010) reports that bearded capuchin monkeys locomoted bipedally primarily (but not exclusively) during foraging contexts, and while carrying something, both while on the ground and in trees. The population of bearded capuchin monkeys studied by Biondi is well-known to use stones as hammers to crack open nuts (Fragaszy et al., 2004). The bearded capuchin monkeys occasionally transport hammer stones (weighing on average 1 kg; adult monkeys weigh 2–4.5 kg) to anvils, carrying these objects in both hands and striding bipedally several meters on the ground, or occasionally along a broad limb (Visalberghi et al., 2009; Biondi, 2010; Fragaszy et al., 2010). Among extant wild primates, to our knowledge authors report observing only bearded capuchin monkeys carrying tools bipedally (although wild chimpanzees have been observed carrying food items bipedally [Carvalho et al., 2012] and objects used in display [Goodall, 1971]).

In sum, quantitative data on the kinematics of BHBK bipedalism by wild primates is limited, and kinematics during carrying of a load by wild primates are not quantified at all (although Watson et al., 2009 provide data for captive apes). Thus, in this study, we describe spatio-temporal and kinematic characteristics of wild capuchins' bipedal locomotion during transport of heavy stones and compare these data with data recently provided by Demes (2011) on tufted capuchin monkeys (*Sapajus (Cebus) apella* spp.²) walking bipedally in a laboratory setting, unloaded. Although wild bearded capuchin monkeys do walk bipedally while carrying light loads or nothing at all, they do so infrequently and unpredictably, and we could not acquire a suitable sample of episodes for analysis of unloaded bipedal walking. This remains a goal for the future.

Materials and methods

Subjects

Six members of one wild group of bearded capuchins voluntarily participated in this study (see Table 1). The monkeys are habituated to human observers. The study site is located at Fazenda Boa Vista and adjacent lands (hereafter, FBV) in the southern Parnaíba Basin (9°S, 45°W) in Piauí, Brazil. Boa Vista is a flat open woodland

¹ Recent molecular analysis has revealed that capuchin monkeys, formerly identified as the single genus *Cebus*, are two genera, with the robust (tufted) forms (including *libidinosus*, *xanthosternos*, and several other species) now recognized as the genus *Sapajus*, and the gracile forms retained as the genus *Cebus* (Lynch Alfaro et al., 2012). The nomenclature for *Sapajus* is registered with ZooBank (urn:lsid:zoobank.org:act:3AAFD645-6B09-4C88-B243-652316B55918). To date, tool use has been observed in some species of wild *Sapajus*, but no species of wild *Cebus*.

² Because colonies of tufted capuchin monkeys held in the USA are derived from animals imported from the wild prior to the elevation of subspecies of *Cebus apella* to true species, and more recently, to species in genus *Sapajus*, distinct from *Cebus*, monkeys in these colonies are now recognized as unknown combinations of species and hybrids of the genus *Sapajus*, rather than as *C. apella*. We designate these individuals as *Sapajus (Cebus) apella* spp. in this report, for clarity and for continuity with the published names, as the compounding name changes in these taxa can be confusing. With particular reference to this report, the changes in taxonomy mean that we cannot specify the taxonomic relation at the species level of the monkeys studied by Demes (2011) to the monkeys studied in this report. They are from the same genus, however (tufted capuchins, *Sapajus*).

Table 1

Characteristics of the subjects (*Sapajus (Cebus) libidinosus*).

Subject number	Sex	Mass (kg)	Leg length (m)	
			Knee to heel	Hip height
1	M	4.2	0.11	0.22
2	M	3.5	0.13	0.24
3	M	3.6	0.12	0.27
4	F	2.1	0.11	0.20
5	M	1.8	0.11	0.21
6	M	3.0	0.12	0.26

For sake of comparison with the literature, the leg lengths are presented as the distance from knee to heel and the hip height at midstance.

(altitude 420 m asl) punctuated by sandstone ridges, pinnacles, and mesas rising steeply to 20–100 m. See Madden et al. (2007) and Visalberghi et al. (2007) for further details of the region.

Monkeys crack nuts throughout the year (Spagnoletti et al., 2011; Verderane et al., in review). They transport the nuts to anvil sites scattered across their home range (Visalberghi et al., 2007). When an anvil site lacks a stone, or when they are displaced from an anvil site, the monkeys routinely carry a hammer stone with them (Visalberghi et al., 2009; Fragaszy et al., 2010) and new hammer stones appear at anvil sites at a low rate (Visalberghi and Fragaszy, in press).

Filming took place in May 2008, during the early dry season. We prepared an area the monkeys were known to frequent so that we could film at appropriate angles and distances as the monkeys carried a stone placed at a predetermined start point to an anvil several meters away. The course the monkeys traveled was flat, horizontal (imperceptibly sloping) and free of vegetation and other obstructions (Fig. 1). The substrate was compacted well-drained sandy soil, free of stones, roots, or other surface irregularities. Other hammer stones present in the immediate area were collected for the duration of filming each day and returned to their original locations at the end of filming. We presented palm nuts (*Orbignya* spp. and *Astrocaryum* spp.) collected locally for the monkeys to carry to the anvil and subsequently crack open and consume. The monkeys routinely crack nuts of these species and several others (Spagnoletti et al., 2011; Verderane et al., in review).

Procedure

Two video cameras (Canon GL2) placed at oblique angles (approximately 90° between cameras) to the line of travel were employed to obtain a three-dimensional reconstruction of the movement. A 1 m cubic calibration object placed at two points in the sagittal plane along the line of travel was filmed prior to and following each session. After calibration, one experimenter placed the hammer stone (930 g, ovoid in shape, quartzite) and a single nut at a fixed start point 4 m from the anvil. The stone was familiar to the monkeys, as they had used it at this site for several years. We placed the nut together with the stone, not at the anvil, because the monkeys prefer to carry both objects together. If the nut is placed on the anvil, they collect it, then collect the stone, and transport the set to the anvil. Each capuchin monkey was filmed transporting the stone and the nut along the middle 2 m of the 4 m straight-line course to the anvil. In this manner, we captured only transport (not pick-up or placement) of the stone and nut. The video was captured at 30 frames per second and each frame was deinterlaced to produce 60 fields per second.

We coded five transports for each monkey. For each transport, two consecutive strides were analyzed, producing ten strides per subject in the data set. A stride is defined as the events between two consecutive initial contacts of the right foot with the ground.



Figure 1. View of the experimental area across which the monkeys transported a stone and a nut on their way to an anvil (off view to the right). The substrate was level, nearly horizontal, compact sandy soil, raked free of vegetation, roots, etc. The flags on the left marked the position where the stone and nut were placed on the ground. The moderately sheer fabric panel behind the monkey was hung on a horizontal pole. The panel provided a homogeneous visual background, improving visibility of the monkey in video playback. The monkeys habituated quickly to these features and carried the stone and nut in a direct line from the pick-up point to the anvil. Photo by Rebecca Greenberg.

The APAS software (Ariel Inc., Trabuco Canyon, CA) was used to synchronize the images and digitize manually ten anatomical landmarks on the monkey from each field of the video (60 fields/s) using the spatial model shown in Fig. 2. The videos from the two cameras were synchronized by detecting a common temporal event such as the first heel strike. As the cameras operated at a 60 Hz frequency, this synchronization procedure results in a temporal error of ≤ 0.017 s. Considering a typical movement speed of the order of 1 m/s, this temporal error can introduce a spatial error of 1.7 cm.

During the filming of the wild capuchins, we were unable to put markers on their skin. The digitization of the anatomical landmarks had to be performed by estimating these point locations in each field of video. This task was performed by one of the authors (ES), who is experienced in movement analysis, following study of the location of the anatomical landmarks on an anatomical model and a true skeleton of a capuchin. Then, ES and MD practiced the digitization with some of the videos until the authors felt confident in performing the coding. This method of manual markerless digitization may have increased the error of the movement

description in comparison with a digitization with markers. We have no alternative, however, to study wild capuchins. The error of the three-dimensional reconstruction employed can be described by the average residual of the reconstruction, a measure of the relative accuracy of the point location in the 3D space, which across all points and subjects was 1.7 cm. All of the spatio-temporal and kinematics data were obtained from the analysis of the right side of the subject's body.

The protocol for this study was approved by the University of Georgia IACUC and followed all applicable regulations for the humane treatment of animals in research.

Data analysis

The real coordinates for anatomical landmarks were reconstructed using a direct linear transformation (DLT) algorithm adapted from a code written by Christoph Reinschmidt and Ton van den Bogert (freely available at <http://isbweb.org/software/>) implemented in the Matlab 7.5 software (Mathworks Inc., Natick, MA). Analyses were performed using the Matlab software. As all of the frames were manually digitized, no points were missing and there was no need for interpolation of the data. Kinematic data were smoothed (digitally filtered) using a fourth order and zero-lag Butterworth low-pass filter with an 8 Hz cutoff frequency. This cutoff frequency was chosen based on a frequency analysis of the signal and noise of the data (Robertson, 2004). The following spatio-temporal variables were calculated for each stride: length [m] (defined as the distance between two consecutive initial contacts of the right foot with the ground), duration [s] (defined as the time interval between two consecutive initial contacts of the right foot with the ground), speed [m/s] (length divided by duration), frequency [Hz], and period of contact of one foot with the ground [s]. To compare the spatio-temporal characteristics of individuals of different sizes, these absolute variables were used to calculate the following dimensionless variables: dimensionless stride length (stride length divided by leg length, defined as hip height at midstance), dimensionless speed (the square root of the Froude number, $[v^2/gL]^{1/2}$, where g is the gravitational acceleration and L is the leg length), dimensionless stride frequency (stride frequency multiplied by $[L/g]^{1/2}$), and duty factor (period of contact of one foot with the ground divided by the stride period).

The angular kinematics of the ankle, knee, and hip joints and of the trunk segment were calculated for each stride according to the convention illustrated in Fig. 2. For each angle time-series, the



Figure 2. A bearded capuchin monkey (*Sapajus libidinosus*) carrying a stone and a nut (left). Photo by Noemi Spagnoli. The anthropometric model employed to describe movement, and the joint angle convention (right). The anatomical landmarks digitized were: 1. Tip of the second toe; 2. Second metatarsal phalangeal; 3. Heel; 4. Lateral malleolus; 5. Knee joint center; 6. Trochanter; 7 Iliac crest; 8. C5 vertebra.

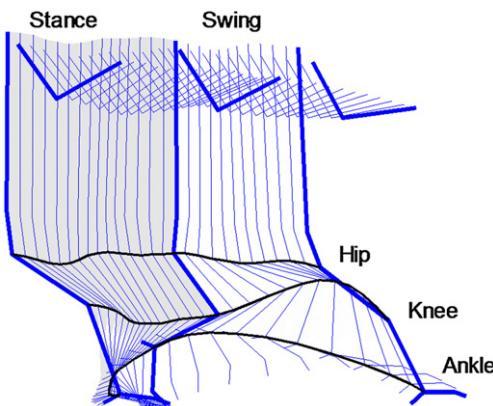


Figure 3. Stick figure of one representative gait stride movement of one bearded capuchin monkey.

following spatio-temporal and kinematic variables were calculated at the first contact of the foot with the ground (touchdown) and at the last contact of the foot with the ground (takeoff): maximum, minimum, mean, range (maximum minus minimum), and the joint angles.

Results

Spatio-temporal characteristics

As expected, during load-carrying bipedalism, bearded capuchins walk with a bent-hip, bent-knee (BHBK) gait (Fig. 3). Table 2 presents descriptive statistics for spatio-temporal variables for data in this study, for unloaded bipedal tufted capuchins (Demers, 2011), and for comparison with unloaded bonobos (*Pan paniscus*) (Aerts et al., 2000), baboons (*Papio anubis*) (Berillon et al., 2011), and gibbons (*Hylobates lar*) (Vereecke et al., 2006). Dimensionless stride length, dimensionless stride frequency, and duty factor versus dimensionless speed during load-carrying were fitted with the equation $y = a \times \text{speed} + b$ using the least squares method (Fig. 4). The linear fits of the capuchin data were all significant for the dimensionless stride length, frequency, and duty factor. Fig. 4 also shows the corresponding fitted lines for bipedal locomotion in *Pan paniscus* (Aerts et al., 2000), *P. anubis* (Berillon et al., 2011), and *H. lar* (Vereecke et al., 2006).

Table 2

Mean and standard deviation values across subjects of the spatio-temporal variables during bipedal locomotion for *Sapajus (Cebus) libidinosus* carrying a load (this study) and for *Sapajus (Cebus) apella* spp. (Demers, 2011) not carrying a load, and for comparison with three other species, all without load: *Pan paniscus* (Aerts et al., 2000), *Papio anubis* (Berillon et al., 2011), and *Hylobates lar* (Vereecke et al., 2006).

Gait variable	Species					
	<i>Sapajus (Cebus) libidinosus</i> (with load)	<i>Sapajus (Cebus) libidinosus</i> (with load)	<i>Sapajus (Cebus) apella</i> (without load) (Demers, 2011)	<i>Pan paniscus</i> (without load) (Aerts et al., 2000)	<i>Papio anubis</i> (without load) (Berillon et al., 2011)	<i>Hylobates lar</i> (without load) (Vereecke et al., 2006)
Duty factor	0.65 ± 0.04	0.65 ± 0.04	0.55 ± 0.05	0.63 ± 0.05	0.70 ± 0.03	0.64 ± 0.06
Stride length [m]	0.56 ± 0.06	0.56 ± 0.06	0.54 ± 0.05	0.92 ± 0.29	0.52 ± 0.03	0.72 ± 0.02
Stride duration [s]	0.46 ± 0.04	0.46 ± 0.04	0.54 ± 0.05	0.68 ± 0.19	NA	NA
Stride frequency [Hz]	2.21 ± 0.20	2.21 ± 0.20	1.71 ± 0.16	1.42 ± 0.33	1.52 ± 0.32	1.51 ± 0.43
Speed [m/s]	1.26 ± 0.18	1.26 ± 0.18	1.00 ± 0.14	1.4 ± 0.40	0.79 ± 0.19	1.1 ± 0.43
Dimensionless stride length	2.4 ± 0.30	4.9 ± 0.70 ^a	4.4 ± 0.40	3.9 ± 1.00 ^a	3.33 ± 0.56 ^a	4.7 ± 1.30 ^a
Dimensionless stride frequency	0.34 ± 0.02	0.24 ± 0.01 ^a	0.19 ± 0.02	0.24 ± 0.04 ^a	0.19 ± 0.04 ^a	0.19 ± 0.05 ^a
Dimensionless speed	0.83 ± 0.15	1.19 ± 0.19 ^a	0.68 ± 0.10	0.95 ± 0.31 ^a	0.64 ± 0.18 ^a	0.90 ± 0.35 ^a

^a Dimensionless variables were calculated with leg length calculated as the distance from knee to heel, rather than with hip height at midstance. 'NA' indicates data not available.

Joint kinematics and coordination

In general, capuchins exhibited large flexion at the hip and knee (Fig. 5) and a larger excursion of the ankle during bipedal load-carrying than when walking bipedally unloaded (Table 3). Load-carrying capuchins showed greater plantarflexion of the ankle than any of the other species included in Table 3.

Discussion

Although bipedal locomotion is a small part of locomotor time budgets among all non-human primates, and bipedal locomotion while carrying a load in the arms is even less common, it is routine among bearded capuchin monkeys at Boa Vista. We were able to study the monkeys' bipedal locomotion as they carried a load because monkeys willingly transport stones to use in cracking nuts. We took advantage of this naturally occurring phenomenon to study the kinematics of bipedal locomotion while carrying a moderately heavy load (930 g; 21–40% of body mass). The benefit of executing this task has been hypothesized as a selective pressure leading to the evolution of bipedalism (Washburn, 1959, 1967; Hewes, 1961, 1964; Lovejoy, 1981; Iwamoto, 1985; Marzke, 1986; Wall-Scheffler et al., 2007; Watson et al., 2009; Carvalho et al., 2012).

Interspecific comparison of unloaded and loaded bipedalism

Spatio-temporal variables After scaling the spatio-temporal variables based on dynamic similarity, the patterns of dimensionless stride length, frequency, and duty factor across the range of dimensionless speed present a few differences between capuchins carrying a load and those not carrying a load. Capuchins carrying a load tend to move more quickly and do so using a higher stride frequency than other capuchins not carrying a load (Demers, 2011). This is in contrast to bonobos that, when carrying a load, move more slowly and use a slower stride frequency (and a shorter stride length) (Table 2). Chimpanzees also appear to use a slower stride frequency during load-carrying bipedal movement.

Even though the capuchins tend to move faster when carrying a load (i.e., in our study), they used a higher duty factor than when not carrying a load (i.e., as in Demers, 2011). As the locomotor speed of an animal increases, it is normally expected that the duty factor should decrease and when there is a transition from walk to run, the duty factor normally drops below 0.5 (indicating there is only

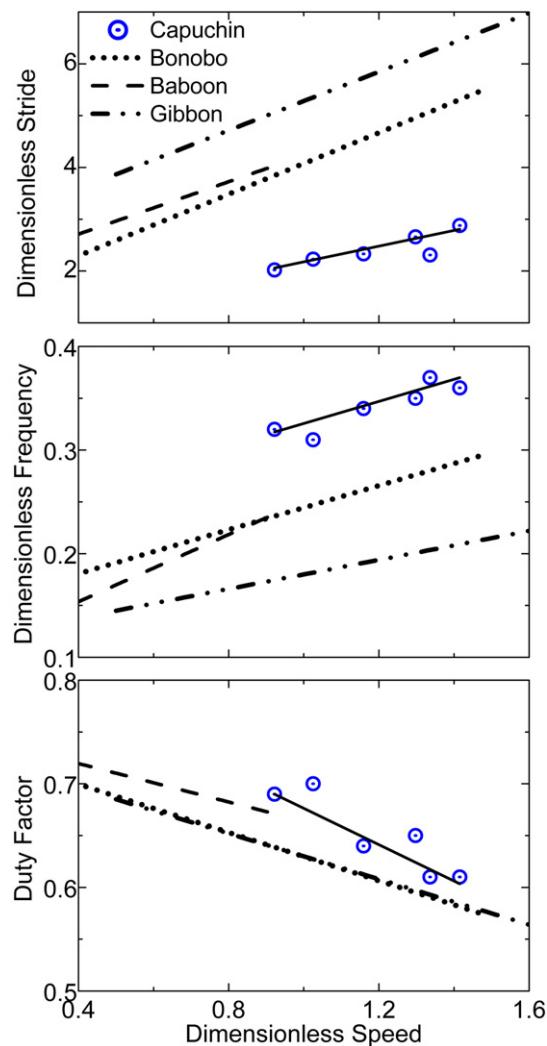


Figure 4. Spatio-temporal gait characteristics compared to dimensionless speed during load-carrying by capuchins (*Sapajus (Cebus) libidinosus* and *apella*) from this study and unloaded bipedal locomotion in bonobos (*Pan paniscus*) (Aerts et al., 2000), baboons (*Papio anubis*) (Berillon et al., 2011), and gibbons (*Hylobates lar*) (Vereecke et al., 2006). Values are derived using leg length defined as the distance from knee to ankle for all groups. The data were fitted with the equation $y = a \times \text{speed} + b$. The linear fits of the capuchin data were all significant for the dimensionless stride length ($a = 1.39$, $b = 0.75$, $R^2 = 0.82$, $p = 0.01$), frequency ($a = 0.11$, $b = 0.21$, $R^2 = 0.73$, $p = 0.03$), and duty factor ($a = -0.18$, $b = 0.87$, $R^2 = 0.72$, $p = 0.03$).

one foot in contact with the ground at a time and there is a flight phase when both feet are not in contact with the ground, as opposed to what is typically observed in walking when there is a double support phase with both feet in contact with the ground) (Alexander, 2003). Another interpretation of these results is that given the high values of dimensionless speed (0.83 ± 0.15 on average when leg length was calculated as hip height at midstance and 1.19 ± 0.19 on average when leg length was calculated as the distance from knee to heel), the capuchins of this study were running instead of walking. Although we cannot negate this explanation with the present data, a similar interpretation could be put forward to the data of some species presented in Table 2. For example, *H. lar* (Vereecke et al., 2006) presented a dimensionless speed of 0.90 ± 0.35 , which is not different from the values for the capuchins in this study if we consider the ranges given by the mean plus/minus one standard deviation.

We hypothesize that because of the relatively large mass of the load for the capuchins, they could not carry the load for long

and the heavy load generated a strong perturbation to their balance while moving. As consequence, the capuchins increased their locomotor speed to decrease the duration of the task and also increased the duration of their double support phase to increase their balance during walking. The increase in dimensionless stride frequency, but not dimensionless stride length, also supports this hypothesis. Of note, however, is that the maximum gait speed found by Demes (2011) for the capuchins not carrying a load was 1.28 m/s, which is higher than the gait speed of two of the six load-carrying capuchins that we analyzed (ranges 0.98–1.45 m/s). Thus the capuchins in the two studies are not very different with regard to their gait speeds. An alternative interpretation of the greater duty factors in the loaded condition is that animals when carrying a load tend to increase the duty factor (or simply the time of contact) in comparison with the unloaded condition for the same speed of locomotion (e.g., Hoyt et al., 2000) and this is thought to be an attempt to decrease the rate of force application and the metabolic cost in the loaded condition (Kram and Taylor, 1990; Farley and Taylor, 1991). However, by the same reasoning, we would expect a decrease in preferred speed in the loaded condition compared with the unloaded condition (for example, horses decreased their preferred speed when transporting a load [Wickler et al., 2001]). Although we do not have data for the same subjects locomoting in these two conditions, the observation that capuchins with load moved with about the same, or even slightly higher, speeds than the capuchins in the unloaded condition found by Demes (2011) does not favor this interpretation.

Kinematic parameters Capuchin monkeys carrying a load, similar to other primates walking bipedally, adopted a BHBK gait. Load-carrying monkeys use greater joint excursion at the ankle than other species throughout almost the entire stride, particularly during the preparation for toe-off (Table 3). These data suggest that capuchins carrying a load rely more heavily on their distal limb segment for movement than other primates. It is likely that the difference is due to load-carrying, although speed may be a factor. For example, researchers have found that in macaques trained for bipedal locomotion, an increase in speed was achieved by increasing stride length and reducing stride frequency, with a trend towards increased range of joint motion as speed increased (Hirasaki et al., 2004; Ogihara et al., 2007). On the other hand, macaques that were not trained to move bipedally moved at higher speeds via an increase in stride length, but with no changes in joint range of motion (Hirasaki et al., 2004). Additionally, in untrained, bipedal gibbons, the hip and ankle angles changed as speed increased, but the knee angle did not (Vereecke et al., 2006). Since our capuchins did not conform to any of these patterns in total, it is difficult to say whether the joint angle or spatio-temporal gait parameter differences seen between the load-carrying versus unloaded bipedal capuchins were due to speed alone. Especially given that the dimensionless speed values are similar (within one standard deviation of one another), it is difficult to argue that speed has a significant effect on the joint kinematics or spatio-temporal gait parameters between these two samples.

There are some studies that examine the biomechanics of human walking while carrying a load in the arms (Neumann and Cook, 1985; Cham and Redfern, 2004; Fiolkowski et al., 2006; Watson et al., 2009). These studies indicate that while there are some changes in lower limb kinematics, similar to changes seen while wearing a backpack, greater differences are seen in the loading regimes and muscle activation patterns of the lower limb during load-carrying compared with unloaded bipedalism. In terms of kinematics during arm-loaded walking, Cham and Redfern (2004) found that the ankle was significantly more plantarflexed

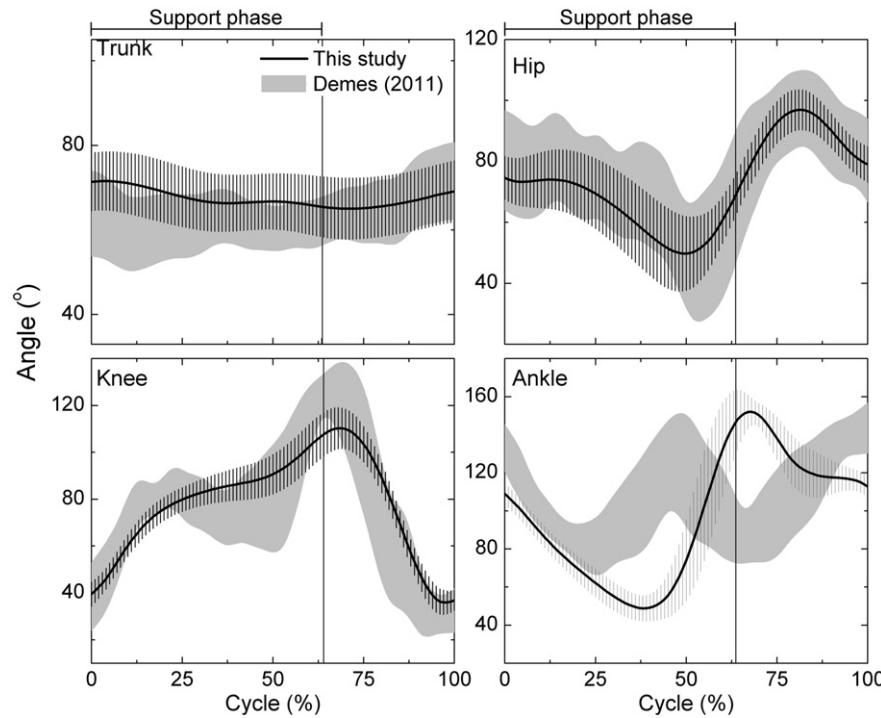


Figure 5. Mean and standard deviation values across subjects of joint and segment angles versus time during bipedal locomotion for the capuchin subjects carrying a load (continuous line). For the trunk, a larger angle indicates greater trunk extension, whereas for the hip and knee, a larger angle indicates greater flexion. Finally, a larger angle for the ankle indicates greater plantarflexion. Range of joint and segment angles versus time for unloaded capuchin bipedalism (gray band) were taken from Demes (2011). It was not possible to calculate mean and standard deviation from Demes' data; thus, the figure illustrates the range for each angle. Support and swing phase for these data were scaled to match the 0.65 duty factor observed in this study (compared with the 0.55 duty factor observed by Demes, 2011).

at 20% of the stance phase. Additionally, they found that arm-loaded walking was associated with a significant increase in angular velocity of the ankle joint. Interestingly, this result is similar to the comparison observed between load-carrying and unloaded capuchins during bipedalism.

Intragenus comparisons

Demes (2011) report kinematic data on bipedal locomotion (unloaded; i.e., not transporting anything) of tufted capuchin monkeys (*Cebus apella*; now *Sapajus apella*) in a laboratory setting. Comparing these data with ours allows us to examine the similarities and differences in limb use across locomotor mode in tufted capuchins. Such a comparison may be confounded by phylogeny and morphology. At present, captive specimens identified as *C. apella* or *S. apella* derived from animals taken from the wild prior to 2000 (and that would include all monkeys in research colonies in the United States, to our knowledge) have an ambiguous taxonomic status, because of the division of *S. (C.) apella* into several different species in 2001 (Groves, 2001; Rylands et al., 2005), including *libidinosus* (previously a subspecies designation of *C. apella*). Thus we cannot know with certainty the taxonomic relationship between the monkeys studied by Demes (2011) and the monkeys at Boa Vista, beyond shared membership in the genus *Sapajus*. Moreover, previous work on the biomechanics of primate locomotion suggests that greater differences are exhibited across genera than within genera (Hanna and Schmitt, 2011). Thus, we feel a comparison of loaded and unloaded bipedalism across *Sapajus*, some known to be *S. libidinosus* and some of undetermined species status (i.e., captive *S. (C.) apella*), is valid and this comparison provides one way to evaluate kinematic and spatio-temporal differences between load-carrying and unloaded facultative

bipedal locomotion. Unfortunately, physical differences among the species of *Sapajus*, including *S. libidinosus* and *S. apella*, have not yet appeared in the literature.

We found limited kinematic differences between wild capuchin monkeys carrying stones (reported here) and captive monkeys locomoting bipedally without a load (as reported by Demes, 2011). For example, there are limited differences in hip and knee angles across carrying treatments in the monkeys (Table 3). One possible difference that was revealed in this study, however, is that the range of ankle excursion may be increased during load-carrying, BHBK bipedalism.

It is interesting that the variable in which load-carrying bipedalism appears to differ from unloaded bipedalism in capuchins occurs at the ankle and specifically at toe-off (Table 3), because the ankle plantarflexors are an important source of power at toe-off during extended-joint bipedalism (normal walking) in humans (e.g., Anderson and Pandy, 1993; Zajac et al., 2003; Neptune et al., 2004). It is possible that the ankle plantarflexors also contribute a significant amount of power to bipedal locomotion in the monkeys, and this power may increase during load-carrying, as the degree of plantarflexion at toe-off increases by almost 20% (~25°) over that exhibited during unloaded bipedalism (Demes, 2011). We hypothesize that the larger excursion in plantarflexion during load-carrying bipedalism by capuchins may be associated with a greater angular velocity of the ankle during carrying, as has been found during human carrying (Cham and Redfern, 2004). Thus, it may be that during load-carrying, the plantarflexors are operating at suboptimal contractile conditions compared with that during the unloaded regime. Some measure of muscle function could be estimated by examining ground reaction force data in concert with muscle activity patterns during loaded bipedalism and comparing such data with unloaded bipedalism (see Neptune and Sasaki, 2005

Table 3

Mean and standard deviation values of segment and joint angles during bipedal locomotion for capuchins with and without load, and for three other species of primates without load.

Angle	Segment/Joint			
	Trunk ^a	Hip ^b	Knee ^c	Ankle
<i>Sapajus (Cebus) libidinosus</i> with load (this study)				
<i>Sapajus (Cebus) apella</i> without load (Demes, 2011)				
<i>Pan paniscus</i> (D'Aout et al., 2002)				
<i>Papio anubis</i> (Berillon et al., 2011)				
<i>Hylobates lar</i> (Vereecke et al., 2006)				
Minimum (°)	61.3 ± 7.7	49.6 ± 12.6	33.3 ± 5.1	44.7 ± 6.7
	63	46	35	77
	61.9 ± 5.3	43 ± 12.9	48.6 ± 10.0	52.1 ± 8.6
	NA	45.4 ± 9.4	NA	89.5 ± 11.7
	NA	28.6 ± 9.6	36.1 ± 8.4	54.7 ± 6.6
Maximum (°)	74.3 ± 6	98.1 ± 6.9	112.6 ± 9.1	158.6 ± 10.0
	73	92	125	146
	75.3 ± 8.3	84.4 ± 10.9	117.7 ± 17.2	88.1 ± 8.5
	NA	NA	116.3 ± 8.8	124.1 ± 13.0
	NA	79.2 ± 10.0	107.4 ± 9.9	119.2 ± 8.8
Range (°)	13 ± 4.4	48.5 ± 7.9	79.3 ± 12.5	114 ± 9.4
	NA	NA	NA	NA
	13.4 ± 6.2	41.3 ± 12.4	69.1 ± 11.5	36.0 ± 13.6
	NA	NA	NA	NA
	NA	50.2 ± 13.7	68.9 ± 10.6	62.8 ± 9.5
Mean (°)	67 ± 6.9	73.3 ± 8.8	78.5 ± 3.9	97.5 ± 6
	67 ± 4	71 ± 6	86 ± 5	105 ± 4
	NA	NA	NA	NA
	NA	34 ± 7.1	65.1 ± 8.3	30.5 ± 6.8
	74.7 ± 5.9	NA	NA	NA
Touchdown (°)	70.8 ± 7.5	74.9 ± 8	39.2 ± 5.9	109.3 ± 6.9
	NA	NA	39 ± 6	133 ± 7
	69.1 ± 6.4	73.8 ± 10.0	54.5 ± 14.5	79.4 ± 11.1
	67.3 ± 4.1	75.2 ± 9.8	55.2 ± 6.6	119.6 ± 8.0
	NA	75.3 ± 10.7	41.1 ± 10.4	113.1 ± 12.4
Takeoff (°)	65.4 ± 7.4	69.4 ± 12.5	108.8 ± 11.6	152 ± 9.6
	NA	NA	95 ± 7	126 ± 10
	NA	48.2 ± 12.6	110.9 ± 16.9	80.2 ± 7.0
	NA	55.5 ± 11.5	113.2 ± 9.0	122.1 ± 12.1
	NA	34.1 ± 9.4	84.5 ± 16.0	87.3 ± 13.1

^a S. (C.) *apella* spp. without load calculated as 90-trunk pitch (Demes, 2011).

^b S. (C.) *apella* spp. without load calculated as 180-hip (Demes, 2011).

^c S. (C.) *apella* spp. without load calculated as 180-knee (Demes, 2011).

for details). We are collecting at least the ground reaction force data currently to begin to address these hypotheses.

Conclusion

This study contributes valuable data for reconstruction of locomotor behavior of extinct hominin species because it provides a comparative reference beyond that of extant great apes. We suggest that capuchins provide a useful model, alternative to that of apes, to understand the evolution of early hominins (Isaac, 1978; Westergaard et al., 1999). Just as diversity of social systems and feeding ecologies in extant primates broadens the range of ideas about these aspects of human evolution, the existence of diverse models of naturally occurring bipedal locomotion broadens our appreciation of the versatility of behavior in primates with generalized quadrupedal anatomy. Bipedal locomotion could certainly be prevalent in advance of specialized anatomy supporting human-typical styles of walking and running, and we show that it could readily involve transport of moderately heavy loads over many meters.

Acknowledgments

We thank the Oliveira family for allowing the EthoCebus research group to work on their land and for logistical assistance,

and Brigitte Demes for sharing data. This research is supported by grants from the National Geographic Society and the L.S.B. Leakey Foundation.

References

- 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, R.M., 2003. *Principles of Animal Locomotion*. Princeton University Press, Princeton.
- Anderson, F.C., Pandya, M.G., 1993. Storage and utilization of elastic strain energy during jumping. *J. Biomech.* 26, 1413–1427.
- Andrews, P., Harrison, T., 2005. The last common ancestor of apes and humans. In: Lieberman, D., Smith, R.J., Kelley, J. (Eds.), *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution*. Brill Academic Publishers, Inc., Boston, pp. 103–121.
- Begun, D.R., Ward, C.V., Rose, M.D., 1997. Events in hominoid evolution. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, pp. 289–415.
- Begun, D.R., 2007. Fossil record of Miocene hominoids. In: Henke, W., Tattersall, I., Hardt, T. (Eds.), *Handbook of Paleoanthropology*. Springer, New York, pp. 921–977.
- Benefit, B.R., McCrossin, M.L., 1995. Miocene hominoids and hominid origins. *Annu. Rev. Anthropol.* 24, 237–256.
- Berillon, G., D'Aout, K., Daver, G., Dubreuil, G., Multon, F., Nicolas, G., de la Villenet, B., 2011. In what manner do quadrupedal primates walk on two legs? Preliminary results on olive baboons (*Papio anubis*). In: D'Aout, K., Vereecke, E.E. (Eds.), *Primate Locomotion: Linking Field and Laboratory Research. Developments in Primatology: Progress and Prospects*. Springer, New York, pp. 61–82.
- Biondi, L., 2010. *Comportamento posicional e uso de substrato de macacos-prego *Cebus libidinosus* Spix*, 1823. Master's Thesis, University of São Paulo.
- Carvalho, S., Biro, D., Cunha, E., Hockings, K., McGrew, W.C., Richmond, B.G., Matsuzawa, T., 2012. Chimpanzee carrying behaviour and the origins of human bipedality. *Curr. Biol.* 22, R180–R181.
- Cham, R., Redfern, M.S., 2004. Gait adaptations during load carrying on level and inclined surfaces. *Occup. Erg.* 4, 11–26.
- Crompton, R.H., Vereecke, E.E., Thorpe, S.K., 2008. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *J. Anat.* 212, 501–543.
- Crompton, R.H., Sellers, W.I., Thorpe, S.K.S., 2010. Arboreality, terrestriality and bipedalism. *Phil. Trans. R. Soc. B* 365, 3301–3314.
- D'Aout, K., Aerts, P., De Clercq, 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.
- Demes, B., 2011. Three-dimensional kinematics of capuchin monkey bipedalism. *Am. J. Phys. Anthropol.* 145, 147–155.
- Doran, D.M., 1992. The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior – a case-study of paedomorphism and its behavioral correlates. *J. Hum. Evol.* 23, 139–157.
- Doran, D.M., 1993. Sex-differences in adult chimpanzee positional behavior – the influence of body size on locomotion and posture. *Am. J. Phys. Anthropol.* 91, 99–115.
- Doran, D.M., 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. *J. Hum. Evol.* 32, 323–344.
- Farley, C.T., Taylor, C.R., 1991. A mechanical trigger for the trot-gallop transition in horses. *Science* 253, 306–308.
- Fiolkowski, P., Horodyski, M., Bishop, M., Williams, M., Stylianou, L., 2006. Changes in gait kinematics and posture with the use of a front pack. *Ergonomics* 49, 885–894.
- Fleagle, J.G., Stern, J.T., Jungers, W., Susman, R.L., Vangor, A.K., Wells, J.P., 1981. Climbing: a biomechanical link with brachiation and with bipedalism. In: Day, M.H. (Ed.), *Vertebrate Locomotion. Symposia of the Zoological Society of London*. Academic Press, London, pp. 359–375.
- Fragaszy, D.M., Izar, P., Visalberghi, E., Ottoni, E.B., De Oliveira, M.G., 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *Am. J. Primatol.* 64, 359–366.
- Fragaszy, D.M., Greenberg, R., Visalberghi, E., Ottoni, E.B., Izar, P., Liu, Q., 2010. How wild bearded capuchin monkeys select stones and nuts to minimize the number of strikes per nut cracked. *Anim. Behav.* 80, 205–214.
- Goodall, J., 1971. *In the Shadow of Man*. Collins, London.
- Groves, C.P., 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington.
- Hanna, J., Schmitt, D., 2011. Interpreting the role of climbing in primate locomotor evolution: are the biomechanics of climbing influenced by habitual substrate use and anatomy? *Int. J. Primatol.* 32, 430–444.
- Harrison, T., 1993. Cladistic concepts and the species problem in hominoid evolution. In: Kimbel, W.H., Martin, L. (Eds.), *Species, Species Concepts, and Primate Evolution*. Plenum Press, New York, pp. 345–371.
- Hewes, G.W., 1961. Food transport and the origin of hominid bipedalism. *Am. Anthropol.* 63, 687–710.
- Hewes, G.W., 1964. Hominid bipedalism: independent evidence for food-carrying theory. *Science* 146, 416–418.

- 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.
- Hoyt, D.F., Wickler, S.J., Cogger, E.A., 2000. Time of contact and step length: the effect of limb length, running speed, load carrying and incline. *J. Exp. Biol.* 203, 221–227.
- Isaac, G., 1978. Food-sharing behavior of protohuman hominids. *Sci. Am.* 238, 90–108.
- Iwamoto, M., 1985. Bipedalism of Japanese monkeys and carrying models of hominization. In: Kondo, S.O. (Ed.), *Primate Morphophysiology, Locomotor Analyses, and Human Bipedalism*. University of Tokyo Press, Tokyo, pp. 251–260.
- Kram, R., Taylor, C.R., 1990. Energetics of running: a new perspective. *Nature* 346, 265–267.
- Lovejoy, C.O., Latimer, B., Suwa, G., Asfaw, B., White, T.D., 2009. Combining prehension and propulsion: the foot of *Ardipithecus ramidus*. *Science* 326, 71–78.
- Lovejoy, C.O., 1981. The origin of man. *Science* 211, 341–350.
- Lynch Alfaro, J.W., Boubli, J.P., Olson, L.E., Di Fiore, A., Wilson, B., Gutiérrez-Espeleta, G.A., Chiou, K.L., Schulte, M., Neitzel, S., Ross, V., Schwobchow, D., Nguyen, M.T., Farias, I., Janson, C.H., Alfaro, M.E., 2012. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *J. Biogeogr.* 39, 272–288.
- Madden, M., Fragaszy, D.M., Izar, P., Hinley, A.J., Ottoni, E.B., Visalberghi, E., 2007. Modelling the monkey habitat in Brazil. *Geospatial Today* 5, 26–35.
- Marzke, M.W., 1986. Tool use and the evolution of hominid hands and bipedality. In: Else, J.G., Lee, P.C. (Eds.), *Proceedings Xth Congress of the International Primatological Society*. Cambridge University Press, London, pp. 203–209.
- Nakatsukasa, M., 2004. Acquisition of bipedalism: the Miocene hominoid record and modern analogues for bipedal protohominids. *J. Anat.* 204, 385–402.
- Neptune, R.R., Sasaki, K., 2005. Ankle plantar flexor force production is an important determinant of the preferred walk-to-run transition speed. *J. Exp. Biol.* 208, 799–808.
- Neptune, R.R., Zajac, F.E., Kautz, S.A., 2004. Muscle force redistributes segmental power for body progression during walking. *Gait Posture* 19, 194–205.
- Neumann, D.A., Cook, T.M., 1985. Effect of load and carrying position on the electromyographic activity of the gluteus medius muscle during walking. *Phys. Ther.* 65, 305–311.
- 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.
- Richmond, B.G., Begun, D.R., Strait, D.S., 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. *Am. J. Phys. Anthropol.* Suppl. 33, 70–105.
- Robertson, D.G.E., 2004. Research Methods in Biomechanics. Human Kinetics, Champaign.
- Rose, M.D., 1993. Locomotor anatomy of Miocene hominoids. In: Gebo, D.L. (Ed.), *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois University Press, DeKalb, pp. 252–272.
- Rylands, A.B., Kierulff, M.C.M., Mittermeier, R.A., 2005. Notes on the taxonomy and distributions of the tufted capuchin monkeys (*Cebus*, *Cebidae*) of South America. *Lundiana* (Suppl.) 6, 97–110.
- Schmitt, D., 2003. Insights into the evolution of human bipedalism from experimental studies of humans and other primates. *J. Exp. Biol.* 206, 1437–1448.
- Spagnoletti, N., Visalberghi, E., Ottoni, E., Izar, P., Fragaszy, D., 2011. Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *J. Hum. Evol.* 61, 97–107.
- Thorpe, S.K., Holder, R.L., Crompton, R.H., 2007. Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* 316, 1328–1331.
- Verderane, M., Izar, P.E.V., Ottoni, E., Fragaszy, D., in review. Socioecology of wild bearded capuchin monkeys (*Cebus libidinosus*): does tool use impact female social relationships? *Behav. Ecol. Sociobiol.*
- Vereecke, E.E., D'Aout, K., Aerts, P., 2006. Locomotor versatility in the white-handed gibbon (*Hylobates lar*): a spatiotemporal analysis of the bipedal, tripodal, and quadrupedal gaits. *J. Hum. Evol.* 50, 552–567.
- Visalberghi, E., Fragaszy, D., in press. The EthoCebus project. Stone tool use by wild capuchin monkeys. In: Sanz, C., Call, J., Boesch, C. (Eds.), *Multidisciplinary Perspectives on the Cognition and Ecology of Tool Using Behaviors*. Cambridge University Press, Cambridge.
- Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M.G., Andrade, F.R., 2007. Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *Am. J. Phys. Anthropol.* 132, 426–444.
- Visalberghi, E., Spagnoletti, N., Ramos da Silva, E.D., Andrade, F.R., Ottoni, E., Izar, P., Fragaszy, D., 2009. Distribution of potential suitable hammers and transport of hammer tools and nuts by wild capuchin monkeys. *Primates* 50, 95–104.
- Wall-Scheffler, C.M., Geiger, K., Steudel-Numbers, K.L., 2007. Infant carrying: the role of increased locomotory costs in early tool development. *Am. J. Phys. Anthropol.* 133, 841–846.
- Ward, C.V., 1997. Functional anatomy and phyletic implications of the hominoid trunk and hindlimb. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, pp. 101–130.
- Washburn, S.L., 1959. Speculations on the interrelations of the history of tools and biological evolution. *Hum. Biol.* 31, 21–31.
- Washburn, S.L., 1967. Behaviour and the origin of man. In: *Proceedings of the Royal Anthropological Institute of Great Britain and Ireland*, 1967, pp. 21–27.
- Watson, J.C., Payne, R.C., Chamberlain, A.T., Jones, R.K., Sellers, W.I., 2009. The kinematics of load carrying in humans and great apes: implications for the evolution of human bipedalism. *Folia Primatol.* 80, 309–328.
- Westergaard, G.C., Haynie, M.K., Lundquist, A.L., Suomi, S.J., 1999. Carrying, sharing, and hand preference in tufted capuchins (*Cebus apella*). *Int. J. Primatol.* 20, 153–162.
- Wickler, S.J., Hoyt, D.F., Cogger, E.A., Hall, K.M., 2001. Effect of load on preferred speed and cost of transport. *J. Appl. Physiol.* 90, 1548–1551.
- Zajac, F.E., Neptune, R.R., Kautz, S.A., 2003. Biomechanics and muscle coordination of human walking: part II: lessons from dynamical simulations and clinical implications. *Gait Posture* 17, 1–17.