

# The strategic role of the tail in maintaining balance while carrying a load bipedally in wild capuchins (*Sapajus libidinosus*): a pilot study

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**Abstract** The ability to carry objects has been considered an important selective pressure favoring the evolution of bipedal locomotion in early hominins. Comparable behaviors by extant primates have been studied very little, as few primates habitually carry objects bipedally. However, wild bearded capuchins living at Fazenda Boa Vista spontaneously and habitually transport stone tools by walking bipedally, allowing us to examine the characteristics of bipedal locomotion during object transport by a generalized primate. In this pilot study, we investigated the mechanical aspects of position and velocity of the center of mass, trunk inclination, and forelimb postures, and the torque of the forces applied on each anatomical segment in wild bearded capuchin monkeys during the transport of objects, with particular attention to the tail and its role in balancing the body. Our results indicate that body mass strongly affects the posture of transport and that capuchins are able to carry heavy loads bipedally with a bent-hip-bent-knee posture, thanks to the “strategic” use of their extendable tail; in fact, without this anatomical structure, constituting only 5 % of their body mass, they would be unable to transport the loads that they habitually carry.

**Keywords** Bipedal locomotion · Torque · Center of mass · Tail use

## Introduction

Non-human primates walk bipedally with a “bent-hip, bent-knee” posture (BHBK), and it is very likely that this is the first form of hominin bipedal locomotion (Lovejoy 2005). Kinematic properties of BHBK bipedal gait have been described for captive chimpanzees, bonobos (*Pan paniscus*), gibbons (*Hylobates lar*), Japanese macaques (*Macaca fuscata*), baboons (*Papio anubis*), and tufted capuchins (*Sapajus spp.*) (Reynolds 1987; Aerts et al. 2000; D’Aout et al. 2001, 2002; Hirasaki et al. 2004; Vereecke et al. 2006a, b; Kimura and Yaguramaki 2009; Berillon et al. 2010; Ogihara et al. 2010; Demes 2011).

Bipedal locomotion leaves the upper limbs free to transport objects and use tools (Fleagle 2013). Wild chimpanzees (*Pan troglodytes*) stand bipedally about 1 % of the daytime (Doran 1992, 1993). They typically locomote bipedally to transport highly valued foods and to carry several food items at once (Carvalho et al. 2012). Wild bearded capuchin monkeys (*Sapajus libidinosus*) offer an opportunity to examine some features of bipedal gait during routine object transport. At Fazenda Boa Vista (hereafter, FBV) these monkeys habitually walk bipedally to transport stone hammers to anvils, where they crack hard-shelled nuts (Fragaszy et al. 2004; Visalberghi et al. 2009). They perform two types of transport: (1) “continuous” transport, in which the capuchin lifts the stone once and carries it directly to the anvil by walking bipedally; or (2) “non-continuous” transport, in which the capuchin moves toward the anvil, lifting the hammer and lowering it to the ground more than once before reaching the anvil

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(Massaro 2013). Continuous transports provide an ideal situation in which to examine spontaneous bipedal carrying of loads.

Duarte et al. (2012) described the kinematics of bipedal locomotion of FBV capuchins transporting a 1-kg hammer stone, and compared it to the kinematics of bipedal locomotion in unloaded capuchins, bonobos, baboons, and gibbons. Loaded capuchins adopted a relatively erect trunk, while the hips and knees remained flexed. These authors noticed that capuchins moved in a walking gait, with a duty factor of 0.65, and tended to move faster than unloaded capuchins (1.26 vs. 1 m s<sup>-1</sup>), likely because the weight of the load, carried in front of the body, pulled the monkey off balance. In contrast, bonobos and chimpanzees carrying out this task tend to walk more slowly. However, this study (Duarte et al. 2012) did not consider the dynamics of transport—that is, the forces acting on the masses of the different body parts—when capuchins moved with bipedal locomotion.

In mid-sized cebids (such as capuchins), the tail can work as a balancing organ in tripodal stance during jumping, climbing, and foraging (Garber and Rehg 1999). In large cebids (such as howlers and atelines), the tail is used as an organ for stabilization during locomotion (Hershkovitz 1977; Jenkins et al. 1978; German 1982; Lemelin 1995; Turnquist et al. 1999). During lifting and striking with the hammer stone, wild capuchins at FBV sometimes held the tail in the air rather rigidly behind the body or placed the tail in contact with the anvil or ground as the third leg of a tripod (Liu et al. 2009). This “tripod posture” does not seem to affect efficiency, i.e., the number of strikes used to crack the nut. Liu et al. (2009), however, did not assess whether the tail provided stability to the body during the stone-lifting phase.

In this pilot study, we examined how bearded capuchin monkeys maintain balance during the transport of hammer stones and the role of the tail for balance. In particular, we investigated mechanical aspects of position and velocity of the center of mass, trunk inclination, forelimb postures, and the torque of the weight force applied on each anatomical segment, and assessed whether capuchins actively adjusted the position of the tail during transport in ways that aided balance.

## Methods

### Study site and subjects

The study was carried out at the outdoor laboratory of the *EthoCebus* Project located in FBV (Piauí, Brazil; for further information, see Massaro et al. 2012). In order to study the dynamics of different body mass, we selected two

subjects: an adult male (Chicao, body mass 4.4 kg) and an adult female (Piassava, body mass 1.9 kg). They belonged to a group of wild bearded capuchins that were fully habituated to human presence and had participated in other field experiments on nut-cracking (see Visalberghi et al. 2009). Capuchins voluntarily participated in this study by approaching the experimental area. They were filmed opportunistically as they transported stones placed by the experimenter at a given distance from the anvil. The research adhered to the principles for the ethical treatment of primates established by the American Society of Primatologists.

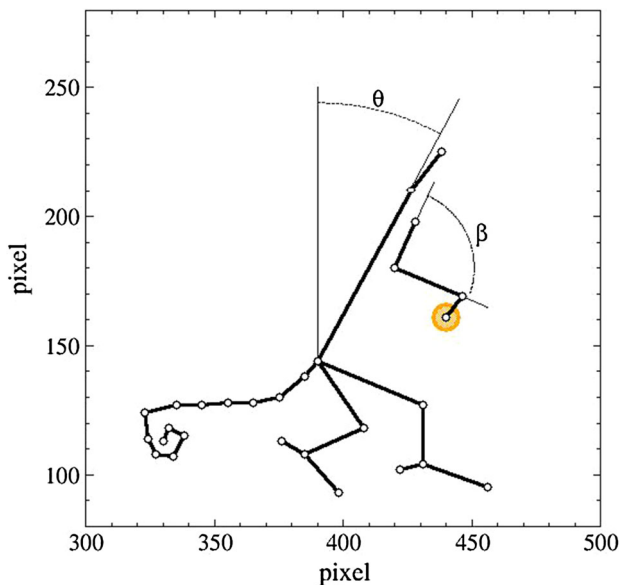
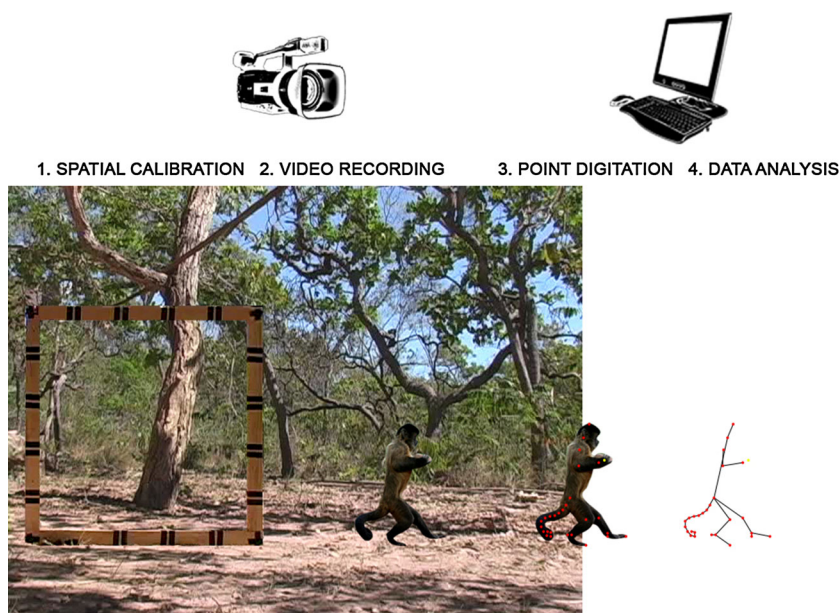
### Procedure

An illustration of the four steps of the procedure (spatial calibration, video recording of the transport, manual digitization of landmarks, and data analysis) is shown in Fig. 1. The camera (Canon GL2 MiniDV) was placed perpendicular to the sagittal plane on which subjects would move. A calibration device (1-m length) was filmed to scale the video images, and the transport events were then recorded (30 frames per second [fps]; 60-Hz sampling rate). Each subject was filmed in July 2007 while transporting a stone over a distance of 2 m on the compacted well-drained sandy soil of the outdoor laboratory. The soil was free of stones, roots, and other surface irregularities that might affect locomotion. The surface was leveled and horizontal. The stone was an ovoid-shaped quartzite weighing 0.93 kg.

For each subject, we selected three transport trials in which locomotion occurred perpendicular to the camera axis. We coded and digitized two strides (one stride for each leg) for each of three trials of each subject. The 2-D coordinates of anatomical locations on the monkey's body and on the stone were manually digitized. They included 31 points: one for the center of the stone, 13 (up to 16) for the tail, and 14 for the rest of the body (Fig. 2). By observing the videos, we determined that transverse rotation of the shoulders was minimal. Hence, as the positions of the left shoulder, left elbow, and left wrist were not visible in the video, we assumed their positions were equal to the corresponding point on the right side. Digitizing was performed by LM by means of the Peak Motus<sup>®</sup> software (v4.2, Vicon Motion Systems, Ltd., Oxford, UK). The raw *x*, *y* coordinates were scaled from pixels to meters.

For the body and extremities, the distal and proximal joint coordinates defined a given body segment. We derived the percentage of mass for each body segment (Table 1) from two individuals of the same genus (reported in Grand 1977) whose body mass was similar to those of our subjects. Given the regular shape of the stone transported, we assumed its center of mass at the center of its image. The curved shape of the tail was described by a

**Fig. 1** The four-step procedure (at scale). From *left*: Step 1. A *squared* calibration device was filmed to obtain the exact scale factor between pixels and meters. Step 2. The transport events were recorded. Step 3. The coordinates of a set of landmarks representing the monkey's body were manually digitized in each frame of the videos. Step 4. All coordinates were processed. Steps 1 and 2 were performed using a video camera placed perpendicular to the sagittal plane on which subjects would move. Steps 3 and 4 were performed using a computer



**Fig. 2** Chicaco' spatial model is represented by 31 points (*open circles*) defining segments and angles ( $\theta$  and  $\beta$ ). The stone is represented in *yellow*. An analogous model was used to represent Piassava's body

series of contiguous linear segments detected in each frame by the highest possible number of points, depending on the extension of the tail (i.e., the distance from the base of the tail to the farthest point). Positions of the hands and stone were considered coincident. The kinematic data were analyzed using original codes generated with LabVIEW software packages (version 7.1; National Instruments Corporation, Austin, TX, USA).

### Center of mass and gravitational torque

We considered the total system to have three components: the stone (*s*), the tail (*t*) and the rest of the body (referred to as "body without tail", *b*) having mass  $M_s$ ,  $M_t$ , and  $M_b$ , and center of mass  $COM_s$ ,  $COM_t$ ,  $COM_b$ , respectively.

The principal external forces acting on the system are the weight of each part of the monkey's body, the weight of the stone, and the ground reaction forces (hereafter, "GRF"). The effect of weight and GRF are distinct, as by definition of the center of mass, the total torque of weight forces with respect to the center of mass is exactly equal to zero, independently of its motion. Therefore, the variation of the angular momentum around the center of mass is due only to the GRF. However, the internal forces (e.g., those due to muscle and tendon activity) indirectly affect the motion around and of the center of mass, as the monkey may modify the GRF by acting on the ground or simply by changing the position of some parts of the body.

Therefore, independently of the effect of GRF and of the acceleration of the center of mass, the null torque produces a balanced relationship between the torque of the weight of the three system components and the center of mass. This relationship not only cannot be violated, but the monkey must be able to produce internal forces that allow it to transport the stone. This relationship does not oblige the monkey to have a fixed posture. On the contrary, the monkey can modify the position of the center of mass of each of the three system components in order to maintain the x-position of the total center of mass between the feet when both touch the ground.

**Table 1** Percentage of body mass and mass of each anatomical part for Chicaco and Piassava

Body segment	Chicaco (4.4 kg)		Piassava (1.9 kg)	
	% of body mass	Body mass (g)	% of body mass	Body mass (g)
Hand	0.7	30.8	1	18.1
Upper arm	2.7	118.8	2.5	46.7
Fore-arm	3.2	140.8	2.8	54
Foot	1.2	52.8	1.9	36.2
Calf	3.3	145.2	2.8	52.3
Thigh	6.5	286	5.4	103.2
Tail	4.8	211.2	5.5	103.6
Trunk	75	1980.6	80	940.5
Head	25	660.2	20	235.6

As the tail and body without tail each comprise segments, we calculated the anteroposterior coordinates of the COM of the components as follows:

$$(\text{COM}_{s,t,b})_x = \sum_j (m_j x_j) / M_{s,t,b}$$

where for each component of interest ( $s, t, b$ ),  $m_j$  refers to the mass of the  $j$ th segment and the sum is calculated for all the  $n$  segments;  $x_j$  refers to the anteroposterior and vertical coordinates, respectively, of the COM of the  $j$ th segment, and  $M_{s,t,b}$  is the total mass of that component. The same algorithm was used for the  $y$  component.

The coordinates of the center of mass of the total system are:

$$\text{COM}_{\text{system}} = (M_t \cdot \text{COM}_t + M_b \cdot \text{COM}_b + M_s \cdot \text{COM}_s) / M_{\text{total}}$$

where  $M_{\text{total}} = M_s + M_t + M_b$  is the total mass of the system.

To test whether subjects manipulated gravitational torque to make balance less effortful, the gravitational torques of the system's components were generated. The rationale is as follows:  $\text{COM}_{\text{system}}$  represents the fulcrum about which the component gravitational torques act. The sum of these torque values equals zero at the fulcrum point, and this is the point at which all of the system's weight is acted upon by gravity. Thus, when the gravitational torque of one component changes—for example, the *stone's* gravitational torque increases because of a modification of component distance values—the location of the  $\text{COM}_{\text{system}}$  changes unless another component's torque (e.g., the *tail*) can counterbalance in response.

The gravitational torque of each component ( $T_{s,t,b}$ ) is the weight of the component ( $M_{s,t,b}g$ ) multiplied by the torque arm (leverage):

$$T_{s,t,b} = (M_{s,t,b}g) |(\text{COM}_{s,t,b})_x - \text{COM}_{\text{system}x}|$$

where  $g = -9.81 \text{ m s}^{-2}$  is the gravitational acceleration. Torque rotating the system counterclockwise (i.e., backwards) was positive.

Gravitational torques (and consequently the location of the  $\text{COM}_{\text{system}}$ ) can be manipulated only by changing the torque arms, as component weights are fixed. Hence, to test whether the monkeys manipulated their component gravitational torques using strategies likely to be less effortful than others, we obtained angular measures that were dependent on how each component's mass location was changed. We generated the trunk inclination relative to vertical ( $\theta$ , see Fig. 2). The elbow flexion angle ( $\beta$ ) was the interior angle formed between the lower and upper arm, and was used to determine whether the monkeys kept the stone close to the body (lower torque arm).

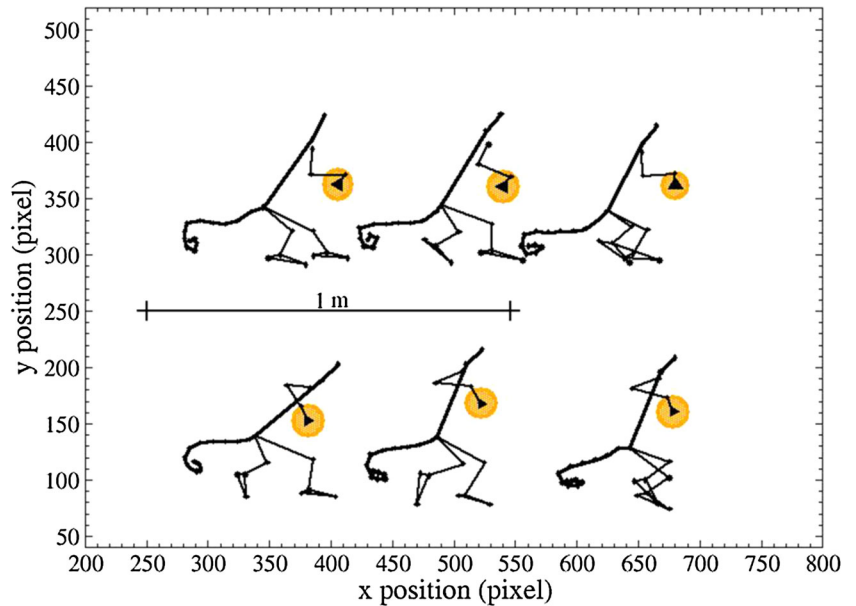
The horizontal velocity of the  $\text{COM}_{\text{system}}$  in each trial was calculated using a linear regression of the  $\text{COM}_{\text{system}x}$  as a function of time.

## Results

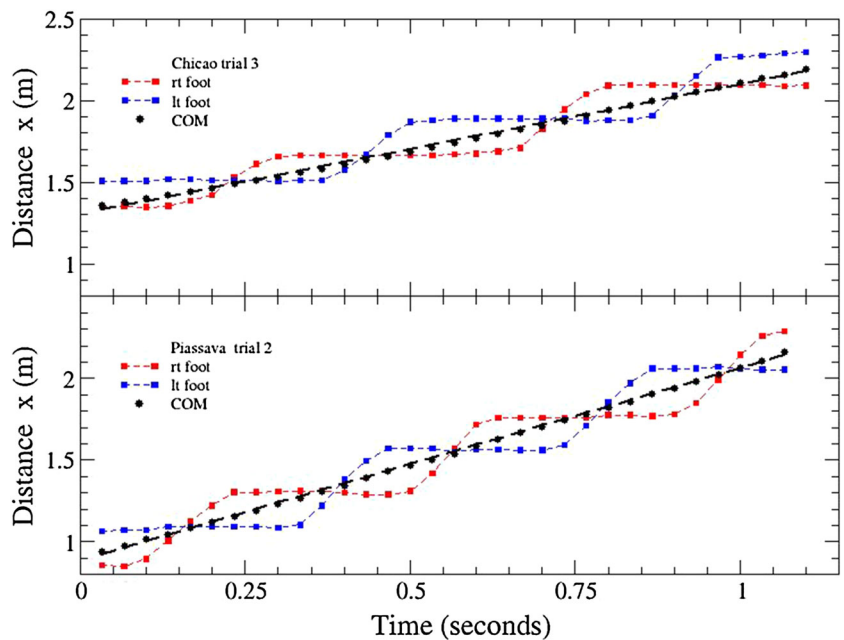
Three representative positions of body posture when carrying the stone reveal interesting differences between Chicaco and Piassava (Fig. 3). Chicaco keeps the stone at a relatively large distance from his chest, while Piassava holds the stone in a much closer position. The average values of  $\beta$  for Piassava are in the range between  $37^\circ$  and  $69^\circ$ , much smaller than the ones of Chicaco that are between  $85^\circ$  and  $90^\circ$ . The angle  $\theta$  is similar between subjects: average values are  $27^\circ$  forward lean for Chicaco and  $25^\circ$  for Piassava. The most upright posture corresponds to a trunk inclination of  $14^\circ$  for Chicaco and  $11^\circ$  for Piassava.

The vertical position of the  $\text{COM}_{\text{system}}$  was at the abdomen level and its anteroposterior velocity was remarkably constant throughout the strides considered for each transport. During each trial the  $\text{COM}_{\text{system}}$  position is the middle of the two feet and changes with a constant horizontal velocity (see trial 3 and 2 for Chicaco and Piassava, respectively, in Fig. 4). Therefore its horizontal

**Fig. 3** Three representative positions of transport for Chicaco (top) and Piassava (bottom)



**Fig. 4** X-positions of the COM<sub>system</sub> (black dotted line), of the right foot (red dotted line), and of the left foot (blue dotted line) vs. time in Chicaco’s trial 3 (upper panel) and Piassava’s trial 2 (lower panel). The x-acceleration of the COM<sub>system</sub> is equal to zero



**Table 2** Horizontal velocity of the center of mass (COM) of the body + stone system (mean ± SD)

COM	Chicaco	Piassava
Velocity trial 1 (m/s)	0.956 ± 0.009	1.063 ± 0.009
Velocity trial 2 (m/s)	0.958 ± 0.004	1.181 ± 0.004
Velocity trial 3 (m/s)	0.791 ± 0.007	1.25 ± 0.003

acceleration is negligible. Our evaluation of the average gait velocity provided values around 0.9 m s<sup>-1</sup> for Chicaco and 1.2 m s<sup>-1</sup> for Piassava (Table 2).

**Mechanics of transport: the role of the tail**

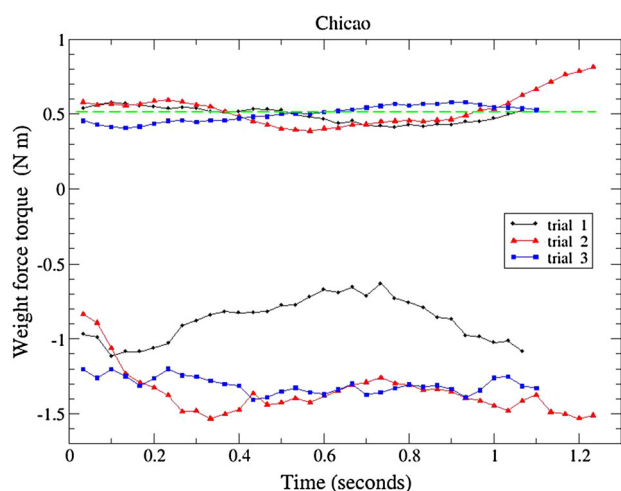
All torque values for the tail and stone are reported in Table 3, together with the ratio of the torque of the tail to that of the total body, which highlights the exact mean fractional contribution of the tail to balance in each trial. The tail weight torque values were constant during each transport trial, with an average value of 0.51 and 0.22 N m for Chicaco and Piassava, respectively (Figs. 5, 6). The average torque of the stone was -1.11 N m for Chicaco and -0.42 N m for Piassava.



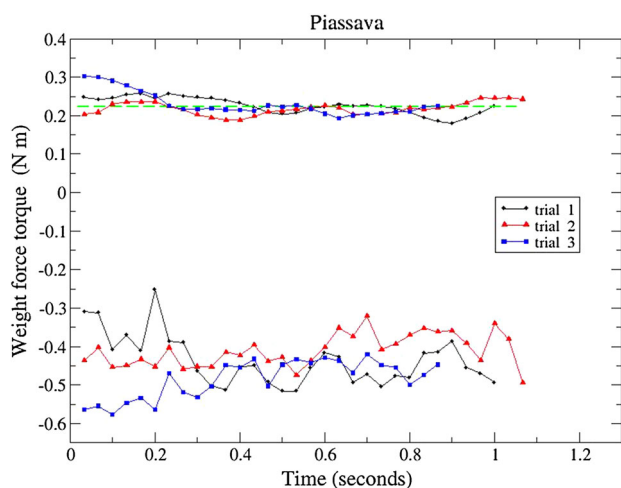
**Table 3** Torque of the tail and stone in the three trials of Chicaco and Piassava (mean  $\pm$  SD), along with the tail-to-body torque ratio

Chicaco	Tail torque (N m)	Stone torque (N m)	Tail torque/body torque
Trial 1	0.494 $\pm$ 0.052	-0.813 $\pm$ 0.134	0.61
Trial 2	0.531 $\pm$ 0.14	-1.265 $\pm$ 0.144	0.42
Trial 3	0.502 $\pm$ 0.054	-1.216 $\pm$ 0.051	0.41
Piassava			
Trial 1	0.226 $\pm$ 0.022	-0.406 $\pm$ 0.061	0.56
Trial 2	0.218 $\pm$ 0.017	-0.382 $\pm$ 0.039	0.57
Trial 3	0.23 $\pm$ 0.031	-0.451 $\pm$ 0.046	0.51

This ratio highlights the exact contribution of the tail to the balance of the system in each trial

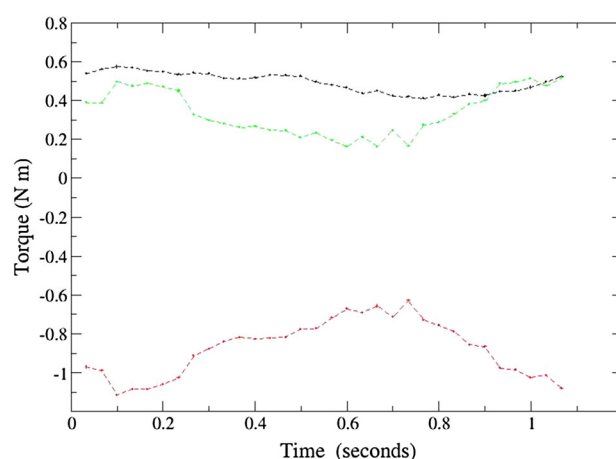


**Fig. 5** Torque of the tail (*top*) and the stone (*bottom*) in the three trials of Chicaco



**Fig. 6** Torque of the tail (*top*) and the stone (*bottom*) in the three trials of Piassava

The stone torque values may exhibit greater variation. As shown in Fig. 7, in the central phase of Chicaco's trial 1 (black lines), the gravitational torques decreased, since



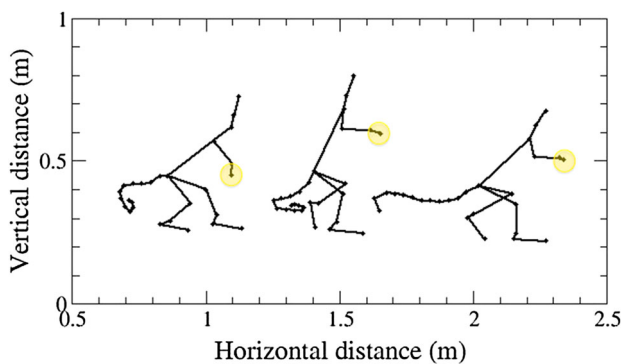
**Fig. 7** The sum of the torques of the body without the tail (*green dotted line*), the tail (*black dotted line*), and the stone (*red dotted line*) is equal to 0

Chicaco drew the stone near the chest, and thus the distance between the stone center of mass and the body without tail center of mass was reduced. At the same time, the torque of the tail component decreased much less, as the length of the leverage changed only slightly. Hence, the balance of the system was maintained. Piassava maintained a more constant posture in all trials by keeping the stone as close as possible to the center of mass, thus reducing the stone torque to about one-third of that of Chicaco.

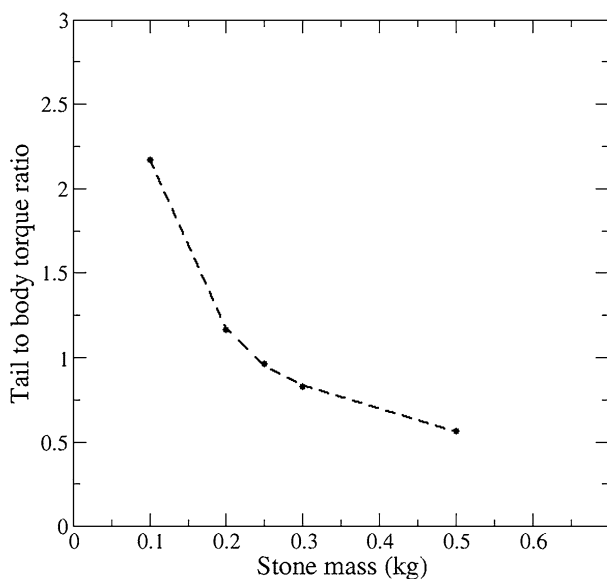
In both subjects, the torque of the tail compensated for 40–60 % of the torque of the stone, indicating that the tail, despite its small mass, had a fundamental role in balancing the capuchins' body during bipedal transport (see Table 3). Moreover, the tail's contribution to balance was dynamic and flexible. For example, in Chicaco's trial 2, we observed an increased torque of the tail, such that by the end of the transport, the torque value of the tail was 0.8 N m. During the same interval, the stone torque increased as well. In fact, as Chicaco was approaching the anvil and extending his arms to drop the stone, both the stone and his trunk

moved forward. Hence, to prevent the center of gravity of the system from moving too far forward, the tail increased its counter-torque, and extended from 0.13 to 0.34 m (Fig. 8). This extension of the tail clearly increased the system's stability.

As reported above, at approximately  $-1.2$  N m, Chicaco's stone torque was about three times that of Piassava. As the weight of the stone was the same for both subjects, it follows that the decreased stone torque of Piassava was achieved by reducing the stone's torque arm. Piassava achieved static equilibrium as a result of her elbow flexion pulling the stone closer to the  $COM_{system}$ . We performed a simulation by means of our numerical code that replaced the mass of Chicaco's body segments with those of



**Fig. 8** Three representative positions of Chicaco's trial 2 showing the increasing extension of the tail to counterbalance the stone torque when approaching the anvil



**Fig. 9** Ratio of the tail torque to the body torque in function of the stone mass assuming that Piassava would have a dynamic asset similar to that of Chicaco. The torque of the tail balances 50 % or more of the torque of the stone for stones with mass up to 0.5 kg

Piassava, while maintaining the same coordinates of Chicaco's body, thus making her assume the same body posture as Chicaco. This was possible because the geometric lengths of the limbs of the two subjects were within 10 % of each other. The simulation with stones ranging from 0.1 to 1 kg (Fig. 9) showed that the torque generated by Piassava's tail was able to maintain a stable transport (contributing at least 50 % to the total torque) only if the mass of the stone did not exceed about 0.5 kg. Thus, only with a stone of about 0.5 kg or lower mass could Piassava assume a posture similar to that of Chicaco (with an arm angle of approximately  $90^\circ$ ) and with a similar distance between the stone and the center of mass of the body. Therefore, the only way in which Piassava could maintain the balance while carrying a 1 kg stone, as she did in our experiment, was by bringing the stone closer to her center of mass, thus minimizing the torque of the stone.

## Discussion

We systematically prompted the transport of hammer stones in order to study wild capuchins' bipedal locomotion while carrying a load (see also Massaro et al. 2012) and to investigate the mechanical aspects of position and velocity of the center of mass and of the anatomical segments, the trunk inclination, the postures, the torque of the force applied on each anatomical segment, and the role of the tail in balancing the body during transport.

In this pilot study, we estimated the position of the center of mass in an adult male and adult female bearded capuchin transporting a 1-kg stone. The anatomical model took into account the mass of each body segment. Our calculations demonstrated that the center of mass was located at the abdomen level, and not at the hip level as inferred in previous kinematic studies on capuchins (Demes 2011; Duarte et al. 2012). Our estimate is in agreement with those proposed for chimpanzees and macaques (Yamazaki et al. 1979).

Trunk inclination and elbow joint angle are important parameters describing body posture during bipedal transport. During transport, the average forward inclination of the trunk of our subjects was about  $25$ – $27^\circ$ , occasionally reaching values lower than  $20^\circ$ . This result is in line with the trunk inclination of  $23^\circ$  reported by Duarte et al. (2012) in loaded capuchins and by Demes (2011) in unloaded capuchins. Therefore, there is convergent evidence that capuchins have a very upright posture while walking bipedally, probably the most upright among primates with the exception of humans and orangutans (Watson et al. 2009; Demes 2011).

The angle of the arm indicated how the stone was held and how close the stone was to the body and, therefore, to

the center of mass. During transport, because of their different body mass, the female and male faced different mechanical demands that led to different postures. Piassava's stability was compromised because she carried a stone weighing about half of her body mass; therefore, she flexed her elbow so that the load was as close as possible to her center of mass. In contrast, Chicaco, who carried a stone weighing about five times less than his body mass, used a more extended elbow (almost 90°) and held the load farther away from his center of mass. Our measurements concerning arm angles and erectness of the trunk are in agreement with those reported by Duarte et al. (2012) for capuchins of the same study group.

### Mechanics of transport

Our analysis of bipedal locomotion demonstrated that the tail and its extension play a key role in balancing the body during transport of loads. The contribution of the gravitational torque with respect to the center of mass provided by the tail was about 50 % of the torque generated by the stone, while the remaining 50 % of the stone's torque was compensated by the torque of the body without tail. This extraordinary tail torque was made possible by extending it and keeping it relatively parallel to the ground during transport such that its center of mass was brought backwards to maximize leverage. In our case, the center of mass of the tail was approximately three times farther from the center of mass of the total system than was the center of mass of the stone.

Moreover, we found that the monkeys changed the extension of the tail depending on the position of the stone with respect to the center of mass. For example, Chicaco's tail in trial 2 reached maximum extension when he approached the anvil and lowered the stone to the ground (Fig. 8). In this phase of the trial, the tail torque completely counterbalanced the other gravitational torques of the body. Without the tail extension, Chicaco would have fallen forward.

Surprisingly, despite constituting only 5 % of the entire body mass, the tail had a fundamental dynamic role. Without this part of their anatomy, the load-carrying capacity of capuchins would be much lower than was observed in this study. Given Piassava's morphological characteristics and body mass, her actual transport of a 1-kg stone was made possible by both extending her tail and by carrying the stone close to the center of mass, so as to decrease the instability related to the stone torque. In fact, by calculating the ratio between tail and body torques in relation to stone mass, and assuming that Piassava would have the posture and the dynamic equivalent of Chicaco, our simulation demonstrated that Piassava's balance could be guaranteed by a stone mass of about 0.5 kg or less.

Here, we described the transport of heavy loads by capuchin monkeys and the function of the tail. In particular, we demonstrated that extending the tail keeps the center of mass closer to the center of the body, thus helping to maintain balance, and that the tail allows the transport of loads not bearable without its extension.

Future research should systematically investigate the extent to which individuals of different body mass are able to modulate tail extension, trunk inclination, and posture in relation to the mass of the stone carried. Furthermore, a full dynamic study should calculate the angular acceleration around the instantaneous center of rotation, which would require complete knowledge of GRFs acting on the feet when both are touching the ground.

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