

Vertical bipedal locomotion in wild bearded capuchin monkeys (*Sapajus libidinosus*)

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Abstract When carrying objects, nonhuman primates often show bipedal locomotion. Studies of primate bipedality, however, in both nature and captivity, have concentrated on locomotion on horizontal substrates, either terrestrially or arboreally. No observational or experimental study seems to have looked at non-horizontal bipedality, yet we show here that it occurs often in nature in *Sapajus libidinosus*, the bearded capuchin monkey. The context is transport of small food items from source to site of consumption, in which the monkeys usually carry handfuls of maize kernels over several meters' distance, both on the ground and in the trees. Most impressively, over a fifth of such bouts are done vertically, when the tree trunk is fully upright. Such vertical bipedality, with or without transport, apparently has not been reported before.

Keywords *Cebus libidinosus* · *Sapajus libidinosus* · Bipedality · Transport · Locomotion

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Introduction

Bipedality has been studied exhaustively, especially because of its important place in human evolutionary origins. This longstanding fascination, since Darwin's day, has yielded plentiful empirical and theoretical treatments, many to do with testing hypotheses of its function (Hunt 1994; Richmond et al. 2001; Niemitz 2010). For living primates, at least, it might be assumed that bipedality's various manifestations in nature are well known, but here we report a previously-undescribed variant.

So far as we can see, all prior descriptions of bipedal locomotion in primates have focused on behavior on horizontal or near-horizontal substrates—e.g., *Hylobates* (Vereecke et al. 2006); *Macaca*, (Nakatsukasa et al. 2004); *Pan* (Aerts et al. 2000; Sockol et al. 2007); *Papio* (Berillon et al. 2010). In nature, these may be terrestrial (on the ground's surface) or arboreal (on tree boughs), including non-experimentally induced situations, like the chimpanzees crop-raiding (Albrecht and Dunnett 1971) and bonobos branch-dragging (Kano 1992). In captivity, these substrates may be treadmills, specially constructed walkways, floors, or other horizontal surfaces. It seems to be assumed that when primates move on tilted surfaces, such as those angled at 0–45°, then bipedality shifts to quadrupedality, although we can find no behavioral evidence or explicit mention of this. Apparently, the possibility of vertical bipedalism (on surfaces angled at 75–90°) is not considered.

Here, we report non-horizontal bipedal locomotion that is spontaneous, habitual, and commonplace in a free-ranging population of New World monkeys. This form of bipedality occurs daily in a dry forest environment, on woody vegetation angled at slopes ranging from 0° to 90°, that is, from flat horizontal to totally vertical. This behavior

is expressed as unassisted bipedality; that is, during its performance the upper limbs play no part in supporting the locomoting individual.

The locomotion of capuchin monkeys (*Cebus* and *Sapajus*) has been well studied, both in captivity (Wallace and Demes 2008; Demes 2011; Demes and O'Neill 2013), and in nature (Duarte et al. 2012; Hanna et al. 2015, Massaro et al. 2016). Captive studies have used a 10-m long runway on the floor, fitted with force plates (see Fig. 1 in Demes 2011); ethological observations have followed monkeys moving on the ground (see Fig. 1 in Duarte et al. 2012). All such studies have focused on horizontal locomotion.

The aim of this paper is to report preliminary ethnographic information on upright, striding bipedal locomotion (Hunt et al. 1996) on both horizontal and non-horizontal substrates, both terrestrial and arboreal. This is a pilot study, but it involves many individuals of both sexes and all ages, showing many more instances of bipedality than is the norm in such studies.

Methods

Study site and subjects

Wild bearded capuchin monkeys (*Sapajus libidinosus*) living in Serra da Capivara National Park (SCNP), Brazil, were observed in free-ranging daily life (see Ottoni and Izar 2008, for general background). The monkeys were from two groups, Pedra Furada (PF) and Gato (GT); PF has been studied since 2007 and was fully habituated to close-range observations (Falótico and Ottoni 2013, 2014, 2016). GT had not been studied before, but was encountered often during research on other study groups (Mannu and Ottoni 2009). At the time of study, PF numbered 41 members and GT approximately 50 members; the groups' combined age-sex make-up was typical for the species in nature (adult males—33 %, adult females—31 %, juveniles—23 %, infants—12 %; adult M/F ratio—1.08 Fragaszy et al. 2004).

The park (08°26'50"–08°54'23"S, 42°42'53"–42°10'21"W) covers 1300 km² of Caatinga ecotype, that is, semi-arid, thorn-bush vegetation, with a highly seasonal climate. Mean annual rainfall is 689 mm and mean annual temperature averages 28 °C (Mannu and Ottoni 2009). Park staff provision the groups regularly during the dry season with dried maize grain and cut-up bananas, pumpkin, and cassava roots, for the benefit of tourists and to encourage the groups to stay inside the park's area. During our data collection, kernels of maize (*Zea mays*) overwhelmingly predominated; it was placed in wooden troughs or secreted in cavities or cracks in dead tree-

stumps. The woody vegetation in the feeding areas is broken-canopy dry forest with little undergrowth; most of the substrate is flat, bare earth. The trees at the feeding sites are broad-leaved, typically have single trunks, and are no more than 10 m tall.

We collected data at three feeding sites, each of these locations were inside one of the group's ranges:

- Old House—GT group—feeding site near an abandoned dwelling. Open dry bush vegetation with some larger trees nearby.
- Guarita—PF group—feeding site close to the park entrance of the Boqueirão da Pedra Furada area. A more open area, with dry bush vegetation.
- Gameleira—PF group—primary feeding site for this group. Near to a high rock face; vegetation with taller/bigger trees was comparable to Guarita.

Sampling

We recorded observational data at the three feeding sites: Old House, $n = 128$ episodes; Guarita, $n = 27$; Gameleira, $n = 23$. We made observations on 29 and 31 July and on 1 and 3 August, 2014, and had 12 h 45 min of contact time with the PF group and 2 h 20 min with the GT group. Data from sites, groups, and days were combined into a single sample for analysis (see below).

WCM took ad lib notes (Martin and Bateson 2007) of the monkeys' locomotion in the feeding sites, over a 4-day period in the dry season. He stood 5–15 m from the monkeys; visibility was excellent, given the sparsity of herbaceous vegetation. He attempted to record complete locomotory sequences that began when the monkeys acquired food and continued uninterrupted until they stopped to consume it. He made no attempt to interact with the monkeys and avoided any intrusion into their social interactions. He recorded data from two groups of monkeys: PF (two sites), $n = 50$ episodes, and GT, $n = 128$.

The following independent variables were noted when possible: date, site, group, type of substrate, orientation of substrate. Sex and age-class were also noted, but sporadically, so will not be investigated here. The following dependent variables were noted: pedality, object transport, style of transport, leap, drop, distance moved. Table 1 gives definitions and explanations for these variables.

Distance traveled by the locomoting monkey was estimated by eye, to the nearest meter or half-meter, depending on distance from the observer. Concurrently, the observer's accuracy of estimation was tested ($n = 3$ times) by pacing off an estimated distance; accuracy was at least 85 %, which was deemed acceptable for this pilot study. Steps occurred too quickly to be counted in the 'live' ethological data but were counted in the video analysis (see below).

Table 1 Definitions and details of variables recorded

Variable	Definition
Episode	Sequence of pedality with transport of food, from acquiring food until settling to eat it. Includes pauses and changes of gait, posture, direction, or substrate. Comprises one or more bouts
Bout	Uninterrupted performance of one type of pedality with transport, thus bout-length determined by change of pedality, pause, or substrate, but not of direction or posture
Pedality	Number of limbs supporting body weight during locomotion, hence unipedality, bipedality, tripedality, or quadrupedality
Substrate	Terrestrial (ground, rocky outcrop); arboreal (woody vegetation, usually tree), or other/unknown. Ground was always flat and horizontal; arboreal varied from horizontal to vertical (see Orientation of transport).
Orientation of transport	From 0° (3 o'clock), horizontal, 0–30° (counter clockwise); oblique, 30–75°; vertical, 75–90° (ca 12 o'clock). Estimated by eye
Tree	Individually identified and numbered tree, sometimes used repeatedly
Object	Maize, other (combines pumpkin, or other foods), unknown
Style	Mode of transport, including: (1) hands held side-by-side, palms upward, carrying one mass of food in both hands as single mass, (2) same but with wrists and forearms also held together, (3) hands held separately, each carrying food, and (4) only one hand carries food. Forearms extended horizontally forward, outstretched in front of trunk, or held against the chest, and parallel to the trunk
Leap	Single bipedal jump up from ground to vegetation, or from one spot to another in vegetation
Drop	Some carried items dropped, then abandoned and not retrieved
Step	Touchdown of <i>a</i> limb in alternating bipedal sequence (cf. stride is touchdown of the <i>same</i> limb in a repetitive sequence. Duarte et al. 2012). Thus, number of steps usually was twice the number of strides, but single steps sometimes occurred, when a monkey changed bouts

Concurrent to WCM's notes, TF and AI recorded 86 episodes ad libitum (Martin and Bateson 2007) using two camcorders at the three sites. The data were recorded from the two groups: PF ($n = 41$) and GT ($n = 45$). The PF group was recorded at two sites: Gameleira ($n = 27$) and Guarita ($n = 14$); the GT group was recorded only at the Old House site.

For video analyses, we used the same variables as for the observational data collection (Table 1), with the only differences being that (1) we recorded the number of the monkeys' steps instead of the estimated distance traveled, and (2) recorded whether the tail was used as support. We used Noldus Observer XT 12 to code the video data.

We also measured the trees at the sites. For all 535 living trees within 10 m of each feeding source, we noted diameter at breast height (DBH) in cm, distance of tree from feeding source in meters, and inclination of the tree trunk to nearest degree using the app TiltMeter on an iPhone 5s.

Data analysis

Locomotor behavior was divided into *episodes*, that is, one sequence of locomotion from acquisition of food to cessation of locomotion, typically to start eating it. Episodes were subdivided into *bouts*, that is, components broken up by either a pause (of only a second or two), a transition from terrestrial substrate to vegetation substrate (typically arboreal), or a change of pedality. Thus, a behavioral episode could have but one bout, if the monkey never paused

or changed gait and stayed on the ground; two or more bouts necessarily meant at least one pause or transition.

Behavioral and habitat data were entered into an Excel spreadsheet and later analyzed in SPSS 20. We used descriptive statistics to analyze the data and a non-parametric test (Kruskal–Wallis) to compare distance and steps between substrates, and tree trunk diameters across sites.

Results

Empty-handed monkeys typically approached the trough or baited stumps quadrupedally and retrieved handfuls of maize kernels. They scooped these up with both hands, then stood up bipedally (with both hands holding batches of maize) or tripedally (with one hand doing so). They then moved away from the food source (Fig. 1, Video in Online Resource 1), apparently to seek shade or to avoid congestion or competition from conspecifics or peccaries (*Pecari tajacu*). When bipedal on the ground, their gait was alternate-striding walking/running; when arboreal, it was alternate-striding walking (Hunt et al. 1996). Occasionally they moved over the ground or low, flattish, rocky outcrops, but often they ascended nearby trees. During this transport, they often paused, apparently to rest briefly, before continuing; they sometimes dropped grains of maize in the process. At the base of trees they were about to ascend, they sometimes did a single leap bipedally from the ground onto the tree trunk, as if to gain momentum before continuing locomotion upwards. Occasionally, a monkey

Fig. 1 Video stills of substrate types and bipedality modes.

a Ground bipedality, **b** oblique bipedality in tree, **c** vertical bipedality in tree, and **d** bipedality on rock face



moved directly, leaping from the feeding source to a tree trunk, if the tree was close by. Once a spot for consumption was reached, the monkey settled to eat, and the episode ended.

Overall, we recorded 265 episodes (direct observation = 179, video = 86) of locomotion with transport. These episodes comprised 505 bouts (Table 2). Most ($n = 143$) of these episodes had two bouts (Table 3), with the typical sequence being locomotion on the ground away from the provisioning site, followed by ascending a tree. However, there were 79 episodes of one single bout, that is going directly from the provisioning site to the eating place, either on the ground only ($n = 186$) or into a tree ($n = 20$). The latter was possible only when the tree trunk was within 1 m of the food source.

For *episodes* of observational data, the mean total distance traveled while carrying food was 11.9 m (median = 10, range = 1–37, SD = 7.7). Again, variation was huge: the longest episode of locomotion comprised bouts of 20 m of bipedal travel on the ground, then 7 m of travel on a branch, then another 10 m of travel on another branch.

From the videos, we analyzed 86 episodes containing 181 bouts of pedality with transport. Each bout had a mean of 10.1 steps (median = 7, range = 1–53, SD = 9.2). The

terrestrial/horizontal step count was greater (mean = 14.6, median = 12, range = 2–53, SD = 10.04) than the arboreal/non-horizontal ones (mean = 5.2, median = 4, range = 1–18, SD = 3.6) ($K-W$, $\chi^2 = 60.9$, $df = 2$, 2-tailed, $p < 0.001$).

More than half (57 %) of bouts were engaged on horizontal substrates, with lesser amounts done vertically or obliquely (Table 2). Proportions were similar across observational and videotaped data, except that more than a third of the observational bouts could not be categorized, because of data-recording constraints. When only videotaped data, which provided complete classification, were analyzed, non-horizontal locomotion accounted for 45 % of bouts. Over a fifth (21 %) of bouts were straight-up vertical in orientation. These vertical/oblique transports also were performed more bipedally (73 %) than tripodally or quadrupedally (27 %).

For *bouts* overall, the mean distance traveled was 6.7 m. (median = 4.2, range = 0.5–35, SD = 6.3). The longest bout was 35 m of bipedal travel on the ground. However, like the step data, terrestrial/horizontal bouts were longer (mean = 9.6 m, median = 7, range = 1–35, SD = 6.7) than arboreal/non-horizontal ones (mean = 2.5, median = 2, range = 0.5–11, SD = 1.8) ($K-W$, $\chi^2 = 146.2$, $df = 2$, 2-tailed, $p < 0.001$).

Table 2 Frequency (bouts) of variables comparing observations and videos

Variable	Observations (<i>n</i> = 324) <i>n</i> (%)	Video (<i>n</i> = 181) <i>n</i> (%)	Total (<i>n</i> = 505) <i>n</i> (%)
Pedality			
Bipedal	240 (74 %)	137 (76 %)	377 (75 %)
Tripedal	84 (26 %)	39 (21 %)	123 (24 %)
Quadrupedal	0	5 (3 %)	5 (1 %)
Style of transport			
Combined wrists and hands	NA	81 (45 %)	81 (45 %)
Combined hands	NA	45 (25 %)	45 (25 %)
One hand	NA	50 (27 %)	50 (27 %)
Separate hands	NA	5 (3 %)	5 (3 %)
Orientation of transport			
Horizontal	189 (58 %)	99 (55 %)	288 (57 %)
Vertical	8 (3 %)	39 (21 %)	47 (9 %)
Oblique	6 (2 %)	43 (24 %)	49 (10 %)
Unknown/other	121 (37 %)	0	121 (24 %)
Substrate			
Ground	190 (59 %)	95 (53 %)	285 (56 %)
Vegetation	133 (41 %)	82 (45 %)	215 (43 %)
Unknown/other	1 (0.5 %)	4 (2 %)	5 (1 %)

NA not available

Table 3 Number of bouts per episode comparing two data sets, observation and videotape

Bouts	Observations	Video	Total
One bout	52 (29 %)	27 (31 %)	79 (30 %)
Two bouts	111 (62 %)	32 (37 %)	143 (54 %)
Three bouts	14 (8 %)	21 (24 %)	35 (13 %)
Four bouts	2 (1 %)	4 (5 %)	6 (2 %)
Five bouts	0	1 (1 %)	1 (0.5 %)
Six bouts	0	1 (1 %)	1 (0.5 %)
Total	179	86	265

Most ($n = 377$, 75 %) of the locomotor transport bouts were bipedal, while the others ($n = 123$, 24 %) were tripedal. Only five (1 %) were quadrupedal (i.e., small amounts of food grasped in the hands or feet simultaneously used for support), and there were no unipedal (i.e., food carried in one foot while the other foot provided only support) transports of food. Thus, bipedality was the norm. During bipedal and tripedal transport, the monkey's tail was recorded as touching the substrate in, respectively, 8.8 and 12.8 % of the videotaped bipedal and tripedal bouts. In only four bouts did the tail grasp vegetation; in the other 13 bouts, the monkey's tail just loosely touched on the substrate. Most of the tail support happened when the monkeys were locomoting on vertical substrates, but it occurred in less than a third of bouts (28.2 % of the vertical bouts). The majority (56 %) of bouts of locomotor transport occurred on the

ground, versus 43 % above the ground, in vegetation. Observational and videotaped proportions were very similar.

Transport of the food (observations obtained only from videotapes) was done using four types of carrying, but most (72 %) were with both hands/wrists (Table 2). One-handed carrying usually was performed when the monkeys were using tripedal locomotion. No data were available on type of transport from the observational data.

The abundance of trees around the feeding source at each site shows that plenty of trees were available close to the feeding sites, with a wide range of size and inclinations, from almost straight up to horizontal. Qualitative differences were observed across sites for all three variables, although some pairwise comparisons showed no differences (see Table 4).

Discussion

The locomotor behavior of capuchin monkeys has been well studied, but primarily on horizontal surfaces (Wallace and Demes 2008; Demes and Carlson 2009; Carlson and Demes 2010; Duarte et al. 2012; Massaro et al. 2016). Some of those studies also focused on bipedal locomotion, but always horizontally. We can find no mention of bipedality being tested or described on other substrate inclinations; until baseline data on activity budgets of these free-ranging monkeys are presented, we cannot judge the validity of this apparent bias.

Table 4 Characteristics of trees at provisioning sites

	Gameleira	Guarita	Old house	<i>K</i> – <i>W</i> test	Pairwise test
<i>n</i>	289	196	50	–	
DBH (cm)					
\bar{X}	18.0	14.1	28.5	$\chi^2 = 43.4, df = 2, \text{two-tailed}, p < 0.001$	Gam-Gua— $p < 0.001$
Med	13.9	11.0	23.7		Gam-Old_H— $p < 0.001$
Range	6.5–71	7.2–44	7.5–94		Gua-Old_H— $p < 0.001$
Feed site dist (m)					
\bar{X}	5.75	5.8	7.4	$\chi^2 = 18.3, df = 2, \text{two-tailed}, p < 0.001$	Gam-Gua— $p = 0.965$
Med	5.9	6.1	7.15		Gam-Old_H— $p < 0.001$
Range	0–10	1–17	3–10		Gua-Old_H— $p < 0.001$
Inclination (degrees)					
\bar{X}	80	71	65	$\chi^2 = 93.9, df = 2, \text{two-tailed}, p < 0.001$	Gam-Gua— $p < 0.001$
Med	84.0	74.5	70.5		Gam-Old_H— $p < 0.001$
Range	5–90	16–90	3–90		Gua-Old_H— $p = 0.322$

n corresponds to all trees in a 10-m radius around provisioning places

The carrying of objects, including food, during bipedal locomotion, has long been known for various species of non-human primates (Hewes 1961; Carvalho et al. 2012). Lacking the cheek pouches of Old World monkeys and apes (Lambert 2005), New World monkeys must use their hands, if they are to transport granulate items. However, a catarrhine exception occurs in Japanese macaques (*Macaca fuscata*) who transport grain from source to processing site, when processing entails treatment of unaltered (e.g., unmoistened) food items (Hirata et al. 2001). For non-granulate items, such as sweet potatoes, the hands are also used if the size of the transported objects exceeds the volume of the cheek pouches.

We have described a new variant of locomotor behavior in capuchin monkeys, showing that capuchins use bipedal locomotion on tilted and even vertical surfaces when carrying objects. That this apparently has not been recorded at the other main study site of this species, Fazenda Boa Vista (FBV), is not surprising, as the monkeys there mostly carry food and tools for processing on the ground (Duarte et al. 2012). Although the different type of food (granulate/non-processed vs one-item/processed) could be a partial explanation for that variant, capuchins in SCNP also transport naturally available cashew nuts and stone tools bipedally up the trees to break the nuts using tree branches as anvils (T. Falótico, personal observation). The transport of tools and cashew nuts up trees to process them has also been reported in FBV, although with no mention of the locomotor type used (Visalberghi et al. 2016).

Vertical climbing is important for several primates, and capuchin vertical bipedality appears to fit well with the data on climbing by spider monkeys (*Ateles geoffroyi*), showing that, during vertical climbing, hind limbs are the ones that generate propulsion rather than fore limbs, used

mostly to keep the body close to the substrate (Hirasaki et al. 2000).

The distances covered by the capuchins were impressively long, in relation to the body size of the monkeys, compared to previous studies. In experimental studies of transport of a stone and nut to an anvil, the capuchin monkeys traveled only 4 m (Duarte et al. 2012; Hanna et al. 2015) and 6 m (Massaro et al. 2012). The authors did not explain why these distances were chosen; perhaps the much heavier weight of the stone dictated the shorter carrying distance. Carvalho et al. (2012) presented observational data on (much bigger) wild chimpanzees transporting hammer-stones, nuts, and pilfered cultigens but gave no data on absolute distances traversed.

We recorded several aspects of normative transport behavior, including locomotion bipedally on oblique and vertical surfaces, using hands and wrists combined to hold the transported items. Individuals may use only one hand to hold the food during transport, which allows them to use tripodal locomotion, but if they choose to use both hands, then they must locomote bipedally. Our data showed that capuchins do both types of locomotion, but predominantly choose bipedality over tripodality, optimizing the quantity of food transported. Use of the tail by the monkeys for additional support during locomotion was registered, mostly during vertical locomotion, but was not the norm.

Bipedal locomotion as reported here seems to be a response to conditions in which it is useful to carry many small items in a batch, in this case, loose kernels of maize. Switching to an upright position frees the hands from locomotion, making them available for carriage. Bipodality is more efficient than tripodality, as it doubles the holding capacity of the hands. Moreover, it allows the use of both hands (and wrists) in combination, thus increasing the

individual's carrying capacity, versus using each hand separately or the mouth to carry objects. At SCNP it was advantageous to maximize the food transported in each attempt, given the direct and indirect competition for food at the troughs. Carrying food to peripheral locations allows consumption with less interference from other monkeys (similar transport of grain to another site, in order to avoid piracy, has been reported for Japanese macaques on Koshima, with wheat grains, Hirata et al. 2001). Another factor encouraging transport is the position of the maize on or just above the ground, where the monkeys are probably more vulnerable to predation: taking the food up into the trees or onto cliff-faces is more secure than eating at the terrestrial provisioning site.

Preliminary data on the hundreds of trees at the feeding sites reveal them to be plentiful and apt for ascent, that is, their range of girths provides ample access to the canopy for a monkey whose hands are occupied with carrying food. As seen in the video footage, the tree trunks suffice for bipedal locomotion, even when they are essentially cylindrical, with few or no side branches. The trees available are quadrupedally climbable but also afford abundant opportunities for bipedally walking along oblique or vertical surfaces. Future study should focus on whether or not monkeys are selective in their choice of trees ascended, and if so, what characteristics of the trees determine their choices. Only one of the sites, Pedra Furada, has a rock face near the provisioning site; it was used but not frequently enough to allow comparison with arboreal ascent.

Because we did not collect systematically sampled data over time, we do not know the true frequency of vertical bipedality in the population, but the qualitative and quantitative data indicate that it occurs often and is widespread. Hundreds of bouts seen over only 4 days of data collection, and the presence of the behavior in both study groups shows it to be customary. Although there seem to be no reports of this kind of locomotion elsewhere, it probably occurs in other populations, especially ones that show frequent terrestriality. Unlike forest populations of *Cebus/Sapajus*, the SCNP monkeys, like other Savannah groups, spend almost half (44 %) of their waking hours on the ground (Falótico 2011).

Fleagle et al. (1981) hypothesize about the link between vertical climbing and bipedalism. The locomotor pattern we describe here shows that bipedality happens even in climbing situations, and that capuchin monkeys climb using only their hind limbs. Maybe monkeys' bipedal climbing is more similar to human bipedality and could be used as a model for understanding bipedal evolution in the human lineage.

Ours was only a serendipitous pilot study, so more detailed studies, including biomechanical, kinematic and functional morphological analyses, are needed — in the

wild, to verify the nuances of this behavior, and in the laboratory, to study its biomechanical features. For example, we were unable in our short observation period to collect enough data on obvious independent variables like age and sex, nor any data on individual differences. Much remains to be done.

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