AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 138:210–220 (2009)

Kinematics and Energetics of Nut-Cracking in Wild Capuchin Monkeys (*Cebus libidinosus*) in Piauí, Brazil

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KEY WORDS tool use; percussion; upright stance; nonhuman primate

ABSTRACT Wild bearded capuchins (*Cebus libidinosus*, quadrupedal, medium-sized monkeys) crack nuts using large stones. We examined the kinematics and energetics of the nut-cracking action of two adult males and two adult females. From a bipedal stance, the monkeys raised a heavy hammer stone (1.46 and 1.32 kg, from 33 to 77% of their body weight) to an average height of 0.33 m, 60% of body length. Then, they rapidly lowered the stone by flexing the lower extremities and the trunk until the stone contacted the nut. A hit consisting of an upward phase and a downward phase averaged 0.74 s in duration. The upward phase lasted 69% of hit duration. All subjects added discernable energy to the stone in the downward phase. The monkeys exhibited individualized kinematic strategies, similar to those of human weight lifters. Capuchins illustrate that human-like bipedal stance and large body size are unnecessary to break tough objects from a bipedal position. The phenomenon of bipedal nut-cracking by capuchins provides a new comparative reference point for discussions of percussive tool use and bipedality in primates. Am J Phys Anthropol 138:210–220, 2009. © 2008 Wiley-Liss, Inc.

The present study provides the first systematic kinematic analysis of percussive tool use in capuchins. Archeological evidence suggests that our ancestors developed percussive tool use as early as 2.7 million years ago (Heinzelin et al., 1999), and this form of tool use is likely among our ancestors' earliest technological discoveries. In contemporary humans, percussive tool use is widespread around the world (Goren-Inbar et al., 2002). Recently, it has been discovered that wild-bearded capuchins crack nuts in seasonally dry forest habitat (Cerrado) using large stones (hereafter, Boa Vista; Fragaszy et al., 2004a, see Fig. 1). This behavior is apparently widespread among capuchins living in the Cerrado of Brazil (Ottoni and Mannu, 2006). Study of these capuchins provides a valuable comparative reference point for hominine percussive tool use, as well as routine bipedality, in a phylogenetically distant member of the primate order.

The best-known example of percussive tool use in nonhuman primates is nut-cracking by wild chimpanzees, reported in many sites in western Africa (reviewed in McGrew, 2004). Chimpanzees use a stone or wooden hammer in a seated position to crack open nuts placed on an anvil. The movement can be performed in a unimanual, or less frequently, a bimanual fashion, depending on the properties of the nuts and the materials available for use as hammers and anvils (Boesch and Boesch-Achermann, 2000).

Chimpanzees use relatively smaller hammers (in proportion to body mass) to crack nuts compared to the capuchins at Boa Vista. Visalberghi et al. (2007) reported that the average mass of the stones found on or near the anvils at Boa Vista was 1.096 kg, which is 30–44% of their adult body mass (assuming masses of adult males and females are 3.7 and 2.5 kg, respectively; Fragaszy et al., 2004b). By comparison, one wild chimpanzee in the Taï Forest used hammer stones that were 6.6% and 14.3% of body mass (Günther and Boesch, 1993).

Given the difference in the proportional mass of the hammer to the body, it is unsurprising that capuchins crack nuts using a very different set of postures and actions than do chimpanzees. Wild capuchins (*Cebus libidinosus*) crack nuts by lifting stones bimanually in a bipedal posture (see Fig. 1), rather than swinging one arm from a seated position.

We assume that during nut-cracking, capuchins concurrently attempt to maximize the force of the strike on the nut (to maximize the effectiveness of their strike) and to avoid injury to themselves. The force of the strike is correlated positively with the vertical distance the stone travels downward. Lifting a heavy weight safely is associated with stable bipedal posture and keeping the stone close to the center of mass of the body (Smith et al., 1995). Therefore, we predict that the capuchins should lift the stone as high as possible while maintaining a strong grip for control, to bring it down with added force, and to keep it (especially while lifting) close to the center of mass of the body.

Grant sponsor: National Geographic Society; Grant number: CRE7749-04; Grant sponsor: National Science Foundation; Grant number: BCS 0125486; Grant sponsor: Fapesp; Grant number: 06/51577-2; Grant sponsors: LSB Leakey Foundation, CNPq.

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Received 22 January 2008; accepted 26 June 2008

DOI 10.1002/ajpa.20920

Fig. 1. Two monkeys cracking a nut on the log. (**a**) An adult male (illustration of upright extension of knee, hip, and trunk). (**b**) A juvenile (jumping off the anvil at this instant). (Photographs by B. Wright). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

Capuchins have the anatomy of a generalized quadrupedal primate (Fleagle, 1999). Like other quadrupedal primates, capuchins have smaller gluteal muscles than humans, and they attach more laterally to the pelvis, different from the dorsal attachment in humans (Stern, 1971; Marzke et al., 1988). The gluteus in a quadrupedal primate is active against rotation of the hip. It can stabilize posture in an upright position when the hip is bent, but not when the hip is extended. This means that capuchins cannot use the gluteus to lift weights as effectively as can humans, and moreover they cannot achieve as full extension of knee or hip during weight-bearing as can humans. Thus, we expect that the capuchins will achieve bent knee–bent hip postures, rather than full extension of the knees and hips, during nut-cracking.

However, capuchins may make facultative postural adjustments (such as turning the feet outward) that in humans enhance the stability of bipedal stance, thus compensating to some degree for the weaker gluteals in achieving and maintaining erect posture. Capuchins may make more use than humans of their relatively stronger musculature of the upper body and fore limb in the lifting action. They may also exhibit more sequential movements of the leg than humans display with the legs during weight lifting, or they may exhibit a different sequence of movements than humans. In humans, during explosive lifts (see Fig. 2), the feet come off the substrate; the lifter "jumps" into the air at the moment of maximum upward acceleration (Baechle et al., 1994). Capuchins may exhibit this movement, even when the knee and hip are less than fully extended by human standards.

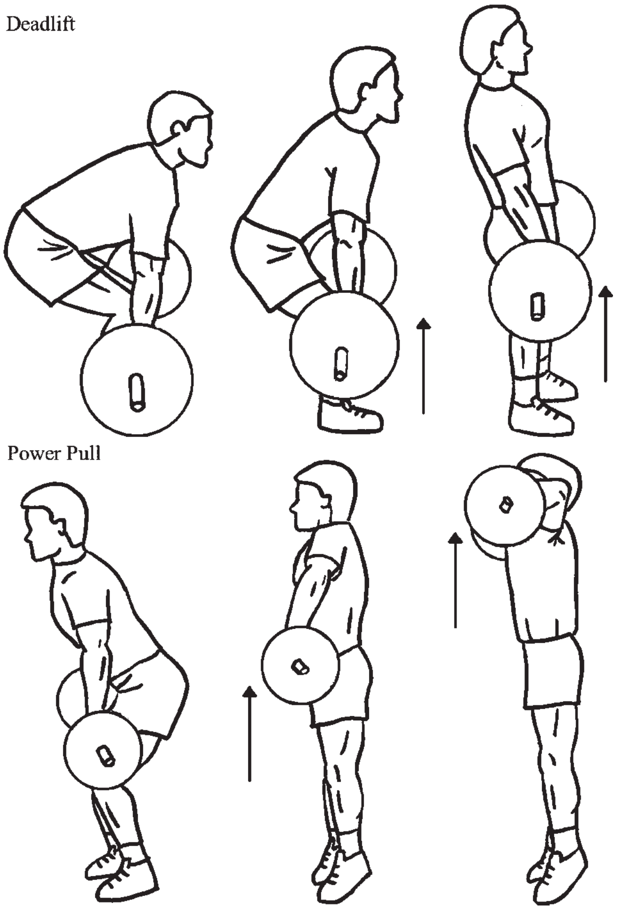

Fig. 2. Deadlift style powerlifting (first row) and power pull (second row). (Illustrated by A. Bradwell; adapted from Baechle et al., 1994).

METHODS

Site and natural resources

The study site (9°south, 45°west, altitude ~420 m above sea level) is located on private property (Fazenda Boa Vista) in a dry woodland plain in Piauí, Brazil. The area is punctuated by sandstone ridges, pinnacles, and mesas rising steeply to 20–100 m above the plain (Visalberghi et al., 2007).

In June 2005 and February 2006, we observed a group of wild capuchin monkeys (*C. libidinosus*) in one nut-cracking site where there were anvils, stones, and trees (Figs. 1 and 3). The nuts the monkeys cracked in this study (*Attalea* sp.) had an oval shape and were up to 5-cm diameter in width and 6-cm diameter in length (Fragaszy et al., 2004a). Several stones of varying shape,

Fig. 3. (**a**) One species of the palm nuts cracked by monkeys in Boa Vista; the rule indicates centimeter. The nuts were cut with a machete. (Photograph by E. Visalberghi) (**b**,**c**) Hammer stones used by the monkeys in the study. (Photographs by T. Faloticò) [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

TABLE 1. Characteristics of subjects and weight of hammer stones they used

Subject	Sex	Estimated body length[a] (m)	Body weight	Weight of hammer stone (kg)
Chicao (CH)	Male	0.59	4.4	1.46 kg
Segundo (SE)	Male	0.59	3.7[b]	1.46 kg
TeNinha (TN)	Female	0.56	2.3	1.46 kg
Piaçava (PI)	Female	0.48	1.9	1.32 kg in 5 hits, 1.46 kg in 5 hits

[a] Body length for each monkey was estimated by adding the lengths of the following body segments: neck (ear–neck), trunk (neck–pelvis), thigh (hip–knee), lower leg (knee–ankle), and foot (ankle-MTP); these segments are defined in Table 2.

[b] The average weight reported for adult males of this species (Fragaszy et al., 2004b) was used as an estimated weight for this individual; a direct weight was not available.

composition, and mass were at the anvil site. In our sample, all the monkeys used one quartzite stone (1.46 kg), and one monkey also used a slightly smaller stone (1.32 kg).

Subjects

Four adult capuchin monkeys (two males, Chicao and Segundo, and two females, Teninha and Piaçava) served as subjects in this study. We determined the monkeys' body lengths (from auditory meatus to ankle) by measurements made from video images (see below), and body weights were obtained for three of the four monkeys by the monkeys' voluntary use of an electronic platform scale (Visalberghi et al., unpublished data). These data are shown in Table 1. The monkeys were judged to be fully adult based on body weight and length, color of facial hair, and shape of the tuft of hair at the crown of the head (Fragaszy et al., 2004b). The larger male weighed 4.4 kg; the smaller female weighed 1.9 kg. Thus, the stone weighing 1.46 kg that was used by all the monkeys was 33–77% of the body weight of these four individuals. The second stone, used only by the smaller female in our samples, was 69% of her body weight.

Data capture setup

We videotaped the monkeys' movements when they were cracking nuts on a log anvil. Standard two-dimensional motion measurement methodology was used (Robertson et al., 2004). A Canon^{TM} GL2 mini-DV camcorder (60-Hz sampling rate; shuttered at 1/2,000 s) was used for video taping. The camcorder was placed within a blind structure ~11.5 m away from the anvil to capture sagittal plane views (field of view was ~1.5 m) of the monkeys during nut-cracking.

TABLE 2. Points coded in the spatial model

Point no.	Point name	Anatomical definition	Landmark identification
1	Ear	Auditory meatus	Center of ear if meatus not identifiable
2	Neck	Cervico-thoracic intervertebral joint	Dorsal edge of cervico-thoracic intervertebral joint, estimated as the point where the neck articulated with the trunk
3	Shoulder	Glenohumeral joint	Center of point where upper arm pivoted with respect to torso
4	Elbow	Elbow joint	Center of point where upper arm and forearm pivot
5	Wrist	The ulnar prominence	Visible
6	MCP	Metacarpophalangeal joint of the third finger	Visible, also used as a proxy for the position of the hammer stone
7	Hip	Center of femoral head	Estimated location of femoral head; center of thigh at articulation with acetabulum of pelvis
8	Knee	Tibio-femoral joint	The midpoint where thigh and lower leg pivoted
9	Ankle	Talocrural joint	Visible, midpoint of lateral malleolus
10	MTP	Metatarsophalangeal joint of the third digit of the foot	Visible
11	Pelvis	Lumbo-sacral joint	Point dorsal and superior to the tail where spinal flexion curvature becomes evident
12	Base of tail	The center point of the sacral-caudal joint	Visible, where the tail connects to the sacrum
13	Tip of tail	The most distal point of the tail	Visible, the end point of the straight part of the tail, before the curl of the tip

Before and after the monkeys used the site each day, we videotaped a calibration device (two rods in vertical alignment) at the anvil. Two reflective markers on two ends of each rod were 0.38-m apart. The horizontal distance (range 1.030–1.075 m) between the two rods was recorded for each calibration video.

Data reduction and digitizing

Video selection. Video clips were selected on the basis of lighting, stability of camcorder, and the subjects' position in the field of view. We preferentially selected episodes during which the monkeys made at least five consecutive hits. An episode started when the monkey began cracking at the anvil and ended when the monkey cracked open the nut. Two episodes for each monkey were selected from all videos. Next, we digitized five hits that were roughly evenly distributed throughout the episode. For example, if a monkey had only five hits in one episode, we digitized every hit. If a monkey had 13 hits in one episode, we digitized the first, fourth, seventh, tenth, and thirteenth hits. Therefore, 10 hits from 2 cracking episodes were digitized for each monkey.

Digitizing unit. A hit consisted of 1) a preparatory prelift phase (defined as five fields prior to start of lifting, 0.083 s in duration), 2) an upward phase (from start of lifting to stone zenith point), and 3) a downward phase (from stone zenith point to stone–nut contact). For each hit, 13 points on the monkey's body, the nut (Point 14) and the top of the anvil (Point 15) were manually digitized (Peak Motus$^{\mathrm{TM}}$ by Vicon, version 9.0) in each field of video (60 fields per second), as shown in Figure 4. The points on the monkey's body that were digitized were in the sagittal plane of the side of the body facing the camcorder. The movements of the monkey were assumed to be bilaterally symmetrical.

Spatial model. Anatomical definitions and landmark identification for the 13 points are given in Table 2. The guiding principle for identifying a point to be digitized at a joint is to estimate from a visible landmark (e.g., the midpoint of the joint space between the two articulating bones). Seven segments were defined (neck, upper arm, fore arm, trunk, thigh and lower leg, and foot). Joint angles (elbow, knee, and ankle) were defined as the interior angle between the two articulating segments. Shoulder angle was defined as the segmental angle between the upper arm and the vertical axis. Hip angle was defined as the interior angle between thigh and trunk. Trunk inclination was defined as the segmental angle between the trunk and the horizontal axis. Figure 4 shows the points and segments.

Critical events. For each hit, three critical events were marked: "start of lifting," "MCP zenith point," and "stone–nut contact". Start of lifting was defined as the instant when the stone began to move upward. The MCP zenith point was the instant at which the metacarpophalangeal joint of the third finger (MCP, hereafter) reached the highest vertical height. Because the MCP joint was used as a proxy for the stone's center of mass, this instant is also referred to as the stone zenith point. The stone–nut contact occurred in the subsequent downward phase, at the instant when the stone contacted the nut. Start of lifting was defined as 0% of hit duration (hereafter, HD) and stone–nut contact was defined as 100% of HD. Data points before start of lifting were therefore marked with negative percent values for HD.

Filtering. After manually digitizing the points, the raw coordinates were filtered using a fourth-order Butterworth filter with a cutoff frequency of 6 Hz. As the vertical displacement-time function of the stone is a discontinuous function just prior to the end of the downward phase, to obtain a more accurate maximum velocity of the stone just prior to the stone–nut contact, a line of best fit of the vertical velocity was generated using the five fields of data just prior to the inflection point that occurred before the contact. The fields from the inflection point to the contact were then extrapolated and

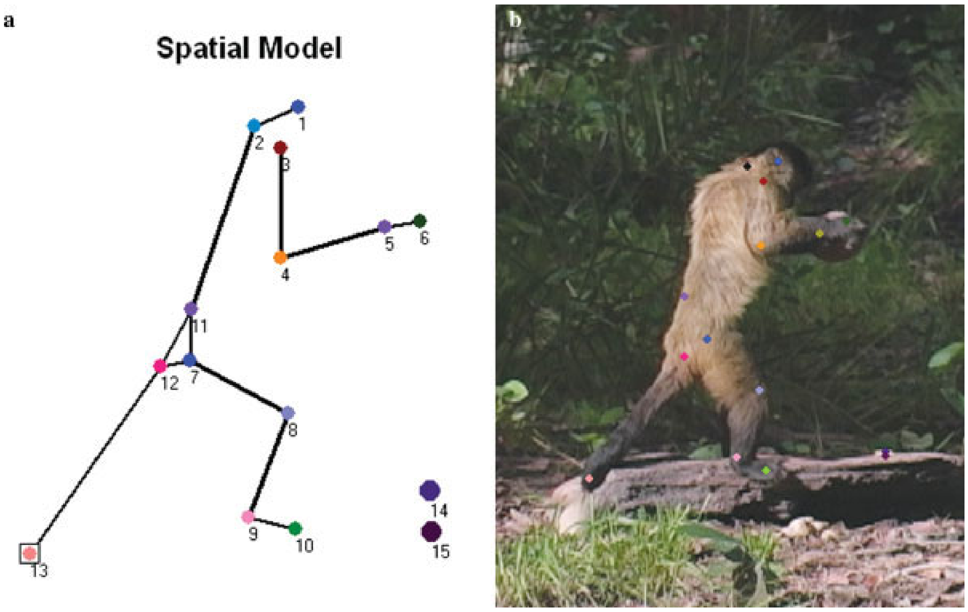

Fig. 4. Spatial model. (**a**) Points (refer to Table 2 for anatomical definition and landmark identification) and angles. (**b**) A digitized field of a male monkey cracking nut.

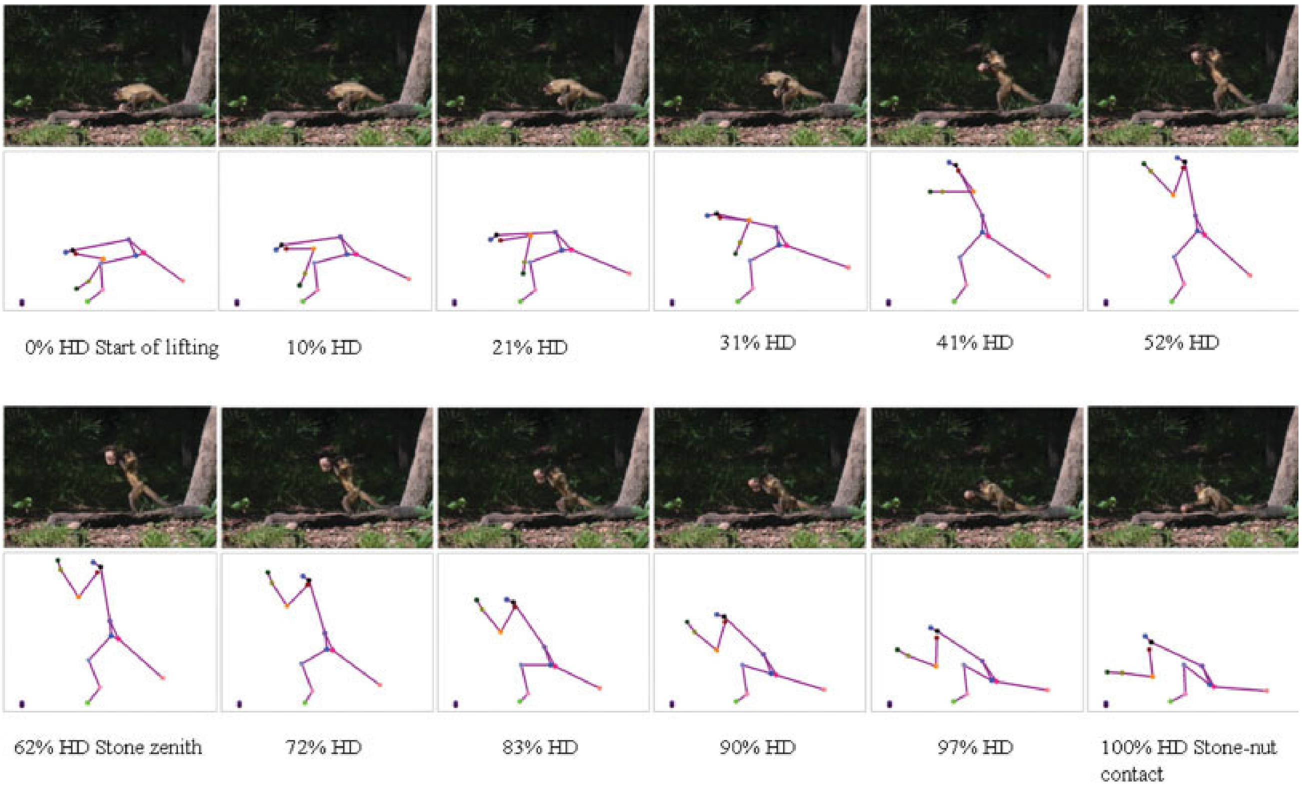

Fig. 5. Stick figure illustration of a representative hit (by a female, Piaçava), with corresponding fields of video shown above.

replaced. The maximum vertical velocity of the stone just prior to the contact was then obtained.

Coding reliability

We assessed the reliability of our coding in two ways. First, we measured the variation in the lengths of five major segments over successive coded fields within hits, using one hit per monkey (10% of the data set). Perfectly accurate data would provide no variation in measurement. The ratio of minimum to maximum values for segment lengths for the four monkeys ranged from 0.81 to 0.89, upper arm; 0.64–0.80 for fore arm; 0.79–0.90 for trunk; 0.76–0.82 for thigh, and 0.78–0.88 for lower leg, and average proportion of minimum to maximum length for each segment ranged from 0.74 to 0.84. Average min/max

TABLE 3. Variables, definitions, and computational methods

Categories	Variables	(Operational) Definition	Computational method
Durations	Duration of one hit (s)	From the instant when the stone starts moving upward to the instant when the stone contacts the nut	=Number of fields from start of lifting to stone–nut contact × 1/60 s
	Duration of upward phase (s)	From the instant when the stone starts moving upward to the instant when the stone reaches the maximum vertical height (zenith point)	=Number of fields from start of lifting to stone zenith point × 1/60 s
	Duration of downward phase (s)	From the instant when the stone reaches the maximum vertical height (zenith point) to the instant when the stone contacts the nut	=Number of fields from stone zenith point to stone–nut contact × 1/60 s
	Duration of free fall (s)	Time needed if the stone movement is free fall from the same vertical height	$t_{\text{free fall}} = \sqrt{2h/g}$ ($h = 1/2gt^2$, $g = 9.8$ m/s^2)
	Difference between duration of down phase and free fall time (s)	Time saved due to extra downward force put by the subject onto the stone	=free fall time − duration of down phase
Maximum vertical height of the stone	Absolute maximum vertical height (m)	Vertical displacement of MCP joint point from the instant when the stone reaches the zenith point to the stone contacts the nut	=Y coordinate of MCP point at nut–stone contact − Y coordinate of MCP joint at zenith
	Relative maximum vertical height (%)	The proportion of the maximum vertical height to estimated body length	=Maximum vertical height of hammer stone/estimated body length × 100
Energetics	Potential energy at the maximum vertical height (J)	The potential energy of the stone at the maximum vertical height	=mgh, m = mass of the stone, in kilograms; g = 9.8 m/s^2; h = maximum vertical height, in meters
	Maximum kinetic energy prior to stone–nut contact (J)	The kinetic energy of the stone when it is moving downward to the nut at the maximum velocity	=1/2 mv^2, m = mass of the stone, in kg; v = velocity of the stone, in m/s
	Production of work (J)	The work the monkeys put onto the stone during the downward phase	=maximum kinetic energy − maximum potential energy

proportions for the five segment lengths per individual varied from 0.83 to 0.84.

Second, we measured the variation in angles calculated per coded field from data coded by the same coder at two different coding runs. We randomly selected four hits (one hit for each individual), recoded 20 fields of motion (10 fields before MCP zenith point and 10 fields after), and recalculated values of six angles (shoulder, elbow, trunk, thigh, knee, and ankle). The comparison with previous values showed that the average absolute angle difference is 4° across all monkeys. The difference values for all monkeys ranged from 1 to 6°, shoulder; 2–4°, elbow; 1–4°, trunk; 1–6°, thigh; 2–6°, knee, and 4–7°, ankle. Average absolute angle difference per individual ranged from 3 to 4° for all six angles.

We conclude from these evaluations that our data are moderately accurate with respect to segment lengths (and thus, point positions), highly accurate with respect to angular variables, and that we were consistently accurate in scoring across individuals.

Data computation

For each hit, durations, maximum vertical height of the stone (using MCP joint as a proxy for the stone), and the mechanical energetics (maximum gravitational potential energy, maximum kinetic energy, and the production of work) of the stone were computed (see Table 3).

Values of joint angles for the elbow, hip, knee and ankle, and segmental angles for the shoulder and trunk were computed for each hit in Peak Motus. Angular displacement for extension and flexion was generated. Temporal durations to maximum/minimum angles were expressed relative to the total hit duration (% HD).

RESULTS

In all episodes analyzed, the stones were on or close to the anvil when the monkeys arrived. The monkeys came to the anvil and picked up the stones at the beginning of the episodes. They either came to the anvil with a nut or picked up a nut at the anvil. The monkeys positioned their arms inside the knees (67.5% of 40 hits), outside the knees (20% of 40 hits), or in front of the knees (12.5% of 40 hits) at the start of the upward phase.

Durations

The 40 hits averaged 0.74 (SD = 0.05) seconds in duration. The upward phase lasted 69.4% HD. The downward phase lasted 30.6% HD. Table 4 presents mean and SD for the duration of the hit for each subject. Given that the video was digitized by field (one

TABLE 4. Duration of a hit (mean and SD per 10 hits per subject)

Subject	Duration of hit (s)	Down duration (s)	Free fall (s)	Difference (free fall-down) (s)
Chicao	0.78 ± 0.05	0.23 ± 0.02	0.26 ± 0.01	0.04 ± 0.03
Segundo	0.75 ± 0.05	0.23 ± 0.01	0.28 ± 0.02	0.05 ± 0.02
TeNinha	0.72 ± 0.05	0.23 ± 0.02	0.25 ± 0.02	0.02 ± 0.02
Piaçdava	0.73 ± 0.05	0.23 ± 0.02	0.25 ± 0.02	0.02 ± 0.01

TABLE 5. Maximum vertical height to which the monkeys lifted the hammer stone (mean and SD per 10 hits per subject)

Subject	Absolute maximum vertical height (m)	Relative maximum vertical height (% of body length)
Chicao	0.34 ± 0.03	57 ± 5
Segundo	0.38 ± 0.04	66 ± 8
TeNinha	0.30 ± 0.04	53 ± 8
Piaçava	0.31 ± 0.04	65 ± 9

field = 1/60 s), the resolution of measurement is ±1/60 s, or approximately ±0.017 s.

To test the prediction that monkeys exerted external downward force onto the stone during the downward strike phase, we compared the duration of the downward phase to the duration of a free fall movement from the same vertical height. If the actual duration is less than free fall duration, the monkey presumably exerted downward force on the stone.

For the two males, in 18 of 20 hits, the downward phase duration is shorter than free fall duration; for the two females, in 10 of 20 hits, the downward phase duration is shorter than free fall duration. This indicates that in these hits, the monkeys exerted downward force onto the stone to strike on the nut. The average difference between free fall and actual durations for those hits in which the actual duration is shorter, is greater for the two males ($\text{mean}_{\text{diff.}} = 0.04 \pm 0.02$ s, $n = 18$) than for the two females ($\text{mean}_{\text{diff.}} = 0.02 \pm 0.01$ s, $n = 10$).

Maximum vertical height

The monkeys lifted the stone to an average vertical height of 0.333 (SD = 0.051) meters (range of all hits: 0.251–0.449). The relative maximum vertical height of the stone in proportion to estimated body length averaged 60% (± 9). Absolute maximum vertical height and relative maximum vertical height that each monkey lifted the stone are shown in Table 5. Across all hits, males lifted the stone vertically to 47–77% of their body length and females to 45–76% of their body length.

Velocity and energetics

Table 6 presents the mean and SD of maximum vertical velocity of the stone before stone–nut contact, maximum potential energy, maximum kinetic potential, and the production of work for each subject for all coded hits. The two males achieved greater maximum vertical velocities than the females (mean = 3.81 m/s vs. 3.16 m/s; males and females, respectively). Therefore, the males generated higher maximum kinetic energy than the females. As the males lifted the stones to a higher maximum vertical height (in accord with their longer body length), the potential energy that they generated was also higher than the potential energy generated by females. All the monkeys produced work in the downward phase; that is, they added energy to the stone in the downward direction. Table 6 also shows that the males produced nearly twice the work that females produced (mean = 5.61 J vs. 2.89 J; males and females, respectively).

Angles and angular kinematics

To analyze angular kinematics, we selected three hits exhibiting the highest stone zenith points for each subject. The higher the stone zenith point, the more erect the subject became and the more pronounced the angular movement pattern was. To assess the uprightness of their posture, we examined the maximum trunk inclination, hip and knee angles during each hit. In our samples, the maximum trunk inclination angle ranges 61−80°, the maximum hip angle achieved ranges 99−130°, and maximum knee angle ranges 121−148°.

Commonalities among subjects. The basic pattern of the nut-cracking movement in these adult capuchin monkeys is illustrated in Figure 5. We adopt the conventions used to describe human movements in a standing position (Robertson et al., 2004) to describe the movements of nut-cracking. Starting from a crouched position, all four monkeys hyper-extended the upper arms to pull the stone closer to his/her center of mass in all 12 hits (three hits per monkey) in prelift phase or in the beginning of the upward phase. Hyper-extension of the upper arm resulted in an increase in the shoulder angle. The shoulder continued to hyperextend, moving the upper arm further past the vertebral column. Then the trunk, hips, and knees extend explosively until the stone reaches the maximum vertical height (stone zenith point). In the downward phase, the trunk, hips, and knees flex until the moment of stone–nut contact such that the monkey returns to a crouched position.

Individual strategies. Aside from these common features of lifting and striking, we observed four distinctive strategies within and between individuals across prelift, upward lifting, and downward striking.

1. Three subjects exhibited a specific lifting strategy in the upward phase. In one female (Piaçava, two of three hits) and the two males (all hits), the trunk started extending earlier (−9% ± 3% HD) than the knees (12% ± 15% HD), indicating that the trunk moved the stone first. The fourth monkey extended trunk and hips simultaneously.
2. One female (Teninha) jumped when the stone was about to reach the zenith point. She started dorsiflexing her ankles at the beginning of the hit (5% ± 5% HD) from 126 ± 19°. Then at 30% ± 8% HD, she started plantar flexing her ankles from an angle of 113 ± 7°. Her ankles reached maximum plantar flexion (155 ± 7°) at the zenith point, then began to dorsiflex again until the angle was 105 ± 4° at 84% ±

TABLE 6. Energetics of nut-cracking (mean and SD per 10 hits per subject)

Subject	Maximum potential energy (J)	Maximum velocity of the stone before stone–nut contact (m/s)	Maximum kinetic energy (J)	Production of work (J) (=maximum kinetic energy − maximum potential energy)
Chicao	4.81 ± 0.41	3.59 ± 0.42	9.50 ± 2.25	4.70 ± 1.87
Segundo	5.51 ± 0.64	4.04 ± 0.46	12.04 ± 2.65	6.52 ± 2.07
TeNinha	4.27 ± 0.61	3.18 ± 0.20	7.42 ± 0.98	3.15 ± 1.00
Piaçava	4.24 ± 0.37	3.14 ± 0.27	6.86 ± 0.89	2.62 ± 0.65

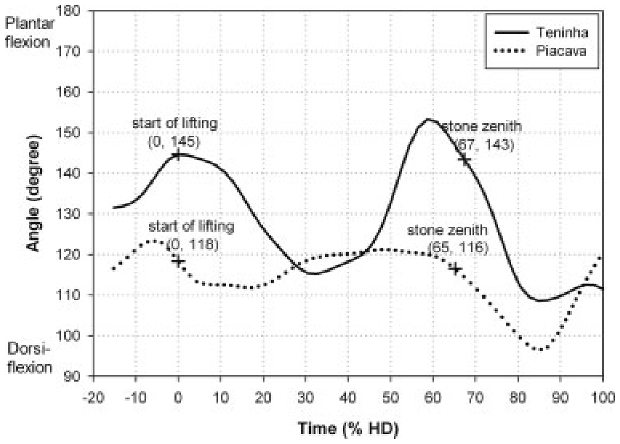

Fig. 6. Angle displacement of Teninha's ankle from one hit and ankle displacement of Piaçava from one hit for comparison. The crosses represent the start of lifting and the stone zenith point. Values in parentheses are % HD and the value of the angle (degree) at the time point. Teninha began dorsiflexing at the beginning of the lifting phase then plantar flexed later in the lifting phase as her feet came off the anvil. After stone zenith point, she dorsiflexed the ankle again in the downward phase.

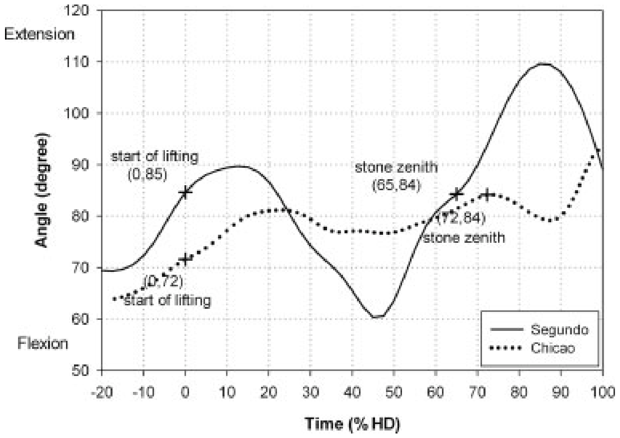

Fig. 7. Angle displacement of Segundo's elbow from one hit and elbow displacement of Chicao from one hit for comparison. The crosses represent the start of lifting and the stone zenith point. Values in parentheses are % HD and the value of the angle (degree) at the time point. Segundo had a clear pattern of flexing and extending the elbow.

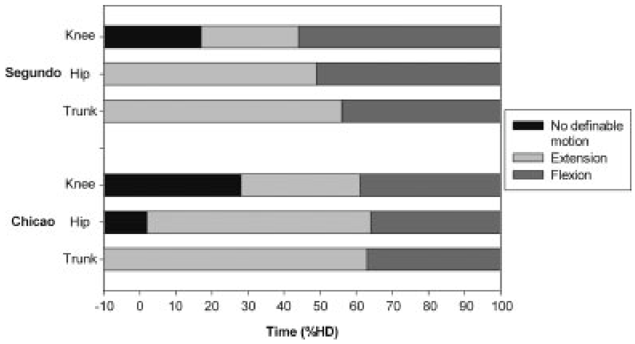

Fig. 8. Sequence of knee, hip, and trunk movement (Segundo) from one hit and simultaneous pattern of Chicao from one hit for comparison. Segundo started flexing knees earlier than trunk while Chicao flexed knee, hip, and trunk simultaneously.

1% HD. The other three monkeys kept their feet in contact with the anvil throughout every hit and their ankles did not show patterned movements. The change of their ankle angles was due to movement of the lower leg, rather than movement of the foot. Figure 6 illustrates ankle angles from one hit from Teninha and one from the other female for comparison.

3. In one male (Segundo), the elbows exhibited a clear pattern of flexing and extending. In the upward phase at 20% ± 6% HD, he started flexing his elbows from 89 ± 1°. At 48% ± 4%HD, his elbows reached maximum flexion of 60 ± 5°. Then, he started extending the elbows close to the zenith point and continued to extend his elbows in the downward phase. At 88% ± 6% HD, his elbows reached maximum extension of 105 ± 5°. Segundo's pattern and for comparison the pattern of the other male are depicted in Figure 7.
4. Three subjects exhibited a sequential movement pattern. In one male (Segundo) and both females, the knees flexed, then the hip, then the trunk, whereas the timing of these was much closer in Chicao, the other male. This pattern is illustrated in Figure 8 for Segundo, together with the essentially simultaneous pattern of the other male for comparison.

Use of the tail

The monkeys placed the tail in contact with the anvil or ground; or held it in the air rather rigidly behind the body during nut-cracking. No particular posture was predominant and we did not observe any apparent link between position of the tail and effectiveness of the strike or features of the movement or posture of the monkeys.

DISCUSSION

Nut-cracking in the wild capuchins can be considered as an integrated dynamic system with biomechanical, morphological, and environmental components. Despite the morphological constraints of the body and environmental constraints such as the mass of the hammer stone and toughness of the nuts, the monkeys successfully exploited the mechanics of their body to crack open nuts using stones that weighed 33–77% of their body weight. We assume that the monkeys maximized the effectiveness of their performance and minimized the risk of injury in nut-cracking. Below we discuss the monkeys' diverse kinematic strategies and compare the monkeys' movements during nut-cracking to those of human weight lifters to evaluate how each species accomplishes the same goal (lifting a heavy object to a maximal height and bringing it down again, with control and without injury to the body). Next, we compare how capuchins crack nuts with how chimpanzees crack nuts. Finally, we discuss the significance of the capuchins' bipedal stance during nut-cracking and its relation to their morphology.

Kinematic strategies

The monkeys showed several different kinematic strategies during each phase of the nut-cracking movement. The first strategy observed likely serves as a potential injury prevention mechanism as it likely reduced the amount of trunk extensor muscle torque and increased postural stability (reducing risk of falling). Before the start of the lift or at the beginning of the lift, to reduce the lever arm of the weight of the stone and the moment of inertia of the stone, all the monkeys hyperextended the upper arms to pull the stone closer to their center of mass ($\mathrm{COM_{body}}$). A shorter lever arm of the weight reduces the gravitational torque of the stone that must be counteracted with trunk muscle extensor torque (Preuschoft, 2004). Skilled human weight lifters and occupational workers who lift heavy loads also use this strategy when it is feasible to pull in the load closer to their $\mathrm{COM_{body}}$ before lifting the load. This strategy keeps the antero-posterior location of the $\mathrm{COM_{body}}$ further from the front edge of their base of support, thereby increasing stability before lifting the stone (Smith et al., 1995).

In the upward phase, the mechanical goal is to lift the stone as high as needed. Three subjects used the back first to move the stone upward. Then, the strong leg muscles accelerated the stone vertically to a high upward velocity. This strategy is sometimes employed by humans lifting heavy objects (Harman, 1994). McGill (2002) demonstrated that skilled occupational workers generate rapid trunk extension early in the lifting phase, and that this strategy reduces back extensor muscle torques compared to those generated when slowly extending the trunk.

One female showed another lifting strategy, in which the body comes off the ground during the end of the upward lifting phase. Her ankle joint displayed plantar flexion at the stone zenith point (as shown in another individual in Fig. 1b). This may reflect use of a technique employed in human power pull style lifting (see Fig. 2), in which maximal force is applied to the ground early in the upward phase, generating momentum that helps carry the body and stone upward later in the lifting phase (Baechle et al., 1994).

One male showed a pattern of elbow flexion–extension in the hit cycle. We interpret the extension–flexion pattern as a strategy to help lift the stone near the end of the upward phase and push the stone in the downward phase. The other three monkeys held the elbows at a relatively constant angle; so elbow displacement did not make a major contribution to raising the stone.

In the downward phase, the mechanical goal is to gain the maximum controllable kinetic energy before stone–nut contact on all strikes until the nut cracks. All the monkeys added discernable energy onto the stone during the downward phase. Three monkeys also showed a sequential movement pattern in which they flexed the knees earlier than the trunk, lowering the stone by dropping the lower body first and dropping the trunk later. We surmise that by using the back extensors later in the downward phase (closer to the stone–nut contact), the monkeys could strike the nut with more control. Trunk flexion movements indicate that contraction of the abdominal muscles adds force to the strike.

In summary, each monkey apparently developed its own style of managing the strenuous and risky task of lifting a heavy stone and striking it forcefully onto a nut. We assume that these strategies represent the monkeys' individually crafted solutions to the concurrent goals of maximizing mechanical advantages and minimizing the risk of injury. Future studies can evaluate the relation between reliance on varying strategies and proficiency at cracking nuts.

Comparison with human lifters

The capuchins' form of lifting the hammer stone is similar to the descriptions of the deadlift and power pull style weight lifting by humans (Baechle et al., 1994). These two weight lifting actions are also bimanual, bipedal, and relatively strenuous. Figure 2 illustrates a deadlift and a power pull. In a deadlift, the lifter starts in a squat position with arms straight and pointing down. The bar is positioned in front of the lifter's feet. The lifter reaches down, grasps the bar, and lifts it up until the legs and back are upright. The power pull has the same upward phase but includes a phase in which the lifter moves the bar explosively from a position on the thighs by extending the lower extremities and pulling the bar to neck-level before returning the bar to the floor. For either lift, the highly skilled human lifters keep the bar close to the body, which enhances performance and minimizes risk of injury.

In human sumo style deadlifts, the lifter's feet are positioned further apart and turned out with arms positioned inside the knees, compared to the conventional style in which the lifter's feet are positioned closer together and the lifter's arms are positioned outside the knees (Escamila et al., 2001). Turning the feet outward enhances postural stability in human lifters (Smith et al., 1995) by broadening the base of support beneath the center of mass. Placing the arms inside the knees allows the trunk to go lower, permitting an absolutely greater distance for upward acceleration from extension of the legs. The capuchins resemble the sumo style lifters in some aspects. The monkeys' feet were often turned out at the calcaneofibular ligament on the lateral edges of the anvil (~20 cm in width). Their arms were positioned inside the knees two-thirds of the time, resembling the sumo style. In addition, Teninha's ankle plantar flexion strategy, as discussed above, showed resemblance to the jumping action in human power pull style weight lifting (Baechle et al., 1994).

Comparison with nut-cracking by chimpanzee

The adoption of bipedal posture versus a sitting posture for striking suggests that nut-cracking is a more strenuous action for capuchins than for chimpanzees. Despite being 1/10 or less of the mass of adult chimpanzees, adult capuchins crack open nuts that are as tough as those cracked by chimpanzees (compare Peters, 1987 with Visalberghi et al., in press). Günther and Boesch (1993) estimated that a wild male chimpanzee used hammers 6.6% and 14.3% of his body mass (estimated body mass was 35 kg and mass of the hammers was 2.3 and 5 kg) to crack a Coula nut. They calculated in one hit that the chimpanzee generated 14.5 J of maximum kinetic energy and the production of work was 8.2 J with the 2.3-kg hammer. In comparison, the two hammer stones (1.32 and 1.46 kg) used by monkeys in our samples were 33–77% of their body mass. On average, the monkeys generated 9.0 J of maximum kinetic energy and produced 4.3 J of work in one hit. The capuchins reached an even greater maximum downward velocity (4.04 m/s) during striking than the chimpanzees (3.55 m/s), and they produced essentially the same maximum kinetic energy (14 J). In a more dramatic comparison, a captive male chimpanzee generated 0.58 J of mean maximum kinetic energy and produced 0.25 J of work in one hit when he was cracking macadamia nuts using a light hammer (443 g; Foucart et al., 2005). The strenuous nature of the activity for capuchins raises interesting questions about the nutritional benefits of nut-cracking, the developmental pathways resulting in this "extreme skill," and the consequences for morphology resulting from routine practice.

Bipedal stance in nut-cracking by capuchins

The monkeys in Boa Vista achieved semivertical stance during every hit. The degree of verticality achieved repetitively by the capuchins during nut-cracking is surprising, considering that capuchins are considered anatomically and behaviorally quadrupedal. Theoretically, in perfect bipedal stance, hip and knee angles are 180° and trunk inclination is 90°. However, given the arrangement of the gluteal muscles in capuchins (Stern, 1971; Marzke et al., 1988), as expected, they achieved a bent-hip, bent-knee posture during hits. In our samples, the maximum hip angle that the monkeys achieved is 130°, the maximum trunk inclination angle is 80°, and maximum knee angle is 148°. The maximum knee extension is greater than that achieved by bonobos (*Pan paniscus*) during bipedal locomotion (130°), but bonobos extend the hip (140°) during bipedal locomotion somewhat farther than capuchins extend the hip during nut-cracking (D'Août et al., 2002). Capuchins hold the trunk more vertical during nut-cracking than do bonobos during bipedal walking (~70°; D'Août et al., 2002).

Japanese macaques that have been trained to walk bipedally provide an interesting comparison to capuchins standing bipedally to crack nuts. Hirasaki et al. (2004) compared three trained Japanese macaques (*Macata fuscata*) to two ordinary macaques during bipedal walking. The trained macaques showed a more upright trunk (maximum trunk inclination is 80°) and more extended hip (maximum hip extension is 160°) and knee (maximum knee extension is 160°) joint angles than the ordinary macaques (maximum trunk inclination is about 72°, maximum hip extension and knee extension are both about 120°). The capuchins in Boa Vista showed the same extent of trunk uprightness as that of the trained macaques. They showed greater knee and hip extension than the ordinary macaques, but not as great as the trained macaques. This implies that individuals lacking anatomical correlates of bipedal stance in humans (e.g, knees that extend less than 180°) may achieve upright trunk and head posture even when they do not achieve fully upright lower extremities and efficient bipedal locomotion. A similar interpretation that functional bipedal stance can be achieved without all the features of modern human anatomy has been suggested by Richmond and Strait (2000) and Kingdon (2003), following analyses of Australopithecine fossils.

Morphology

Nakatsukasa et al. (1995), studying the postcranial skeleton of a Japanese macaque, showed that 11 years of training to walk bipedally had modified the monkey's hind limb bones considerably, in terms of joint morphology, articular dimensions, and shape-dependent strength of long bones. They also described how this monkey's gait pattern more closely resembled human bipedal walking than did the gait of untrained monkeys. If trained macaques can develop human-like characteristics of bipedal gait and routine bipedal walking can cause morphological changes in Japanese macaques, one may wonder if routine nut-cracking in bipedal stance over years affects the skeletal anatomy of the capuchins, and further if these skeletal changes may support more efficient bipedal walking than other capuchins can achieve. Further studies on the morphological adaptations and characteristics of bipedal locomotion in wild capuchins that routinely crack nuts, and comparison of their bipedal gait to the bipedal gait of other capuchins that do not crack nuts, will provide valuable insights into this issue. Similar phenomena of morphological (skeletal) adaptation to functional use have been documented in diverse taxa (Hurov, 1991; Carrier, 1996).

Aspects of the limb morphology of tufted capuchins (a group to which *C. libidinosus* belongs) suggest that these monkeys do routinely move from pronograde to orthograde postures, perhaps during climbing (Wright, 2007). Wright (2007) suggested that a higher intermembral index (aka IM or fore limb/hind limb index) (relatively longer fore limbs, or relatively shorter hind limbs) promotes easier transition from a pronograde posture to orthograde posture, which is exactly what the monkeys do in every hit in nut-cracking. Wright found that *C. apella* has a significantly higher IM index than *C. olivaceus*. *C. apella* and *C. libidinosus* belong to the "tufted" group of species in the genus and are considered to be more closely related to each other than to other "non-tufted" species in the genus, including *C. olivaceus* (Fragaszy et al., 2004b). Wright (2007) also found that *C. apella* has relatively short hind tibias and slightly shorter fore limbs, bringing the center of mass lower to the substrate and adding more stability for orthograde posture compared to *C. olivaceus*. Therefore, *C. libidinosus*, until recently considered a subspecies of *C. apella*, may have an advantage over nontufted species of *Cebus* in lifting and striking heavy stones in a bipedal stance. A phylogenetic perspective leads us to predict that bipedal nut-cracking, as observed in *C. libidinosus*, will be less common or perhaps absent in untufted species of *Cebus* (that is *albifrons*, *olivaceus*, and *capucinus*).

Future directions

This is the first examination of the kinematics and energetics of tool use in bipedal stance in wild nonhuman primates. We look forward to further investigations of the phenomenon in wild capuchins at Boa Vista, and in additional populations of nut-cracking capuchins in the Cerrado of Brazil. For example, further energetic analysis of nut-cracking activities and caloric analysis of the nuts are essential to understand the energetic consequences of nut-cracking. We also seek to understand how young monkeys become skillful, and the sources and consequences of individual variation in nut-cracking. Morphological and anatomical work can reveal the consequences for the body of routine strenuous actions by these capuchins. Finally, because these monkeys lift heavy stones while standing bipedally and carry them while walking bipedally (from one anvil to another, for example; personal observation), the capuchins provide a new model for bipedal lifting and carrying in primates.

ACKNOWLEDGMENTS

This work was conducted in compliance with all institutional and governmental regulations regarding humane use of animals in research. The authors thank K. Wright and B. Demes for commenting on a previous version of the manuscript, P. Siggurdson for helping with the Peak Motus™ system, K. Brakke for the use of her Peak Motus™ system for initial coding, A. Bradwell for drawing Figure 2, Q. Li for helping with computation in Matlab®, and the Oliveira family for logistical assistance. Permission to work in Brazil was granted by IBAMA and CNPq to QL, DF, and EV. They also thank Fundação BioBrasil for initial logistical support. Finally, they thank their reviewers and editor Ruff for their helpful comments during the review process.

LITERATURE CITED

Baechle TR, Earle RW, Allerheiligen WB. 1994. Strength training and spotting techniques. In: Baechle TR, editor. Essentials of strength training and conditioning. Champaign, IL: Human Kinetics. p 380, 395.

Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Taï forest. Oxford: Oxford University Press.

Carrier DR. 1996. Ontogenetic limits on locomotor performance. Physiol Zool 69:467–488.

D'Août 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.

Escamila RF, Lowry TM, Osbahr DC, Speer KP. 2001. Biomechanical analysis of the deadlift during the 1999 Special Olympics World Games. Med Sci Sports Exerc 33:1345–1353.

Fleagle JG. 1999. Primate adaptation and evolution. San Diego, CA: Academic Press.

Foucart J, Bril B, Hirata S, Morimura N, Houki C, Ueno Y, Matsuzawa T. 2005. A preliminary analysis of nut-cracking movement in a captive chimpanzee: adaptation to the properties of tools and nuts. In: Roux V, Bril B, editors. Stone knapping: the necessary conditions for a uniquely hominid behavior. Cambridge, UK: McDonald Press. p 147–158.

Fragaszy D, Izar P, Visalberghi E, Ottoni EB, de Oliveira MG. 2004a. Wild capuchin monkeys *Cebus libidinosus* use anvils and stone pounding tools. Am J Primatol 64:359–366.

Fragaszy D, Visalberghi E, Fedigan L. 2004b. The complete capuchin. Cambridge, UK: Cambridge University Press.

Goren-Inbar N, Sharon G, Melamed Y, Kislev M. 2002. Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. Proc Natl Acad Sci USA 99:2455–2460.

Günther MM, Boesch C. 1993. Energetic cost of nut-cracking behaviour in wild chimpanzees. In: Preuschoft H, Chivers DJ, editors. Hands of primates. New York: Springer-Verlag. p 109–129.

Harman E. 1994. The biomechanics of resistance exercise. In: Baechle TR, editor. Essentials of strength training and conditioning. Champaign, IL: Human Kinetics. p 38.

Heinzelin J, Clark JD, White T, Hart W, Renne P, WoldeGabriel G, Beyene Y, Vrba E. 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284:625–629.

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.

Hurov JR. 1991. Rethinking primate locomotion: what can we learn from development? J Mot Behav 23:211–218.

Kingdon J. 2003. Lowly origin: where, when and why humans first stood up. Princeton, NJ: Princeton University Press.

Marzke MW, Longhill JM, Rasmussen SA. 1988. Gluteus maximus muscle function and the origin of hominid bipedality. Am J Phys Anthropol 77:519–528.

McGill SM. 2002. Low back disorders: evidence based prevention and rehabilitation. Champaign, IL: Human Kinetics.

McGrew WC. 2004. The cultured chimpanzees: reflections on cultural primatology. New York, NY: Cambridge University Press.

Nakatsukasa M, Hayama S, Preuschoft H. 1995. Postcranial skeleton of a macaque trained for bipedal standing and walking and implications for functional adaptation. Folia Primatol 64:1–29.

Ottoni EB, Mannu M. 2006. An overview of the occurrence and diversity of spontaneous tool use in tufted capuchin monkeys. Int J Primatol 27 (Suppl 1):108.

Peters CR. 1987. Nut-like oil seeds: food for monkeys, chimpanzees, humans and probably ape-men. Am J Phys Anthropol 73:333–363.

Preuschoft H. 2004. Mechanisms for the acquisition of habitual bipedality: are there biomechanical reasons for the acquisition of upright bipedal posture? J Anat 204:363–384.

Richmond BG, Strait DS. 2000. Evidence that humans evolved from a knuckle-walking ancestor. Nature 404:382–385.

Robertson GE, Caldwell G, Hamill J, Kamen G, Whittlesey S. 2004. Research methods in biomechanics. Champaign, IL: Human Kinetics.

Smith LK, Weiss EL, Lehmkuhl LD. 1995. Brunnstrom's clinical kinesiology. Philadelphia: F.A. Davis.

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

Visalberghi E, Fragaszy D, Ottoni E, Izar P, de Oliveira MG, Andrade FRD. 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, Sabbatini G, Spagnoletti N, Andrade FRD, Ottoni E, Izar P, Fragaszy D. Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). Am J Primatol 70:884–891.

Wright KA. 2007. The relationship between locomotor behavior and limb morphology in brown *Cebus apella* and weeper *Cebus olivaceus* capuchins. Am J Primatol 69:1–21.