KINEMATICS AND ENERGETICS OF NUT-CRACKING IN WILD CACPUHIN MONKEYS (*CEBUS LIBIDINOSUS*) IN PIAUI, BRAZIL

by

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(Under the Direction of Dorothy M. Fragaszy)

ABSTRACT

Wild bearded capuchins (*Cebus libidinosus*) in Brazil crack nuts using large stones. The biomechanics of the nut-cracking action of two males and two females were examined. From a bipedal stance, the monkeys raised a heavy hammer stone (1.46 kg and 1.32 kg) to an average height of 0.333 meters, 60% of body length. The stone was then rapidly lowered 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 0.744 seconds in duration. The upward lifting phase lasted 69% of hit duration. The two males added substantial energy to the stone in the downward phase. The monkeys developed individualized kinematic strategies. Kinematic results are compared to human weight-lifters and chimpanzees, indicating nut-cracking is strenuous for capuchins. The current study provides a reference point for the evolution of percussive tool use and bipedality in primates.

INDEX WORDS: tool use, percussion, nut-cracking, kinematics, energetics, biomechanics, capuchin, *Cebus libidinosus*, nonhuman primates, lifting, upright stance, bipedality

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DEDICATION

This work is dedicated to my soul mate Qingyang, my dearest parents and grandpa, and the wild capuchins in Brazil that have been the inspiration of my work.

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CHAPTER 1

INTRODUCTION

The present study provides the first systematic kinematic analysis of percussive tool use in capuchins. Percussive tool use is a challenging, natural and ancient behavior in humans. Archaeological evidence suggests that our ancestors developed percussive tool use as early as 2.5 million years ago (Heinzelin et al., 1999). It might have been our ancestors' very first technological discovery. In contemporary humans, percussive tool use is widespread around the world (Goren-Inbar, Sharon, Melamed, & Kislev, 2002). Recently, it has been discovered that wild bearded capuchins crack nuts using large stones in their natural environment (Fragaszy et al., 2004). Study of these capuchins will provide a valuable reference point for hominine percussive tool use and its evolution, and routine bipedality in primates.

Spontaneous nut-cracking by wild chimpanzees has been reported in many sites in western Africa (Sugiyama & Koman, 1979; Kortlandt, 1986; Kortlandt & Holzhaus, 1987; Boesch & Boesch-Achermann, 2000; Matsuzawa, 2001). The chimpanzees usually sit close to an anvil and use a stone or wooden hammer to crack open nuts placed on the anvil. The movement can be performed in a unimanual or a bimanual fashion depending on the hardness of the nuts and the materials available for use as hammers.

To date, there is only a single quantitative analysis of the movements of wild chimpanzees cracking nuts. Günther and Boesch (1993) calculated the energetic cost of nut-cracking using wooden hammers (mass: 2.3 kg and 5 kg) in wild chimpanzees in Taï forest. From video records, they estimated the energy expended transporting of the nuts and hammers, cracking open the nuts and sitting and eating the nuts and compared energy expended to energy gained from the nuts. They found that energy gained by eating nuts exceeded energy expended by 9 to 1. This is strong evidence that using tools to crack nuts provide significant energy benefit. We also have another analysis of nut-cracking movement in a captive subadult male chimpanzee that had been trained to crack nuts (Foucart et al., 2005). The chimpanzee cracked nuts in a sitting position, similar to that adopted by the wild chimpanzees. He put the anvil between his legs and used one arm to strike the nuts with a stone (443g). Using a three-dimensional recoding and reconstruction method, Foucart and colleagues (2005) described maximum vertical height, striking angle, temporal parameters and energetics of the upper arm as the chimpanzee cracked nuts. They concluded the chimpanzee adjusted to different conditions (anvil with or without cavities, macadamia nuts or artificial nuts) by altering the angle and maximum vertical height of the striking action.

In contrast to chimpanzees, wild capuchins (*Cebus libidinosus*) crack nuts by lifting stones bimanually in a bipedal posture (see Figure 1). Visalberghi and colleagues (2007) reported the average mass of the stones found on or near the anvils was 0.988 kg on average in the site (Boa Vista, hereafter). The mass of one stone that the monkeys used routinely is 1.46 kg, which indicates the monkeys have the ability to use a stone that is 40%-58% of their body mass (assuming mass of adult males and females are 3.7 kg and 2.5 kg, respectively; data from Fragaszy, Visalberghi & Fedigan, 2004). By comparison, one wild chimpanzee in the Taï forest used hammer stones that were 6.6% and 14.3% of body mass (Günther & Boesch, 1993).

In another site in the same state in northeastern Brazil, wild capuchins (also *C. libidinosus*) were also found to use stones as tools (Moura & Lee, 2004). Although this site (Serra da Capivara, hereafter) and Boa Vista are geographically close, and the capuchins in both sites use stones to crack open food items, the monkeys use stones differently in the two sites. In Serra da Capivara, the monkeys use stones primarily for digging to uncover underground food items (65% of observed tool use events, n=87 out of 134 events) rather than cracking (19% of observed tool use events, n=25 out of 134 events) (Moura & Lee, 2004). When the monkeys do use stones for cracking, the target food items are seeds, hollow branches and tubers. The mass of the stones used by the monkeys to dig and crack (n=14) ranges from 0.01 to 0.625 kg, much less than the mass of stones used by the monkeys in Boa Vista. The light mass of the stone and the ways of using the stones are compatible with the fact that monkeys in Serra da Capivara usually use the stone in a unimanual manner, hitting the ground three to six times while using the other hand to scoop away the loose soil; then they release the stone to dig bimanually or use the stone to hit again (Moura & Lee, 2004). In the sense of bimanual cooperation, monkeys in Serra da Capivara resemble nut-cracking chimpanzees in that they both use one hand to do percussive movement with the stone while using the other hand for different actions (position nut and pick kernel for chimpanzees and scoop away soil for capuchins).

Because the chimpanzees use smaller stones (in proportion to body mass) compared to the capuchins in Boa Vista and the chimpanzees swing one arm while the capuchins use a whole body movement, nut-cracking for capuchins is very different from nut-cracking for chimpanzees. But it is similar to the descriptions of deadlift and power pull style weight-lifting by humans (Baechle, Earle & Allerheiligen, 1994). Those two weight lifting actions are also bimanual, bipedal and 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 (see Figure 2). Then the bar is returned to the floor with control. The power pull has the same upward phase but includes a phase in which the lifter moves the bar explosively from the thighs by extending the lower extremities and pulls the bar to the neck-level. Next, the bar is returned to the floor.

Deadlift can be performed using a conventional style or a sumo style. For the sumo style, the lifter's feet are positioned further apart and turned out with arms positioned inside the knees, whereas in the conventional style, the lifter's feet are positioned closer together and the lifter's arms are positioned outside the knees (Escamila, Osbahr & Speer, 2001). Escamila et al. (2001) found that the sumo style group had a more upright trunk and a more horizontal thigh at barbell liftoff and a more horizontal thigh when the barbell passed the knees in the upward phase. They also found that the sumo group exhibited ankle dorsiflexor, knee extensor, and hip extensor moments, whereas the conventional group produced ankle plantar flexor, knee flexor and extensor, and hip extensor moments. Compared to less-skilled lifters, high-skilled lifters using either style kept the bar closer to the body, which enhanced performance and minimized risk of injury.

In the current study, I will describe the kinematics and mechanical energetics of the nut-cracking action of the capuchins in Boa Vista. I will discuss how the capuchins achieve the linked goals of maximizing performance effectiveness and minimizing risk of injury, presumably by using various lifting strategies. I will discuss similarities in skills and lifting strategies of the capuchins with those of human lifters as described in the literature. I will also compare the energetics of capuchins to those of chimpanzees as described in the literature. Finally, I will discuss the implications of capuchins' effective regulation and control of dynamic balance in an upright stance for understanding bipedality in primates.

CHAPTER 2

METHODS

Site and Natural Resources

The study site (9°south, 45°west, altitude 420 m above sea level) is located 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). The filming site is located on private property (Fazenda Boa Vista).

I observed a group of wild capuchin monkeys (*Cebus libidinosus*) in one nut-cracking site where there were anvils, stones and trees. Observation took place in June 2005 and February 2006. Nuts were provided around a log anvil by local residents, although nuts were abundant in the area. 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., 2004). A few stones of different shape and mass were brought to the anvil from adjacent areas by the researchers, but the monkeys' favorite stone (Stone 11, 1460g) was at the site already. Figures 3 and 4 show the stones used in the study and one species of the nuts. The mass of the stone used by each subject is shown in Table 1.

Subjects

Four adult capuchin monkeys from one group in our study site served as subjects in this study. Subjects' body lengths (from auditory meatus to ankle) are shown in Table 1. They were judged to be fully adult based on body length, color of facial fur and shape of the tuft of hair at the crown of the head (Fragaszy, Visalberghi & Fedigan, 2004). Of the four capuchins, two were males (Chicao and Secondo Chefe) and two were females (TeNinha and Piacava). Each of the females had offspring in the group but neither one had an infant on the back during coded episodes. During the observation period, all four monkeys cracked nuts frequently (nearly on every observation day).

Data Capture Setup

The movements of the monkeys were videotaped when they were cracking nuts on a log anvil (Figure 5 illustrates the setup). Standard two-dimensional motion measurement methodology was used (Robertson et al., 2004). A Canon ^{TM} GL2 mini-DV camera (60 Hz sampling rate; minimum exposure time 1/2000s) was used for video taping. The camera was placed within a blind structure so the monkeys' activity was undisturbed. The camera was placed approximately 6 meters away from the anvil to capture sagittal plane views (field of view was approximately 1.5 m) of the monkeys during nut-cracking.

After the monkeys left the site, the calibration device consisting of two rods was videotaped for calibration, as shown in Figure 5. The rods were placed in vertical alignment. Two reflective markers on two ends of each rod were 0.38 m apart. The horizontal distance (range 1.03-1.075 m) between the two rods was recorded for each calibration video.

Data Reduction and Digitizing

Video clips were selected on the basis of lighting, stability of camera and the subjects' position in the field of view. I 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, I digitized five hits that were roughly evenly distributed throughout the episode. For example, if a male had only five hits in one episode, I digitized every hit. If a female had thirteen hits in one episode, I digitized the first, fourth, seventh, tenth and thirteenth hits. Therefore, ten hits were digitized for each monkey, which came from two different cracking episodes.

A hit consisted of an upward phase (from start of lifting to stone zenith point) and a downward phase (from stone zenith point to stone-nut contact) and a preparatory pre-lift phase (five fields prior to start of lifting, 0.083s in duration) before start of lifting. For each hit, thirteen points on the monkey's body, the nut and the top of the anvil were manually digitized (Peak Motus™ by Vicon, version 9.0), as shown in Figure 6a. The points digitized of the monkey were in the sagittal plane of the side of the body closer to the camera. The movements of the monkey were assumed to be bilaterally symmetrical.

For each hit, three critical events were marked. The critical events were "start of lifting", "MCP joint of third digit zenith" 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 very instant when the MCP joint reached the highest vertical height. Because the MCP joint was used as a proxy for the stone's center of mass, this instant is referred to as 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 and stone-nut contact was defined as 100% of hit duration. The five data points before start of lifting therefore were marked with negative percent values.

After manually digitizing the points, raw coordinates of all points were filtered using a fourth-order Butterworth filter with cut-off frequency of 6Hz (Jackson, 1979). Filtered coordinates were then scaled to actual measurement units using calibration video.

In further analysis for angular kinematics, three hits exhibiting the highest stone zenith points were selected for each subject. The higher the stone zenith point, the more erect the subject became and the more pronounced the angular movement pattern was.

Data Computation

For each hit, durations, maximum vertical height of stone (using MCP joint as a proxy for the stone) and the mechanical energetics of the stone were computed. The energetics variables of maximum gravitational potential energy and maximum kinetic energy were computed. The kinetic energy/potential energy ratio was also computed to evaluate if the monkeys added energy to the stone in the downward phase. Table 2 illustrates how the above variables were defined and computed.

Joint angles for the shoulder and elbow joints and the lower extremities (hip, knee and ankle), and segmental angle for the trunk were computed in Peak Motus™ (see Figure 6b). Angle values and angular velocity for the six angles were generated for each hit. Angular displacement for extension and flexion was calculated by using maximum and minimum values (e.g., flexion displacement = [minimum angle value]-[maximum angle value]). Temporal durations to maximum/minimum angles were expressed relative to the total hit duration (%HD).

CHAPTER 3

RESULTS

In all episodes analyzed, the stones were already on the anvil or close to the anvil. 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) and in front of the knees (12.5% of 40 hits) in the start of upward phase. Positioning of the arm was not related to gender or mass of the rock in my samples. The monkeys successfully cracked open the nuts in all coded episodes.

Durations

The 40 hits averaged 0.744 (SD=0.053) seconds in duration. The upward phase lasted 69.4%HD. The downward phase lasted 30.6%HD. Table 3 presents mean and SD for the duration of the hit for each subject. The video was digitized field by field (one field=1/60s), so the measurement error is ±1/60s, which is approximately ±0.0167s.

If the duration of the downward phase is shorter than the duration of a free fall movement from the same maximum vertical height, the monkey must have exerted external downward force onto the stone. If the two durations are the same with measurement error allowed, the downward phase must have been a free fall movement; therefore the monkey did not put downward force onto the stone.

As depicted in Figure 7, for the two males, in 18 out of 20 hits, the downward phase duration was shorter than free fall duration; for the two females, in 10 out of 20 hits, the downward phase duration was 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 is greater for the two males ($\text{mean}_{\text{diff.}}$=0.044±0.023 s) than for the two females ($\text{mean}_{\text{diff.}}$=0.020±0.014 s).

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 of the stone are shown in Table 4.

As one can see in Table 4, when the average maximum vertical height is expressed as a proportion of body length, one male (Chicao) lifted the stone on average to the height of 57±5% of his body length, while the other (Secondo) lifted 66±8%; one female (TeNinha) lifted on average to 53±8% and the other female (Piacava) lifted to 65±9% of body length, although she has the smallest body length among the four subjects. Across all hits, males lifted the stone to height of 47%-77% of in body length and females to the 45%-76% in the body length.

Velocity, Maximum Potential Energy and Maximum Kinetic Energy

Table 5 presents the mean and SD of maximum vertical velocity of the stone before stone-nut contact, maximum potential energy, maximum kinetic potential and the potential/kinetic energy ratio for each subject. Both males achieved maximum vertical velocity of 3.19 m/s; the two females reached 2.48 m/s (TeNinha) and 2.69 m/s (Piacava). Therefore, the males generated higher maximum kinetic energy than the females. As males lifted the stones to higher maximum vertical height, the potential energy of stones they generated was also higher than the potential energy generated by females. The males achieved mean kinetic energy/potential energy ratios of 1.39 and 1.24, compared to 0.91 and 1.04 for the two females, suggesting both males added substantial energy in the downward phase while females did not.

Angular Kinematics

Commonalities among Subjects

The basic pattern of the nut-cracking movement in these adult capuchin monkeys is illustrated with a stick figure in Figure 8, and can be described as the following. Starting from a crouched position, the monkey first hyper-extends the upper arms to pull in the stone closer to his/her center of mass. Then the trunk and lower extremities (hip and knee) start extending in an explosive manner until the stone reaches the maximum vertical height (stone zenith point, hereafter). In the downward phase, the trunk and lower extremities all flex until the moment of stone-nut contact such that the monkey returns to a crouched position.

Next, details of movement will be described for each major joint, with representative angle-time graphs shown in Figures 9-12. Temporal durations are marked in the form of percent of hit duration (%HD). The shoulder joint showed an extension-flexion pattern of movement. Subjects started shoulder extension at -4±6%HD from the angle of 155±7°. Maximum shoulder extension reached 186±9° at 36±5%HD in the upward phase. Next the upper arm started flexing, resulting in flexion of the shoulder joint. The shoulder reached the maximum flexion of 101±15°

at 90±6%HD near the end of the downward phase. Mean and SD for shoulder extension and flexion times, angles and displacements for each subject are shown in Table 6.

Three subjects did not show any discernable pattern of movement of the elbow. There was some motion at the elbow joint but the displacement never exceeded 46° (30±9°) and there was no discernable pattern within or among these three subjects. Only one male (Secondo) displayed a clear pattern, which will be addressed below in the section on strategies.

The trunk, hip and knee all reached maximum extension close to the instant of the stone zenith point, and all flexed continuously in the downward phase. The trunk extended from a position parallel to the ground (1±16°) at -5±10%HD. The trunk kept extending until 6%HD past stone zenith point and reached maximum extension of 68±5° at 63±4%HD. In other words, the trunk continued to straighten for a brief period after the stone reached its zenith. Then the trunk began flexing and reached the maximum flexion of 23±6° at the very end of downward phase. Table 7 shows the mean and SD for trunk extension and flexion times, angles and displacements for each subject.

The hip started extending from 6±13° at -3±7%HD. The hip then continued extending 3%HD past the stone zenith point and reached the maximum extension of 120±8° at 60±6%HD. Then the hip began flexing and reached the maximum flexion of -5±13° at the end of downward phase. Mean and SD for hip extension and flexion times, angles and displacements for each subject are shown in Table 8.

The knee began extending from 85±16° at 8±15%HD. The knee reached maximum extension of 129±9° at 54±7%) 3%HD before the stone zenith point. Then the knee began flexing and reached the maximum flexion of 50±7° at 99±1%HD near the end of the downward phase. Table 9 presents the mean and SD for knee extension and flexion times, angles and displacements for each subject.

Only one subject (TeNinha) showed a clear pattern of ankle movement, which will be addressed in the individual strategy section. The other three monkeys firmly gripped on the lateral edges of the anvil with their feet. Although there was some motion about the ankle joint, the displacement never exceeded 42° (31±7°) and there was no discernable pattern within or among these three subjects.

Strategies

Besides commonalities, there are several pronounced strategies within and between individuals in my samples. Across the three phases (pre-lift, upward lifting and downward striking), I found the following strategies.

1. Pre-lift: preparatory phase

Upper arm hyper-extends to pull in stone

All four monkeys hyper-extended the upper arms to pull in the stone closer to his/her center of mass in all 12 hits in pre-lift phase or in the beginning of the upward phase. Hyper-extension of the upper arm resulted in extension of the shoulder angle, which is illustrated in Figures 8, 9, 13-16.

2. Upward lifting phase

Trunk extends earlier than knees

Three subjects exhibited a specific lifting strategy in the upward phase. In one female (Piacava, 2 out of 3 hits) and the two males (all hits), the trunk started extending earlier

(21±15%HD) than the knees, indicating that the trunk moved the stone first with knees extending later. This sequence is illustrated in Figures 13, 15 & 16.

Jump near the end of lifting

One female (TeNinha) jumped when the stone was about to reach the zenith point. This action resulted in her lifting the stone to a higher maximum vertical height than she would have without jumping. She started flexing her ankles at beginning of the hit (5±5%HD) from 126±19°. Then at 30±8%HD, she started extending her ankles from an angle of 113±7°. Her ankles reached maximum extension (155±7°) at the zenith point, showing plantar flexion. Then her ankles started flexing until the angle was 105±4° at 84±1%HD. A representative graph of TeNinha's ankle angle displacement is presented in Figure 17.

Use of elbow

In one male (Secondo), the elbows played a part in raising the stone and his lower arms exhibited a clear pattern of flexing and extending. In the upward phase at 20±6%HD he started flexing 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 to raise stone higher. He kept extending his elbows in the downward phase, which added downward force to help push the stone. At 88±6%HD, his elbows reached maximum extension of 105±5°. The pattern is depicted in Figure 18.

3. *Downward striking phase*

Dropping lower body first

Three subjects exhibited a specific pulling strategy in the downward phase. In one male (Secondo) and the two females, the knees started flexing earlier (13±9%HD) than the trunk.

This indicates the monkeys lower the stone by dropping the lower body (as shown in knee flexion) first and dropping the trunk later. This sequence is illustrated in Figures 13-15.

A comparison of Figures 13-18 illustrates the individually distinctive pattern of joint movement and joint displacement evident in the capuchins. For example, Piacava began extending her shoulders before extending trunk and lower extremities. Her knees extended last and started to flex first. TeNinha has the same pattern as Piacava. In addition, her ankles showed extension until the end of upward phase, reflecting the “jump”. Secondo’s hips and trunk started extending from the very beginning. His elbows showed a clear pattern of flexion and extension. Chicao’s shoulders and trunk started extension at 0%HD. Then his hips started to extend. His knees extended last but started to flex approximately at the same time as the hip and the trunk.

CHAPTER 4

DISCUSSION

General 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 hardness of the nuts, the monkeys successfully exploited the mechanics of their body and achieved the goal of cracking open nuts. I presume that the monkeys maximized the performance effectiveness and minimized the risk of injury in nut-cracking, which is further discussed in the next section.

To recap major findings, capuchins cracked nuts in a bipedal stance, using both hands to grasp the heavy hammer stone. They exhibited control of the stone's movement over the course of lifting and striking. A single hit consisting of lifting and striking lasted three quarters of a second in duration. The monkeys lifted the hammer stone to a vertical height of 45%-77% of their body length. The downward strike lasted less than a quarter of a second. The two males were taller than the females, so they achieved greater maximum potential energy and kinetic energy. But in addition, the fact that the males had a larger energy/potential energy ratio than females suggests that they added more energy to the hammer stone in the downward phase than did the females.

In a typical hit, starting from a crouched position, the monkeys first hyper-extended the upper arms to pull in the stone closer to their body, then extended the trunk and lower extremities (hips and knees) in an explosive manner until the hammer stone reached its zenith point. In the downward phase, the trunk and lower extremities all flexed until the stone contacted the nut and the monkeys returned to a crouched position and released the stone or repositioned it for another hit.

Kinematics Strategies

To crack open the hard nuts, the monkeys must lift the heavy hammer stone and strike it onto the nut. The monkeys showed several different kinematic strategies in each phase of the movement to achieve the goal.

All the monkeys hyper-extended the upper arms to pull in the stone closer to their center of mass in the pre-lift phase or in the beginning of the upward phase. Skilled human weight lifters also pull in the barbell closer to their center to mass at the beginning of lifting. This action reduces the torque that must be counteracted by trunk extensor muscle torque. The back muscles need to produce less force to counteract lesser resistance torque. Therefore, keeping the heavy mass closer to the center of mass minimizes risk of injury and produces better lifting mechanics. This strategy also serves to add more postural stability before lifting the stone (Smith, Weiss & Lehmkuhl, 1995).

In the upward phase, the mechanical goal is to lift the stone as high as possible. Three subjects showed a specific lifting strategy in this phase. They extended the trunk earlier than lower extremities, so that they used the back first and legs later to move the stone upward. The movement of the trunk produced acceleration in the beginning to bring the stone from a zero to an upward velocity. Then the strong leg muscles accelerated the stone vertically to a high upward velocity. This is an effective strategy often employed by human lifters (Harman, 1994).

One female showed another strategy: jumping near the end of upward lifting phase. This indicates that the extension of the lower extremities was so explosive that the ankle joint also extended, producing plantar flexion at the stone zenith point. It is surmised, although not provable from these data, that either the monkey created plantar flexor torque to push the feet down against the ground and/or kinetic energy was transferred from the lower legs to the feet enabling the foot to apply more force to the ground. Either way, by jumping off the anvil near the end of the upward phase, she raised the stone as high as possible. This strategy is also used by human lifters in power pull style weight lifting (See Figure 2) (Baechle, Earle & Allerheiligen, 1994).

One male showed a pattern of elbow flexion-extension in the upward phase and downward phase. I 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 the elbows did not make a major contribution to raising the stone. However, by doing this, they kept their arms rigid so that they used trunk and legs to raise the stone.

In the downward phase, the mechanical goal is to get the maximum controllable kinetic energy before stone-nut contact. Three monkeys showed a pulling strategy of flexing the knees earlier than the trunk. This means they lowered the stone by dropping the lower body first and dropping the trunk later. I surmise that by using the back muscles later in the downward phase (closer to the stone-nut contact), the monkeys could strike the nut with more control and possibly with more force generated from the back muscles.

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. I assume that these individualized strategies represent the monkeys' solutions to the linked goals of maximizing mechanical advantages and minimizing the risk of injury.

Comparison with Human Lifters

The general pattern in the upward phase is strikingly similar to the skills showed by professional human weight lifters. 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, Osbahr & Speer, 2001). The capuchins resemble the sumo style lifters in some aspects. The monkeys' feet were turned out on the lateral edges of the anvil (approximately 20 cm in width). Their arms were positioned inside the knees two thirds of the time, resembling the sumo style. Similar to the human lifters, the capuchins showed trunk, hip and knee extension in the lifting phase. In addition, TeNinha's ankle extension strategy, as discussed above, showed resemblance to the jumping action in human power pull style weight lifting (Baechle, Earle & Allerheiligen, 1994).

Comparison with Chimpanzee Nut-cracking

Despite their smaller size, these wild capuchins astonishingly outshone chimpanzees, their nut-cracking counterparts, in several aspects. First, compared to chimpanzees cracking nuts, these capuchins use a proportionally much heavier stone. In the 1993 study by Günther and Boesch, one wild male chimpanzee used two wooden hammers which were estimated to be 6.6% and 14.3% of his body mass (estimated body mass was 35 kg and mass of the hammers was 2.3 kg and 5kg). The mass of the two hammer stones used by monkeys in my samples was 1.46 kg and 1.32 kg, an estimated 39.5%-58.4% of body mass (Fragaszy, Visalberghi & Fedigan, 2004). Second, the maximum velocity in the downward phase right before nut-stone contact is 3.36 m/s in my samples, which is close to the velocity of 3.55 m/s generated by a wild male chimpanzee in Günther and Boesch's study (1993). The maximum kinetic energy of the hammer stone reached 8.17 J in my samples while the male chimpanzee generated 14.5 J with a 2.3 kg hammer stone. Wild capuchins have approximately 1/10 of the body mass of the Taï forest male chimpanzee, yet they managed to lift a stone that was more than half of the mass that the chimpanzee used, to a vertical height greater than that of the chimpanzee, and reached approximately the same maximum velocity during striking, and they produced kinetic energy that is more than half of what the chimpanzee generated. In a more striking comparison, the mean maximum kinetic energy generated by a captive male chimpanzee to crack macadamia nuts was 0.581J using a stone of 443 grams (Foucart et al., 2006), which is about 1/14 of the kinetic energy generated by wild capuchins. Clearly, nut-cracking is more strenuous for capuchins than for chimpanzees.

Bipedal Stance in Nut-cracking by Capuchins

In terms of angular displacement, the monkeys in Boa Vista achieved semi-vertical stance during the hit. In perfect bipedal stance, hip and knee angles are 180º and trunk inclination is 90º. In my samples, the maximum hip angle that the monkeys achieved is 128º, the maximum trunk inclination angle is 80º and maximum knee angle is 137º. Considering capuchins are anatomically and habitually quadrupedal, these monkeys have to work against their anatomical inheritance to adopt an upright posture routinely and to maintain control over a heavy hammer stone during nut-cracking.

To examine the extent of bipedality in the capuchins, the Japanese macaques trained to walk bipedally provide an interesting reference. Hirasaki and colleagues (2004) compared three highly trained Japanese macaques (*Macata fuscata*) to two ordinary macaques during bipedal walking. The highly 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 (max trunk inclination is about 72°, max hip extension and knee extension are both about 120°). The capuchins in Boa Vista showed the same extent of trunk inclination as that of the highly trained macaques. They also showed greater knee and hip extension than the ordinary macaques but not as great as the trained macaques. Knee and hip extension is more important in walking than in lifting and striking a stone in bipedal stance, so the capuchins did not have to extend the knee and hip as extremely to crack nuts as would be expected in bipedal walking. But in nut-cracking, it is advantageous to lift the stone to a vertical height as great as possible, so uprightness of the trunk is more important than hip and knee extension. In any case, the wild capuchins exhibited the same extent of uprightness in nut-cracking to that of the highly trained macaques in walking.

Morphology

Nakatsukasa and colleagues (1995), studying the postcranial skeleton of a Japanese macaque, showed that 11 years of training had modified the hindlimb bones considerably, in terms of joint morphology, articular dimensions and shape-dependent strength of long bones. The authors suggested these changes reflected the causal relationship between function and morphology. If the trained macaques can develop human-like characteristics of bipedal gait and bipedal walking can cause morphological changes, one cannot help wondering if routine nut-cracking in bipedal stance over years affects the skeletal anatomy of the capuchins, and if these skeletal changes 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.

Wright (2007) suggested a higher IM (intermembral or forelimb/hindlimb index) index (more similar length of arms and legs) 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, Visalberghi & Fedigan, 2004). Wright (2007) also found that *C. apella* have relatively short hind limbs and slightly shorter forelimbs, bringing the center of mass lower to the substrate they are on, adding more stability for orthograde posture compared to *C. olivaceus*. Therefore, *C. libidinosus,* as close cousin of *C. apella*, may have an advantage over non-tufted species of *Cebus* in lifting and striking heavy stones in a bipedal stance.

Human have an IM index of 72 (Fleagle, 1999). The index for *C. apella* is 88 (Wright, 2007), and I assume the value for *C. libidinosus* is similar to that for C. apella. Therefore, our legs are much longer than our arms and our center of mass is proportionally as well as absolutely higher than that of the tufted capuchins, which gives the monkeys an advantage over us in stabilizing the movement in nut-cracking.

Problem Encountered

One limitation of the study is that through the filtering of the raw data points that were manually digitized, abrupt changes in velocity and direction of the movement can be artificially smoothed. As a result, the velocity values prior to stone-nut contact point are underestimated for all subjects in all hits. This explains why the kinetic energy/potential energy ratios are smaller than 1 for the females. It is also the reason why I did not calculate acceleration data, which would be severely influenced by errors of measurement. However, filtering is necessary to reduce substantial amount of noise in the signal caused by manual digitizing. In the future, I will adopt a different filtering strategy to accommodate abrupt changes in the raw data. A different approach is to use an accelerometer attached to the hammer stone to record real-time acceleration data. With this, I can calculate force and movement parameters more accurately.

Future Directions

The current study opens new questions as this is the first to examine the kinematic properties of tool use actions in bipedal stance in nonhuman primates. I look forward to further investigations with many aspects of behavior, physical components and body structure of these wild capuchins. For example, energetic analysis of nut-cracking activities and caloric analysis of the nuts are essential to compare the energy expenditure and gain. I will also expand sample size to capture potential sex difference in adults and to study the development of nut-cracking skills in juveniles. Meanwhile, morphological and anatomical work is also necessary to reveal the consequences for the body of routine strenuous actions by these capuchins. Because these monkeys lift while standing bipedally and also carry heavy hammer stones while walking bipedally, while apes generally do not, the capuchins provide a new model for bipedal lifting and carrying in primates, which can provide ideas about alternative origins of bipedality in human ancestors.

REFERENCES

Baechle, T. R., Earle, R. W., & Allerheiligen, W. B. (1994). Strength training and spotting techniques. In: T. R. Baechle (Ed), *Essentials of Strength Training and Conditioning* (380 & 395). Champaign, IL: Human Kinetics.

Boesch, C. & Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest.* Oxford: Oxford University Press.

Escamila, R. F. et al. (2000). A three-dimensional biomechanical analysis of sumo and conventional style deadlifts. *Medicine & Science in Sports & Exercise*, *32*, 1265-1275.

Escamila, R. F., Lowry, T. M., Osbahr, D. C., & Speer, K. P. (2001). Biomechanical analysis of the deadlift during the 1999 Special Olympics World Games. *Medicine & Science in Sports & Exercise, 33*, 1345-1353.

Fleagle, J. (1999). *Primate Adaptation and Evolution*. San Diego: 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: V. Roux & B. Bril (Eds.), *Stone Knapping: the necessary conditions for a uniquely hominid behavior* (147-158). Cambridge, UK: McDonald Press.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., & de Oliveira, M. G. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, *64*, 359-366.

Fragaszy, D., Visalberghi, E. & Fedigan, L. (2004). *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. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 2455-2460.

Groves, C. P. (2001). *Primate Taxonomy*. Washington, DC: Smithsonian Institution Press.

Günther, M. M. & Boesch, C. (1993). Energetic cost of nut-cracking behaviour in wild chimpanzees. In: H. Preuschoft & D. J. Chivers (Eds.), *Hands of Primates* (109-129). New York: Springer-Verlag.

Harman, E. (1994). The biomechanics of resistance exercise. In: T. R. Baechle (Ed), *Essentials of Strength Training and Conditioning* (38). Champaign, IL: Human Kinetics.

Heinzelin, J. et al. (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. *Journal of Human Evolution, 46*, 739-750.

Jackson, K. M. (1979). Fitting of mathematical functions to biomechanical data. *IEEE Transactions on Biomedical Engineering, 26*, 122-124.

Kortlandt, A. (1986). The use of tools by wild-living chimpanzees and earliest hominids. *Journal of Human Evolution, 15*, 77–132.

Kortlandt, A. & Holzhaus, E. (1987). New data on the use of stone tools by chimpanzees in Guinea and Liberia. *Primates*, *28*, 473-496.

Matsuzawa, T. (2001). Primate foundations of human intelligence: A view of tool use in nonhuman primates and fossil hominids. In: T. Matsuzawa (Ed.), *Primate Origins of Human Cognition and Behavior* (3-25). Tokyo: Springer.

Maura, A. C. de A. (2004). The capuchin monkey and the Caatinga dry forest: a harsh life in a harsh habitat. PhD Dissertation, University of Cambridge.

Maura, A. C. de A. & Lee, P.C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science, 306*, 1909.

Nakatsukasa, M., Hayama, S., & Preuschoft, H. (1995). Postcranial skeleton of a macaque trained for bipedal standing and walking and implications for functional adaptation. *Folia Primatologica, 64,* 1-29.

Robertson, G. E., Caldwell, G., Hamill, J., Kamen, G., & Whittlesey, S. (2004). *Research Methods in Biomechanics*. Champaign, IL : Human Kinetics.

Smith, L. K., Weiss, E. L., & Lehmkuhl, L. D. (1995). *Brunnstrom's Clinical Kinesiology*. Philadelphia: F. A. Davis.

Sugiyama, Y. & Koman, J. (1979). Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea. *Primates, 20,* 513–524.

Sugiyama, Y., Fushimi, T., Sakura, O., & Matsuzawa, T. (1993). Hand preference and tool use in wild chimpanzees. *Primates, 34,* 151-159

Visalberghi, E., Fragaszy, D., Ottoni, E., Izar, P., de Oliveira, M. G., & Andrade, F. R. D. (2007). Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *American Journal of Physical Anthropology, 132*, 426-444.

Wright, K. A. (2007). The relationship between locomotor behavior and limb morphology in brown (*Cebus apella*) and weeper (*Cebus olivaceus*) capuchins. *American Journal of Primatology*, *69*, 1–21.

Table 1 Characteristics of subjects and weight of hammer stones they used

Subject	Sex	Estimated Body Length(m)	Weight of hammer stone (kg)
Chicao (CH)	Male	0.594	1.46 kg
Secondo (SE)	Male	0.586	1.46 kg
TeNinha (TN)	Female	0.562	1.46 kg
Piacava (PI)	Female	0.481	1.32 kg in 5 hits, 1.46 kg in 5 hits

Table 2 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 * 1/60s
	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 * 1/60s
	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 * 1/60s
	Duration of free fall (s)	Time needed if the stone movement is free fall from the same vertical height	$t_{\text{free fall}}$ = the square root of 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 before the 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 kilograms; v = velocity of the stone, in m/s^2.
	Kinetic energy/ potential energy ratio	The ratio reflects how much additional energy the subject adds during the down phase.	K/P ratio = Maximum kinetic energy/maximum potential energy

Table 3 Duration of a hit (mean and SD per 10 hits per subject)

Subject	duration of hit (s)	down duration(s)	free fall (s)	shorter (s)
Chicao	0.778±0.050	0.225±0.016	0.262±0.011	0.037±0.026
Secondo	0.748±0.049	0.228±0.014	0.280±0.017	0.052±0.019
TeNinha	0.723±0.048	0.225±0.024	0.246±0.018	0.021±0.015
Piacava	0.727±0.052	0.233±0.018	0.252±0.017	0.019±0.013

Table 4 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	0.336±0.029	57±5
Secondo	0.385±0.045	66±8
TeNinha	0.298±0.043	53±8
Piacava	0.313±0.041	65±9

Table 5 Energetics of nut-cracking (mean and SD per 10 hits per subject)

Subject	Maximum potential energy (Joule)	Maximum velocity of the stone before stone-nut contact (m/s)	Maximum kinetic energy (Joule)	Kinetic/Potential energy ratio
Chicao	4.81±0.41	2.74±0.35	5.56±1.44	1.14±0.20
Secondo	5.51±0.64	2.93±0.28	6.33±1.16	1.14±0.11
TeNinha	4.27±0.61	2.38±0.13	4.14±0.45	0.98±0.08
Piacava	4.24±0.37	2.40±0.27	4.01±0.70	0.94±0.11

Table 6 Shoulder extension and flexion times, angles and displacements (mean and SD per 3 representative hits per subject)

Subject	Time of start of extension (%HD)	Angle at start of extension (degree)	Time of maximum extension/start of flexion (%HD)	Angle at maximum extension/start of flexion (degree)	Angle displacement from start of extension to maximum extension (degree)	Time of maximum flexion (%HD)	Angle at maximum flexion (degree)	Angle displacement from start of flexion to maximum flexion (degree)
Chicao	-2±8	157±11	33±2	175±2	18±11	92±2	105±3	-70±2
Secondo	-1±5	153±4	38±2	186±3	33±5	83±1	78±3	-108±1
TeNinha	-8±5	159±9	32±6	195±9	36±14	97±3	107±3	-88±11
Piacava	-7±4	151±5	40±6	190±2	39±7	85±3	113±5	-77±4

Table 7 Trunk extension and flexion times, angles and displacements (mean and SD per 3 representative hits per subject)

Subject	Time of start of extension (%HD)	Angle at start of extension (degree)	Time of maximum extension/start of flexion (%HD)	Angle at maximum extension/start of flexion (degree)	Angle displacement from start of extension to maximum extension (degree)	Time of maximum flexion (%HD)	Angle at maximum flexion (degree)	Angle displacement from start of flexion to maximum flexion (degree)
Chicao	-10±1	8±3	65±1	70±1	62±4	100±0	28±3	-43±3
Secondo	-10±3	-4±5	57±2	62±1	66±6	100±0	14±3	-48±4
TeNinha	6±15	20±7	62±3	67±3	47±8	100±0	25±3	-42±3
Piacava	-7±5	-19±8	68±0	72±7	91±2	100±0	26±1	-46±6

Table 8 Hip extension and flexion times, angles and displacements (mean and SD per 3 representative hits per subject)

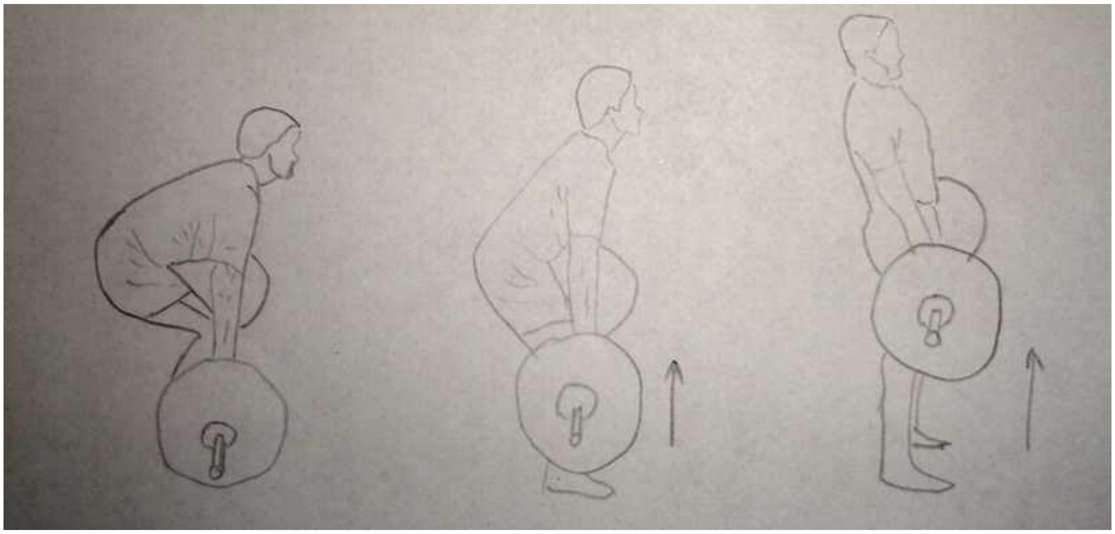
Subject	Time of start of extension (%HD)	Angle at start of extension (degree)	Time of maximum extension/start of flexion (%HD)	Angle at maximum extension/start of flexion (degree)	Angle displacement from start of extension to maximum extension (degree)	Time of maximum flexion (%HD)	Angle at maximum flexion (degree)	Angle displacement from start of flexion to maximum flexion (degree)
Chicao	-4±7	15±10	65±2	123±4	109±14	100±0	-3±3	-126±6
Secondo	-8±7	15±5	55±5	121±4	106±2	100±0	13±4	-108±3
TeNinha	-2±4	-8±14	57±6	120±4	128±10	100±0	-20±2	-140±6
Piacava	1±8	2±7	62±2	115±15	113±12	100±0	-9±8	-124±22

Table 9 Knee extension and flexion times, angles and displacements (mean and SD per 3 representative hits per subject)

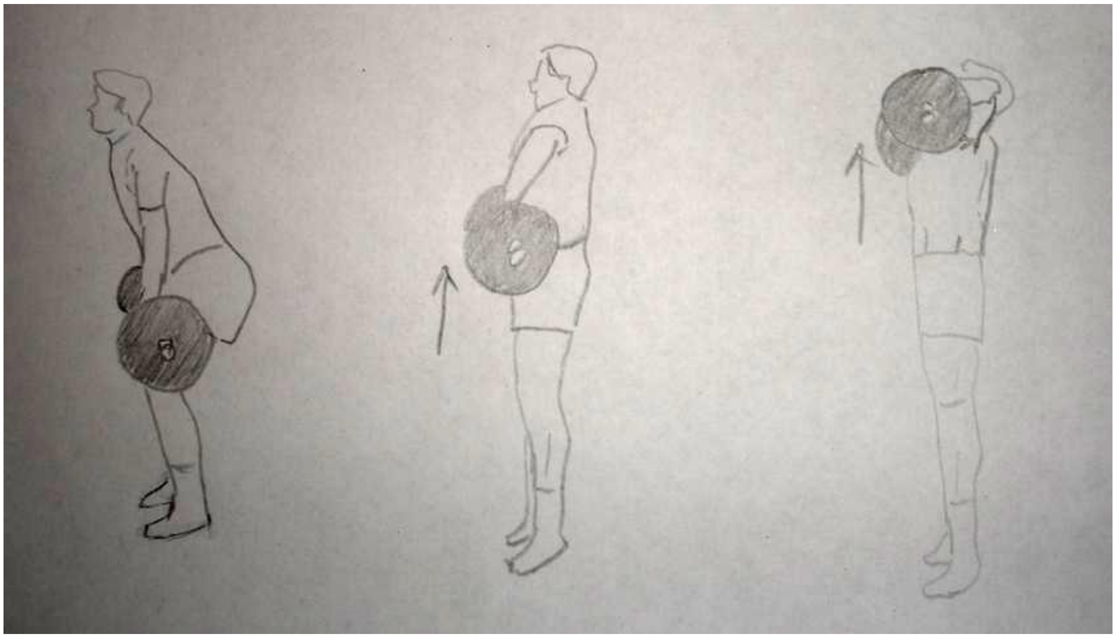
Subject	Time of start of extension (%HD)	Angle at start of extension (degree)	Time of maximum extension/start of flexion (%HD)	Angle at maximum extension/start of flexion (degree)	Angle displacement from start of extension to maximum extension (degree)	Time of maximum flexion (%HD)	Angle at maximum flexion (degree)	Angle displacement from start of flexion to maximum flexion (degree)
Chicao	20±18	90±10	62±2	123±1	34±11	99±1	50±11	-73±11
Secondo	2±13	96±8	51±6	135±3	39±6	100±0	49±7	-86±9
TeNinha	5±15	62±11	55±4	137±10	76±5	98±2	47±7	-91±5
Piacava	6±15	93±4	47±7	121±4	28±3	100±0	53±6	-68±8

Figure 1 TeNinha cracking a nut; she is jumping off the anvil at this instant.

(Photograph by T. Faloticò)



Beginning position Raise bar straight Thrust hips forward



Beginning position Jumping action Highest position

Figure 2 Deadlift style powerlifting (first row) and power pull (second row).

(Figures adapted from *Essentials and Strength Training and Conditioning*, p380&395)

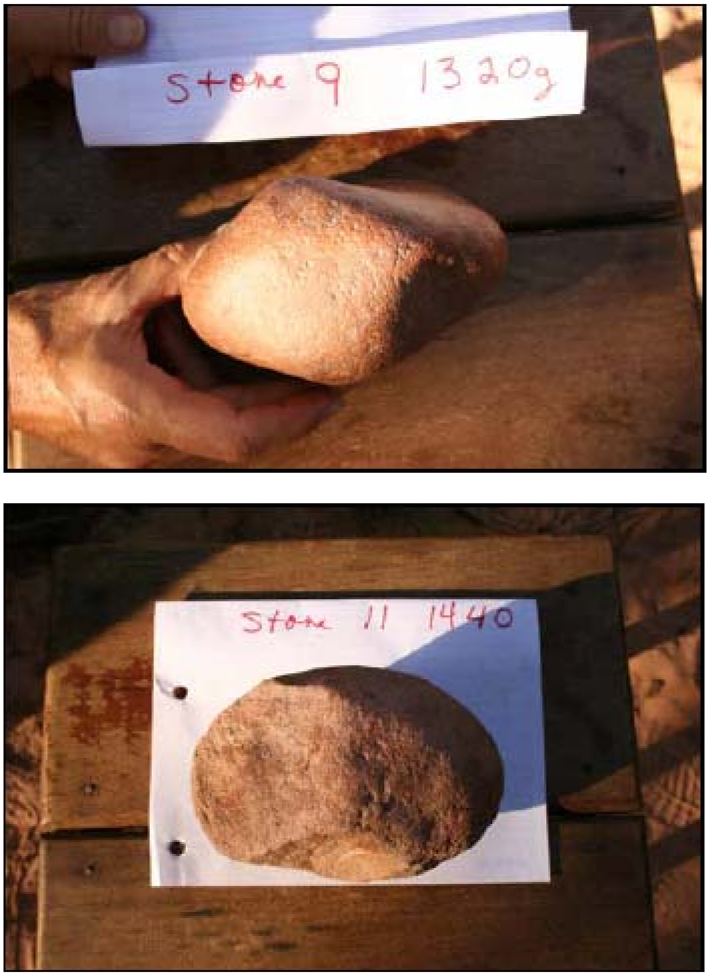
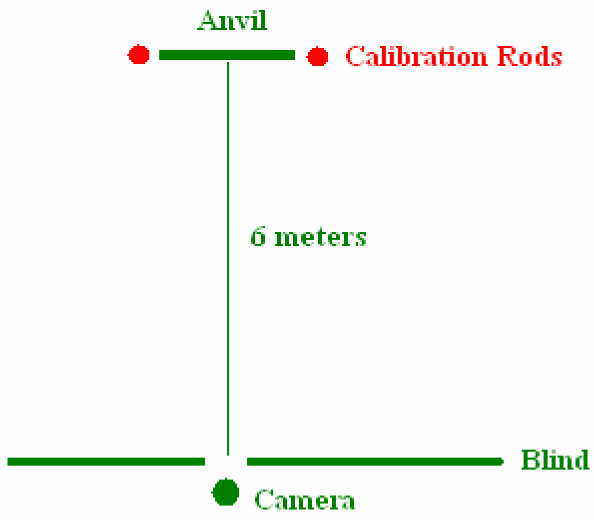


Figure 3 Hammer stones used by the monkeys in the study.

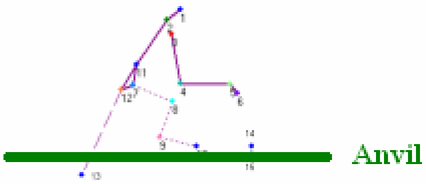
(Photograph by T. Faloticò)

Figure 4 One species of the palm nuts cracked by monkeys in Boa Vista; the rule indicates centimeter.

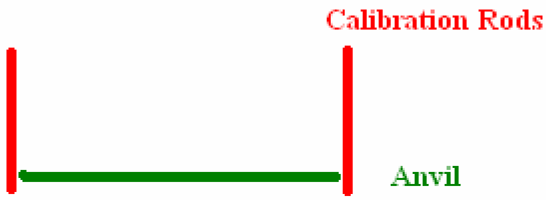
(Photograph by E. Visalberghi)



1. Aerial view



2. Camera's view during video taping



3. Camera's view during calibration

Figure 5 Data capture setup

(The top panel illustrates aerial view of the setup; the middle panel illustrates the camera's view during video taping the nut-cracking movements; the bottom panel illustrates the camera's view during calibration.)

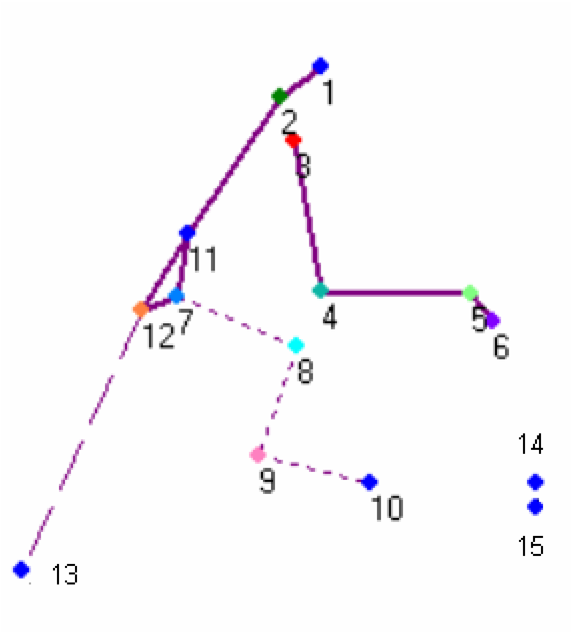


Figure 6a Spatial model

1=ear (auditory meatus)

2=neck (end of cervical vertebra)

3=shoulder

4=elbow

5=wrist

6= Metacarpophalangeal joint (MCP) of the third finger (The MCP joint of the third digit was used as a marker for the hammer stone)

7=hip

8=knee

9=ankle

10= Metatarsophalangeal joint (MTP) of the third digit

11=pelvis

12=base of tail

13=tip of tail (defined as the end point of the straight part of the tail)

14=center of nut

15=top of log where the monkey placed the nut

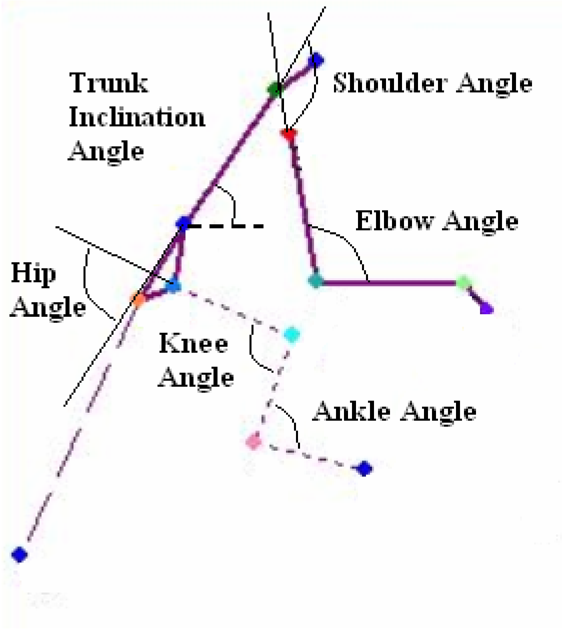


Figure 6b Angles

Shoulder angle= Joint angle between upper arm (elbow-shoulder) and trunk (neck-pelvis)

Elbow angle= Joint angle between upper arm (elbow-shoulder) and lower arm (wrist-elbow)

Trunk inclination angle= Segmental angle between trunk (neck-pelvis) and X axis

Hip angle= Joint angle between upper trunk (neck-pelvis) and thigh (hip-knee)

Knee angle= Joint angle between thigh (hip-knee) and shank (knee-ankle)

Ankle angle= Joint angle between shank (knee-ankle) and foot (MTP-ankle)

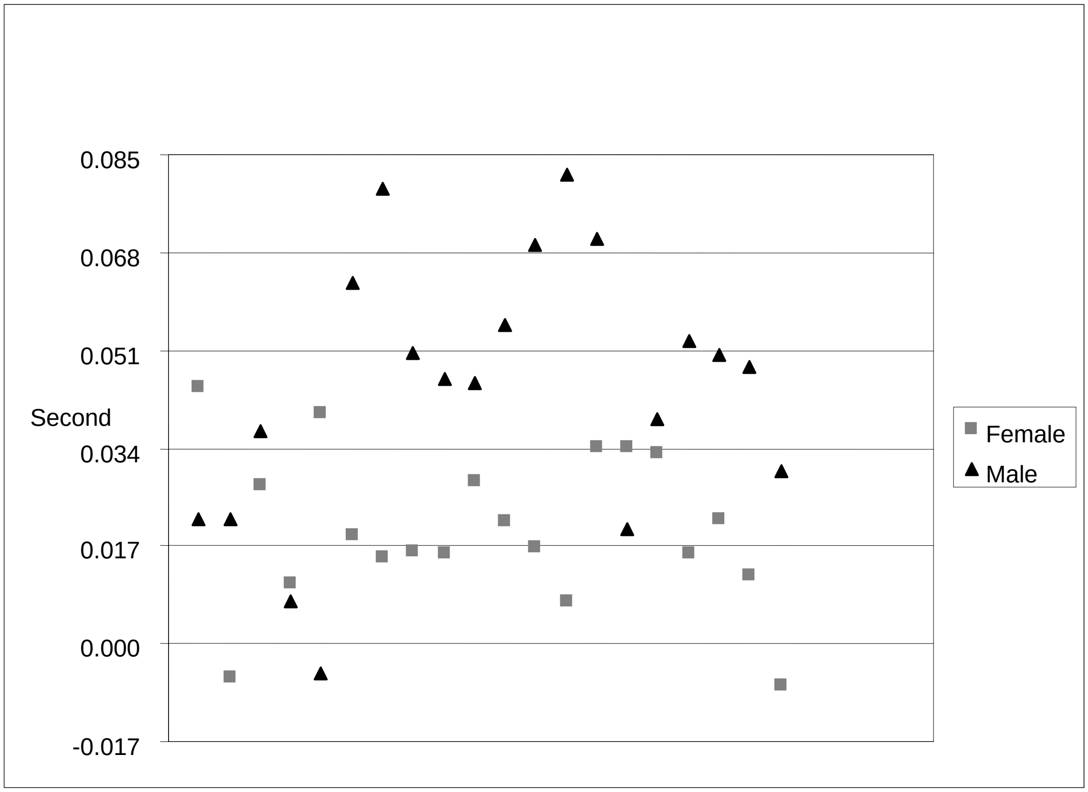
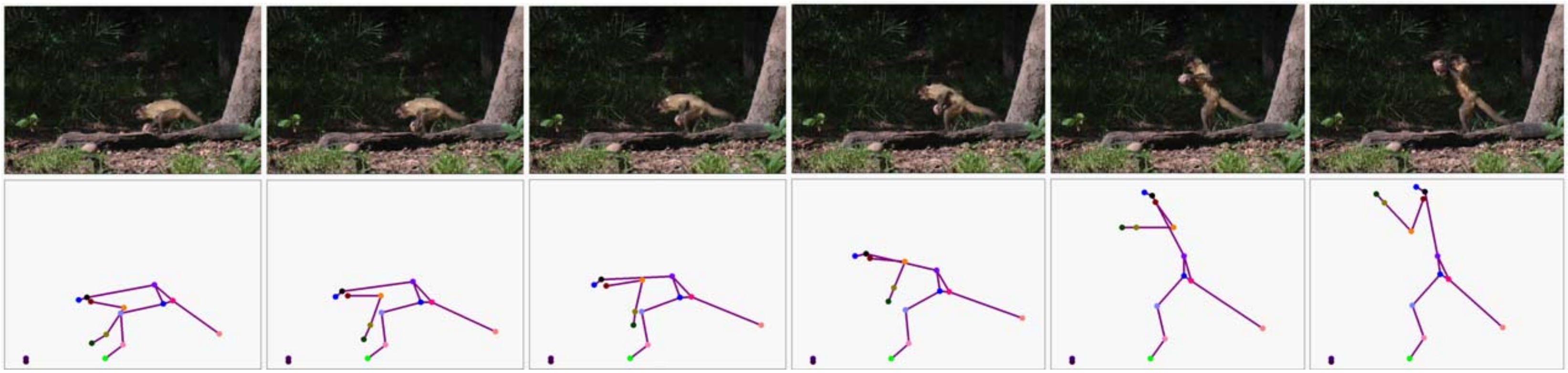
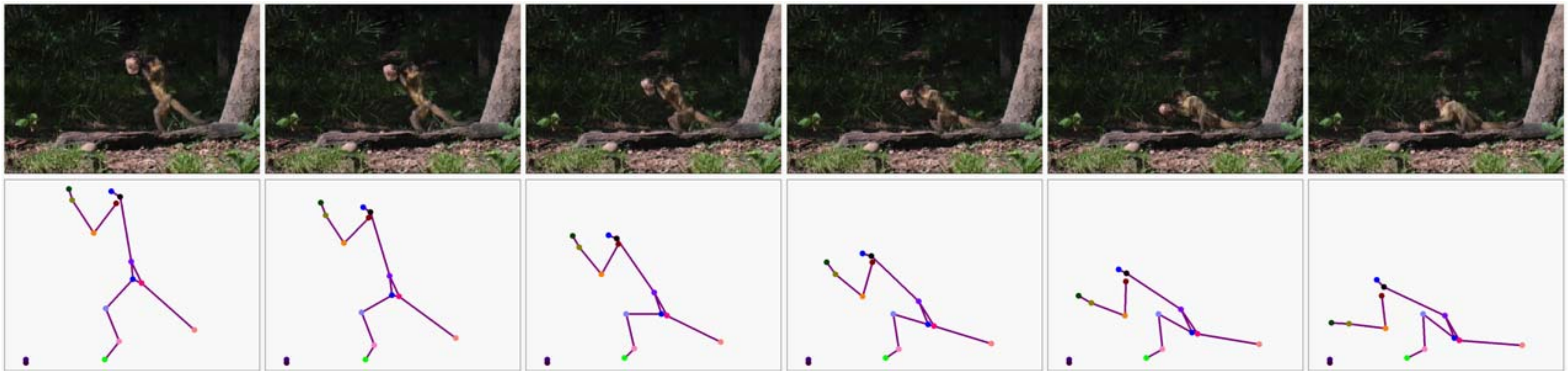


Figure 7 Difference between downward phase duration and free fall time from the same vertical height (positive value means actual down phase duration is shorter than free fall time from the same amplitude) for 40 hits.



0% HD Start of lifting 10%HD 21%HD 31%HD 41%HD 52%HD



62%HD Stone zenith 72%HD 83%HD 90%HD 97%HD 100%HD Stone-nut contact

Figure 8 Stick figure illustration of a representative hit (Piacava).

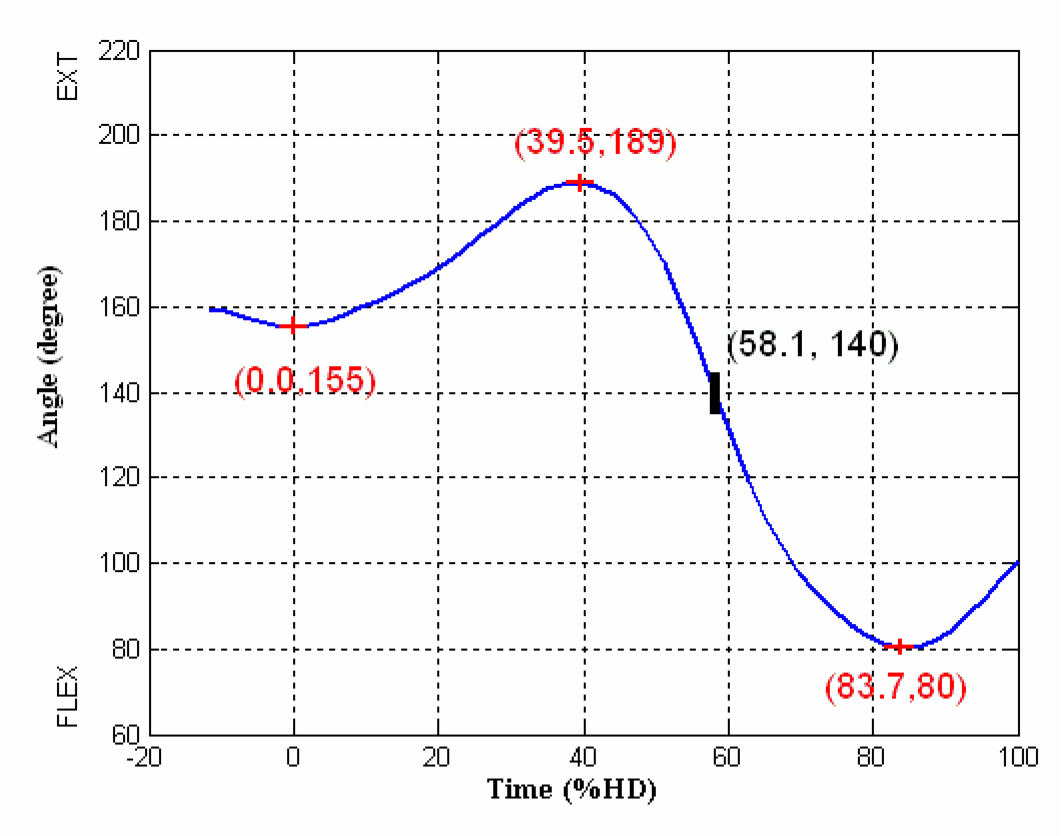


Figure 9 Graph of shoulder angle for one representative hit by Secondo. The crosses represent local maxima and minima; the black line represents the stone zenith point. Values in parentheses are %HD and the value of the angle (degree) at the time point.

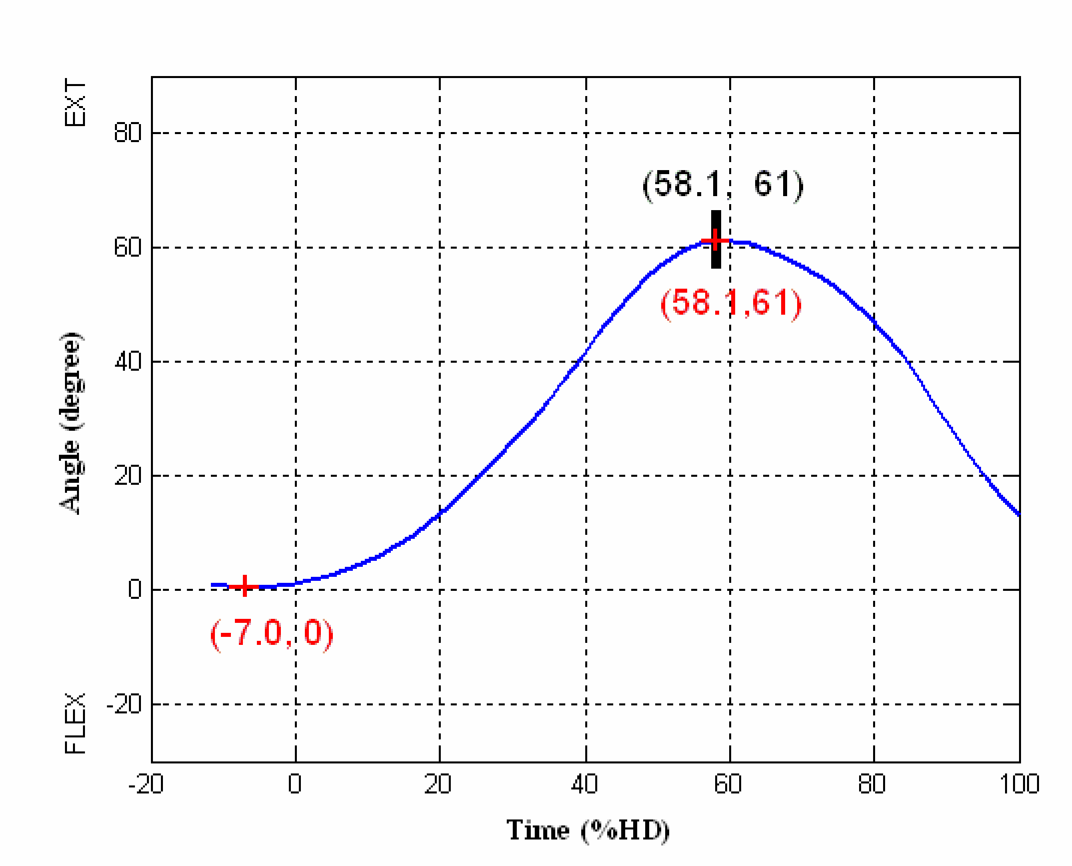


Figure 10 Graph of trunk inclination angle for one representative hit by Secondo. The crosses represent local maxima and minima; the black line represents the stone zenith point. Values in parentheses are %HD and the value of the angle (degree) at the time point.

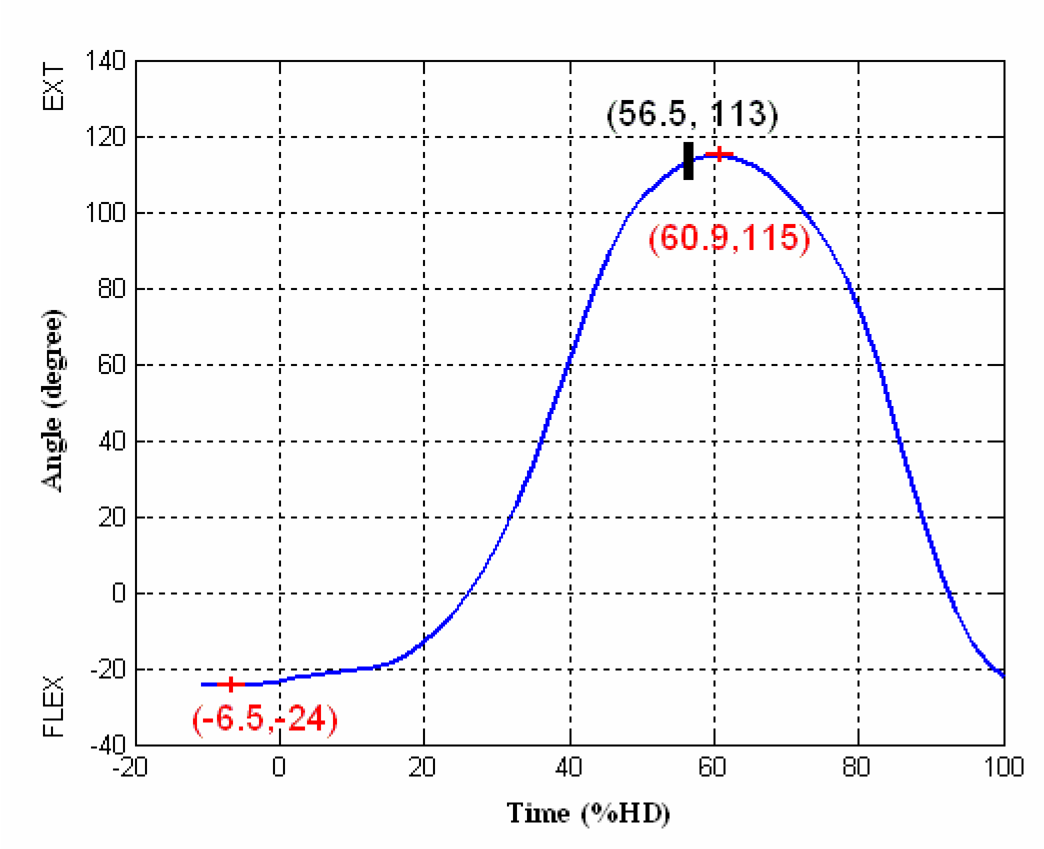


Figure 11 Graph of hip angle for one representative hit by TeNinha. The crosses represent local maxima and minima; the black line represents the stone zenith point. Values in parentheses are %HD and the value of the angle (degree) at the time point.

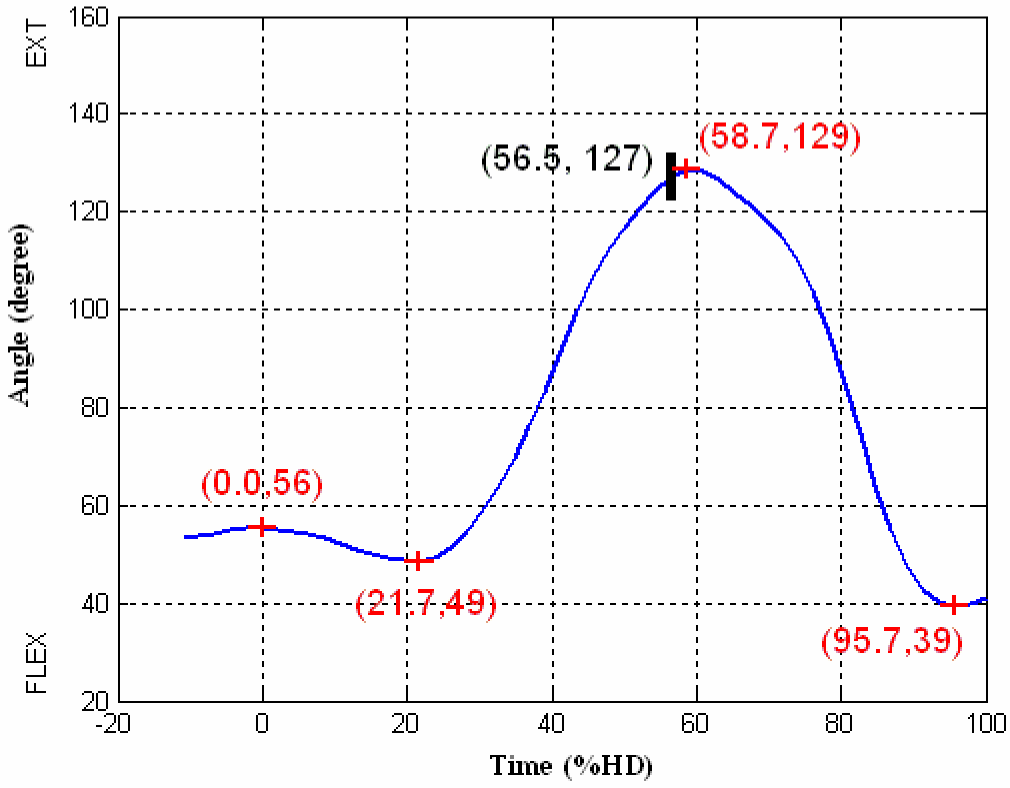


Figure 12 Graph of knee angle for one representative hit by TeNinha. The crosses represent local maxima and minima; the black line represents the stone zenith point. Values in parentheses are %HD and the value of the angle (degree) at the time point.

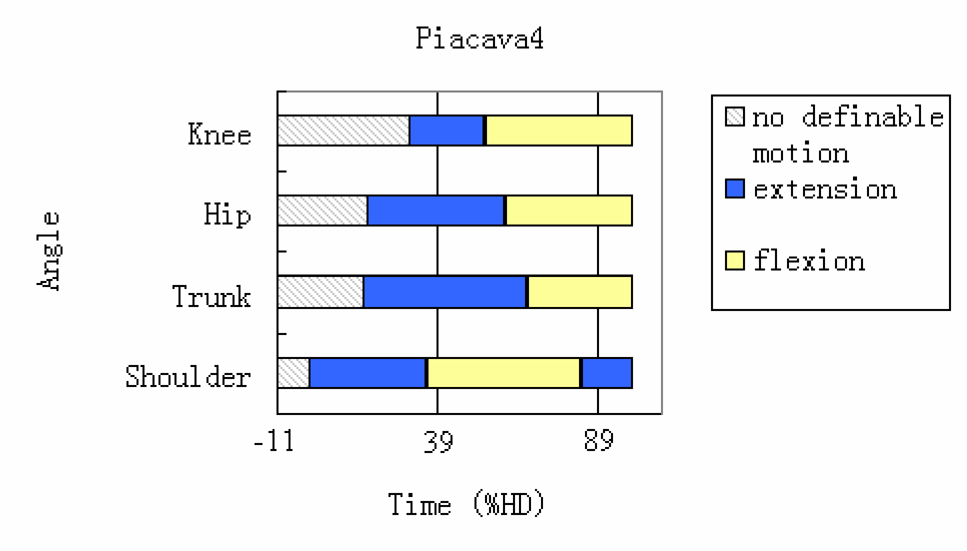


Figure 13 Sequence of angle movement (Piacava) for one representative hit. The figure shows the relative sequence of major joint and segmental angles. The shoulder begins extension before trunk and lower extremities. The knee extends last and starts to flex first. Before the moment of stone-nut contact, the shoulder shows extension again.

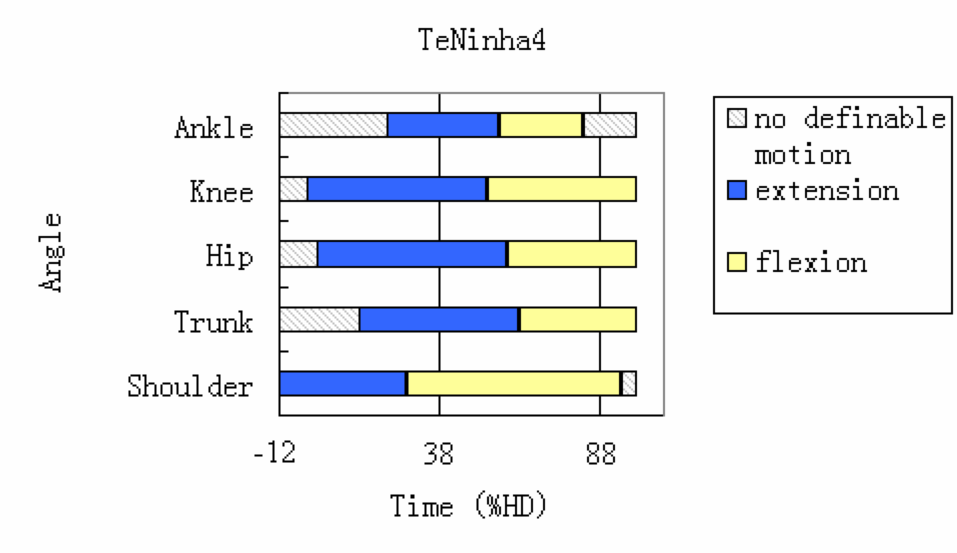


Figure 14 Sequence of angle movement (TeNinha) for one representative hit. The figure shows the relative sequence of major joint and segmental angles. The shoulder begins extension from the beginning of the pre-lift phase. The knee and the hip then start extending followed by trunk extension. The ankle shows extension until the end of upward phase, reflecting the “jump”. In the downward phase, the knee starts to flex first.

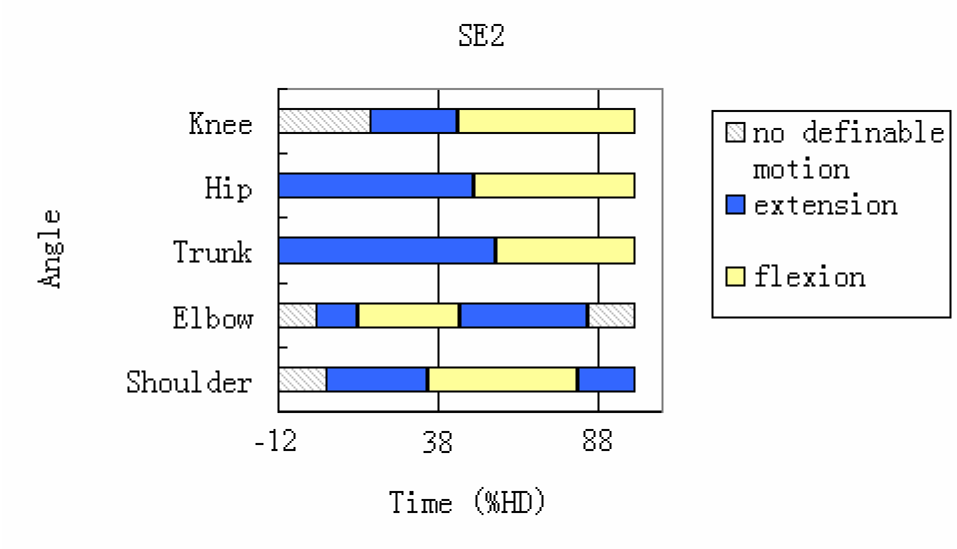


Figure 15 Sequence of angle movement (Secondo) for one representative hit. The figure shows the relative sequence of major joint and segmental angles. The hip and the trunk start extending from the beginning of the pre-lift phase. The shoulder begins extension in the beginning of the upward phase. The knee starts extending last but begins to flex first. The elbow shows a clear pattern of flexion in the upward phase to help raise the stone and extension in the downward phase to help push the stone downward. Before the moment of stone-nut contact, the shoulder shows extension again.

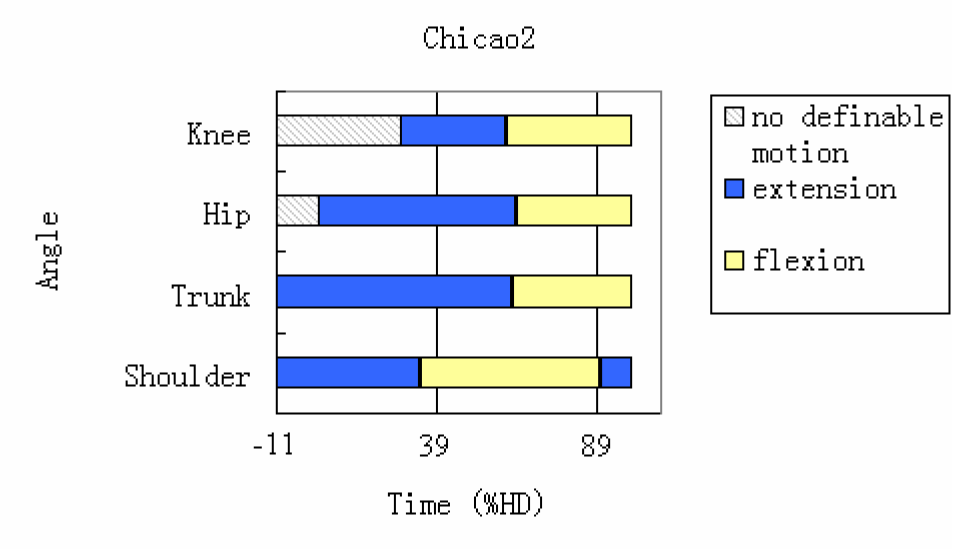


Figure 16 Sequence of angle movement (Chicao) for one representative hit. The figure shows the relative sequence of major joint and segmental angles. The shoulder and the trunk begin extension at the beginning of the pre-lift phase. Then the hip starts to extend. The knee extends last and starts to flex approximately at the same time as the hip and the trunk. Before the moment of stone-nut contact, the shoulder shows extension again.

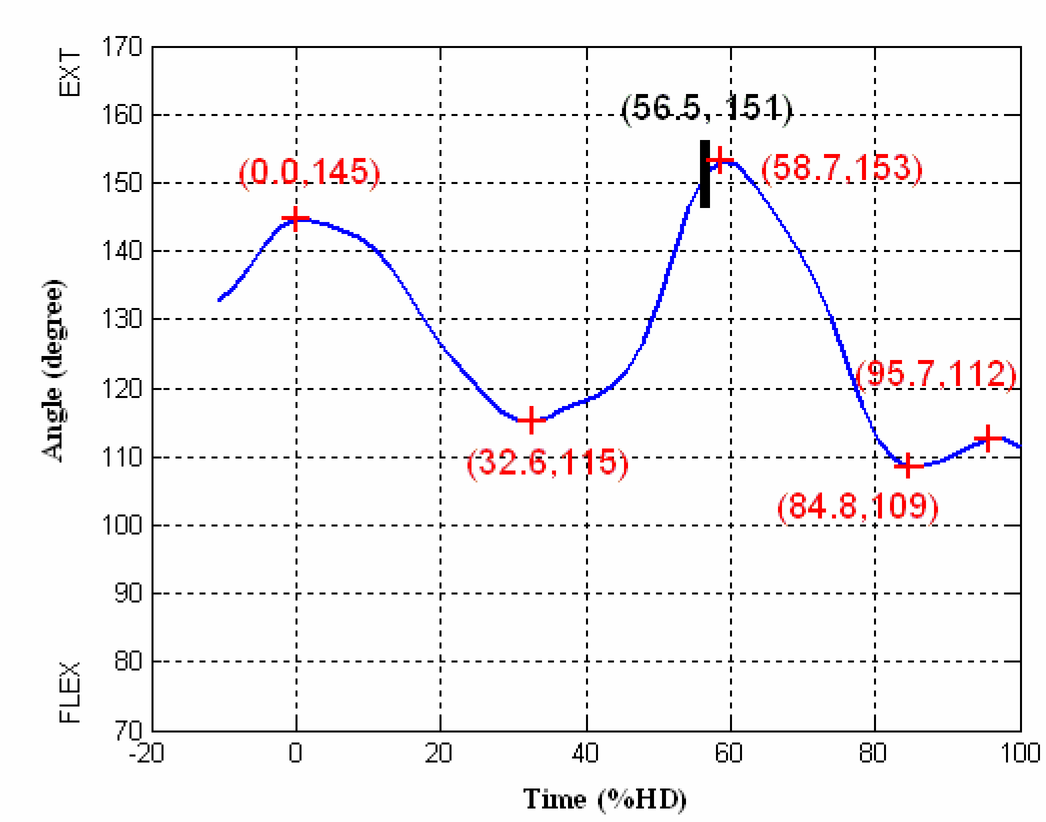


Figure 17 Representative graph of angle displacement of TeNinha’s ankle. The crosses represent local maxima and minima; the black line represents the stone zenith point. Values in parentheses are %HD and the value of the angle (degree) at the time point.

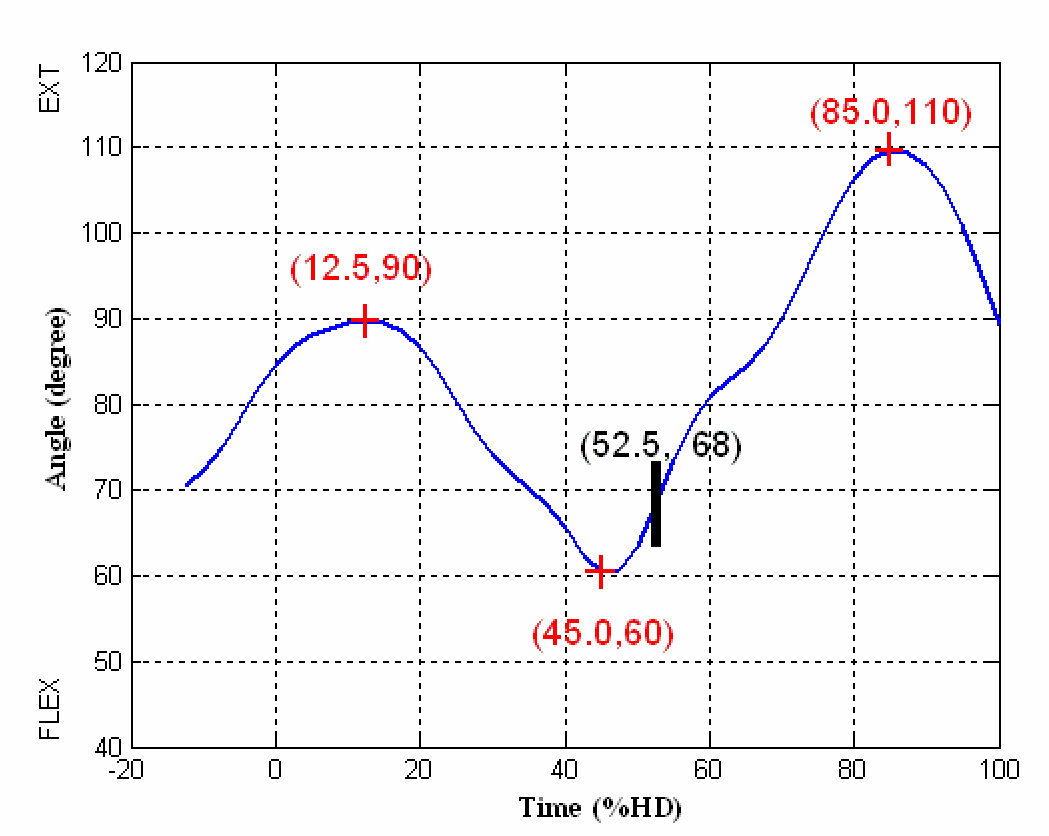


Figure 18 Representative graph of angle displacement of Secondo’s elbow. The crosses represent local maxima and minima; the black line represents the stone zenith point. Values in parentheses are %HD and the value of the angle (degree) at the time point.

APPENDIX

A REVIEW OF THE LITERATURE

Percussive tool use is a challenging, natural and ancient behavior in human evolution. It might have been our ancestors' very first technological discovery and has made our lineage distinctive from our relatives. In contemporary humans, percussive tool use is universally widespread around the world (Goren-Inbar, Sharon, Melamed, & Kislev, 2002). It has been known for several decades that wild chimpanzees use percussive tools to crack nuts (Sugiyama & Koman, 1979; Kortlandt, 1986; Kortlandt & Holzhaus, 1987; Boesch & Boesch-Achermann, 2000; Matsuzawa, 2001). Recently, it has been discovered that wild bearded capuchins crack nuts using large stones in their natural environment (Fragaszy et al., 2004). Study of these capuchins will provide a valuable reference point for hominine percussive tool use and its evolution and routine bipedality in primates.

Human Percussive Tool Use

Archaeological evidence suggests that our ancestors developed percussive tool use as early as 2.5 million years ago (Heinzelin et al., 1999). In the Ethiopian Rift Valley site, Heinzelin and colleagues uncovered hammer stones and anvils and bones of large mammals with hammer stone impact marks. These serve as strong evidence for percussive tool use.

A more recent study yielded more convincing evidence of human percussive tool use in antiquity. Goren-Inbar et al. (2002) reported possible nut-cracking activity by early hominins in a site in Gesher Benot Ya'aqov in Israel. The site dates back to the Early Middle Pleistocene.

Seven species of nuts were uncovered, most of which were found to be so hard that only hard hammers could crack them open (Goren-Inbar et al., 2002). Pitted stone hammers and anvils were together uncovered at this site. The fact that the site yielded both paleobotanical and lithic evidence strongly suggests that nut-cracking was practiced by ancient residents in the site. Moreover, the stone hammers and anvils were found to be pitted in the similar way to those hammers and anvils used by West African chimpanzees and contemporary humans (Goren-Inbar et al., 2002).

Studies on contemporary hunter-gatherer societies have documented extensive use of stone hammers and anvils to extract nut kernels from hard shells (Goren-Inbar et al., 2002). Gender difference is also noted in that females perform nut-cracking more frequently in these societies than males and males play a more important part in hunting. This is consistent with division of labor in hunter-gatherer societies.

Nut-cracking in Wild Chimpanzees

Although tool use was considered one of the hallmarks of human species, it was later found that our nonhuman primate relatives share this trait. Spontaneous nut-cracking by wild chimpanzees has been reported in many sites in western Africa (Sugiyama & Koman, 1979; Kortlandt, 1986; Kortlandt & Holzhaus, 1987; Boesch & Boesch-Achermann, 2000; Matsuzawa, 2001). The chimpanzees usually sit close to an anvil and use a stone or wooden hammer to crack open nuts placed on the anvil. The movement can be performed in a unimanual or a bimanual fashion depending on the hardness of the nuts and the local materials available for use as hammers.

In both sites, longitudinal observations have yielded similar conclusions about the learning of nut-cracking behavior in young chimps. Young chimps learn in the presence of their mothers over several years through apprenticeship by observation, scrounging and active exploratory manipulation of the nuts and stones (Boesch & Boesch-Achermann, 2000; Matsuzawa et al., 2001).

Chimpanzees in the Taï Forest (Boesch & Boesch-Achermann, 2000)

In Taï forest, during the nut-cracking season of four months, the chimpanzees engage in nut-cracking activities for more than 2 hours per day. Those nuts supply a large proportion of their everyday calorific intake (average net gain of 3450 kcal per day from nut-cracking). In the Taï forest, chimpanzees routinely cracked five species of nuts (of different shape and hardness). The researchers reported the chimpanzees were more likely to use wooden hammers (usually fallen branches) when cracking soft Coula nuts and more likely to use stone hammers when cracking hard Panda nuts. Nuts and hammers were transported to the anvils by the chimpanzees. An energetics analysis revealed that by using a stone hammer, 30% to 43% of pounding energy could be saved to crack open a nut compared using a wood hammer.

Anvils used by chimpanzees in Taï forest included surface roots, base of large trees and rocks exposed on the ground; they sometimes also cracked nuts in trees, which required more dexterity. Females were observed to have more hits and more nuts cracked than males, and were often found cracking nuts. Boesch & Boesch argued the sex difference may be due to the fact that male chimpanzees favored social contact and nut-cracking was a solitary activity. They also reported that the female superiority in nut-cracking was mirrored by male superiority in hunting in their study, which is consistent with division of labor in human hunter-gatherer societies.

Chimpanzees in the Bossou Site

In Bossou in Western Africa, wild chimpanzees also crack oil palm nuts open by using a pair of stone and anvil (Matsuzawa, 2001). Like chimpanzees in Taï forest, chimpanzees in Bossou transport nuts and hammers. But unlike chimpanzees in Taï forest, chimpanzees in Bossou sometimes also transport their small anvil stones. Moreover, chimpanzees in Bossou have been reported to sometimes use a third stone to help balance the anvil stones because their small anvils were not stable. This is considered to be meta-tool, reflecting more complexity in their tool use.

Sugiyama et al. (1993) reported in Bossou, adult chimpanzees exhibited consistent hand preference in nut-cracking while there was little difference in left/right handedness in food picking and carrying. In their observation, all adults and many young chimpanzees consistently and exclusively used one hand to hold the hammer stone while cracking nuts. They speculated because chimpanzees nut-cracking requires unimanual striking and cooperative movement of the other hand (holding stone and picking kernel etc.), exclusive hand preference was likely to be developed through the long-term practice.

Nut/ Seed Cracking in Wild Capuchins

Capuchins show a variety of tool use and problem solving behaviors in captivity, including nut-cracking (Fragaszy, Visalberghi and Fedigan, 2004). However, spontaneous nut-cracking in wild populations (*Cebus libidinosus*) has just been reported very recently

(Fragaszy et al., 2004). In another site nearby, wild capuchins (also *C. libidinosus*) were found to use stone to crack open seeds and tubers and also to dig underground food items (Moura & Lee, 2004). Both sites are located in the state of Piauí in northeastern Brazil.

Habitat and food resources

The Fragaszy et al.'s study site (Boa Vista site, hereafter) is located in the southern Parnaíba Basin (9°39' S, 45°25' W; altitude 420 m above sea level) in Piauí, Brazil. The area is a dry woodland plain with sandstone ridges and mesas rising approximately 20-100 m above it. The area supports a small population of humans who have altered the landscape dramatically by burning grazing lands over the recent hundreds of years. There are also cultivated areas, wetlands, private lands where cattle graze and some less disturbed plains and ridge areas, including a biological reserve owned and managed by the Fundação BioBrasil. The present study took place in a private property named Boa Vista.

The climate in the study site is seasonally dry (annual rainfall 1,156.00 mm, dry season: April to September) (Visalberghi et al., 2007). Palms are abundant in the area. The size of the palm nuts varies according to the species: the largest (Attalea sp.) have an oval shape with 5 cm diameter in width and 6 cm diameter in length and the smallest (Astrocaryum sp.) are round and 2.5–3 cm in diameter. The fronds and fruit clusters of the palms in this area emerge from the ground, rather than high above the ground. Capuchins eat the outer part (mesocarp) of the ripe fruit and leave them on the ground, where they dry. Dried palm fruits are probably easier to crack. The EthoCebus research team is currently surveying diet and food availability in the area.

Moura (2004) analyzed diet and food availability including fruit and insects at the Serra da Capivara site. His data are summarized here to provide a reference since the two sites are geographically close. The site is located in the Serra da Capivara National Park (7°30´ S, 41°30´W). Yearly precipitation in the Caatinga dry forest averages 800 mm, with extreme variation between areas and years. There is a marked dry season from May to mid-October, and irregular rainfall resulting in low diversity of trees. Moura's group used 26 species of plants for fruit and other edible parts. After comparing to other capuchin populations living in other dry forest habitat, Moura claimed the number of plants used as food was low. However, the group frequently used the cliff habitat which has even lower density of trees and fruit trees than the Canyon habitat in the area. The reason, Moura suggested, was due to abundance of invertebrates in the cliff habitat and also because the monkey forage for the tubers (from *Thiloa glaucocarpa*) along the cliff habitat. In summary, Moura concluded because the rainfall pattern is very irregular in the area, tree growth and fruit production is highly unpredictable, therefore, using tools to get access to various embedded food items such as seeds, insects hidden in branches and underground tubers can significantly increase the energy gain without too much energy expenditure (Moura, dissertation).

Stones and anvils

Although the two sites are rather close geographically, the capuchins in two sites use stones differently. In the Serra da Capivara, stones are primarily used for digging (65% of observed tool use events) and for cracking (19% of observed events) (Moura & Lee, 2004). Monkeys use stones to dig up food items such as tubers, roots or insects. When the monkeys do use stones for cracking, the target food items are seeds, hollow branches and tubers. A wooden anvil for cracking seeds was found in their study.

In the Boa Vista site, study of stone tools used by capuchins has focused on nut-cracking. It is common knowledge among the local residents that wild capuchins there crack nuts all year long. Compared to Serra da Capivara site, monkeys at Boa Vista site use stones primarily to crack open hard-shelled nuts. Without more extensive survey from Boa Vista site on how the monkeys use stones, we cannot assume the Boa Vista monkeys use stones only to crack nuts. But the ways of stone use are indeed quite different in two sites.

The stones used in these two sites also differ in size. In Serra da Capivara site, digging and hammer stones (n=14) weigh from 10 to 625 grams (Moura & Lee, 2004). The light weight of the stone and the ways of using the stones is compatible with the fact that monkeys in this site usually use the stone in a unimanual manner. In Boa Vista site, however, hammer stones weigh more in average and are scarce in the landscape (Fragaszy et al., 2004; Visalberghi et al., 2007). Visalberghi and colleagues systematically examined the hammer stones found in several areas in the Boa Vista site. They found hammer stones located within one of the surveyed areas weighed 1047 grams in average (ranging from 250-2800 grams, N= 46). Stones found in another surveyed area weighed 600 grams in average (ranging from 220 to 850 grams, N = 7). In their survey, they identified hammer stones based on their proximity to anvils and their resistance to fracture when struck by a geological hammer. Following these criteria, the team reported average weight of stones found near the anvils is 988 grams, all areas combined. This is a sound criteria in this situation where researchers wanted to survey potential hammer stones but researchers could not confirm all selected stones were used as hammer stones by the capuchins. So this might lead to the argument that the hammer stones are much heavier in this site because the stones weighed may include heavy ones that the monkeys do not usually use. On the other hand, one stone that the monkeys routinely have been seen using weighs 1460 grams, indicating the monkeys do have the ability to use a heavy stone that is 40%-58% of their body weight (assuming adult male weighs 3.7 kg and adult female weighs 2.5 kg; data from Fragaszy, Visalberghi & Fedigan, 2004).

There are no data on stone availability from Serra da Capivara. Moura reported stones were obtained from nearby rocky substrate or ground (Moura, dissertation). In Boa Vista site, Visalberghi and colleagues reported the hammer stones found near the anvils appear rather rarely across the area. However, in places near anvil sites, the hammers stones were found to be significantly more abundant than expected by chance (Visalberghi et al., 2007). This implies the possibility that monkeys transport the stones to the anvils, although this awaits further evidence.

Action

In the Serra da Capivara, capuchins use stones primarily to dig underground tubers and roots. The monkeys usually unimanually hold the stone and hit the ground 3 to 6 times while using the other hand to scoop away the loose soil; then they release the stone to dig bimanually or use the stone to hit again (Moura & Lee, 2004). In the sense of bimanual cooperation, monkeys in Serra da Capivara resemble nut-cracking chimpanzees in that they use one hand to do percussive movement with the stone while using the other hand for different actions (position nut and pick kernel for chimpanzees and scoop away soil for capuchins).

Wild capuchins in Boa Vista crack nuts very differently from that Serra da Capivara capuchins and also wild chimpanzees. Usually they come to a stone or log anvil located on the ground or slightly above the ground (approximately < 1 meter) with nuts. Hammer stones can already be on the anvils or sometimes are carried to the anvils by the monkeys. The monkeys crack nuts in a bimanual bipedal manner. They bimanually lift the stone from anvil in a bipedal stance and strike the nut. When they successfully crack the nut, they use both hands and teeth to get the kernel to eat.

Anatomy

Capuchins are quadrupeds. Considering the stone weight, nut-cracking as performed by the monkeys at Boa Vista is a strenuous physical action, accomplished in a posture unusual for arboreal monkeys. A brief review of skeletal anatomy relevant to bipedal stance is helpful here to understand how the monkeys accomplished such actions. If difference emerges in comparison to anatomy of other non-nut-cracking capuchins, it would suggest these capuchins either have a better suited body to perform this kind of action or these capuchins have developed anatomical adaptations for nut-cracking. Either way, it is expected that long-term nut-cracking behavior is correlated with certain morphological features.

Since *C. libidinosus* was formerly considered a subspecies of *C. apella* and was recently promoted to species status by Groves (2001), we do not yet have studies solely focusing on the anatomy of *C. libidinosus.* But due to the close phylogenetic relationship between *C. libidinosus* and *C. apella*, it is reasonable to use data from the latter as a reference for the former. *C. apella* is generally considered to be the most robust species in the genus (Fragaszy, Visalberghi & Fedigan, 2004).

A recent comparative study examined difference of locomotor behavior and limb morphology between *C. apella* and *C. olivaceu*s. In this study, Wright (2007) found that *C.*

apella has significantly higher IM (forelimb/hindlimb) index than *C. olivaceus*. This morphological feature promotes easier transition from a pronograde posture to orthograde posture (Wright, 2007). Wright also found that *C. apella* also has relatively short hind limbs and slightly shorter forelimbs, bringing the center of mass lower to the substrate they are on. This feature adds stability for orthograde posture. These findings can help explain how these wild *C. libidinosus* (as close cousins to *C. apella*) manage to stand up in a bipedal posture while striking the nuts.

Nut-cracking Movement and Models of Action

Nut-cracking movement has been addressed in terms of body posture, amplitude of the movement, force produced and number of hits necessary to crack open the nut (as reviewed by Foucart et al., 2005). So far, there is a single report focusing on quantitative analysis of the movement of wild nut-cracking chimpanzees. Günther & Boesch (1993) calculated the energetic cost of nut-cracking in wild chimpanzees in Taï forest. From video records, they estimated the energy expended transporting of the nuts and hammers, cracking open the nuts and sitting and eating the nuts and compared energy expended to energy gained from the nuts. They found that energy gained by eating nuts exceeded energy expended by 9 to 1. This is strong evidence that using tools to crack nuts provide significant energy benefit.

Foucart et al. (2005) studied a captive subadult male chimpanzee that had been trained to crack nuts. The chimpanzee cracked nuts in a sitting position, similar to that adopted by the wild chimpanzees. He put the anvil between his legs and used one arm to strike the nuts with a hammer stone (443g). Using a three-dimensional recoding and reconstruction method, Foucart et al. described amplitude, striking angle, temporal parameters and energetics of the upper arm.

They concluded the chimpanzee adjusted to different conditions (anvil with or without cavities, macadamia nuts or artificial nuts) by altering the angle and amplitude of the striking action.

However, studies done with the nut-cracking in chimpanzees are of limited relevance to understanding the nut-cracking actions of capuchins. One must consider that nut-cracking of wild capuchins is very different from that of wild chimpanzees. Capuchins use two hands to hold a proportionally heavier stone and lift in a bipedal posture which involves a whole body movement, compared to chimpanzee's one arm swing in nut-cracking. Simply judging from the posture and stone weight, nut-cracking for capuchins is much more strenuous and energy-consuming than nut-cracking is for chimpanzees. Therefore, the closest model of action might be deadlift and power pull style weight-lifting by humans (Baechle, Earle & Allerheiligen, 1994). Those two weight lifting actions are also bimanual, bipedal and strenuous. 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. Then the bar is returned to the floor with control. The power pull has the same upward phase but includes a phase in which the lifter moves the bar explosively from the thighs by extending the lower extremities and pulls the bar to the neck-level. Next, the bar is returned to the floor.

Deadlift can be performed using a conventional style or a sumo style. For the sumo style, the lifter's feet are positioned further apart and turned out with arms positioned inside the knees, whereas in the conventional style, the lifter's feet are positioned closer together and the lifter's arms are positioned outside the knees (Escamila, Osbahr & Speer, 2001). As reviewed by Escamila et al. (2001), past studies suggested sumo and conventional deadlifts exhibited significant differences in kinematics and kinetics. Escamila et al. (2001) found that the sumo style group had 100% more stance width and a more upright trunk and a more horizontal thigh at barbell liftoff and a more horizontal thigh when the barbell passes the knees (in the upward phase). They also found that the sumo group exhibited ankle dorsiflexor, knee extensor, and hip extensor moments, whereas the conventional group produced ankle plantar flexor, knee flexor and extensor, and hip extensor moments. Compared to less-skilled lifters, high-skilled lifters kept the bar closer to the body to produce better lifting mechanics. Keeping the weight closer to the body enhanced performance and minimized risk of injury.

Morphological Adaptations to Bipedal Stance

Nakatsukasa and colleagues (1995) suggested changes in function caused changes in morphology in a Japanese macaque that 11 years of training in bipedal walking. The macaque had considerably modified hindlimb bones (specifically in the joint morphology, articular dimensions and shape-dependent strength of long bones). From our observation in Boa Vista, wild capuchins transport hammer stones frequently in a bipedal walking posture over up to 10 meters of distance at anvil sites. One cannot help wondering if the nut-cracking movement promotes bipedal carrying in these wild capuchins through possible anatomical adaptations. If so, this phenomenon may give us insights about alternative origins of bipedality in human ancestors.