AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 132:426–444 (2007)

Characteristics of Hammer Stones and Anvils Used by Wild Bearded Capuchin Monkeys (*Cebus libidinosus*) to Crack Open Palm Nuts

E. Visalberghi,[1]* D. Fragaszy,[2] E. Ottoni,[3] P. Izar,[3] M.G. de Oliveira,[4] and F.R.D. Andrade[5]

[1]*Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, 00197 Rome, Italy*
[2]*Psychology Department, University of Georgia, Athens, GA 30602*
[3]*Department of Experimental Psychology, Institute of Psychology, University of São Paulo, CEP 05508-030 São Paulo, Brazil*
[4]*Fundação BioBrasil, CEP 42700-000 Lauro de Freitas, Brazil*
[5]*Department of Mineralogy and Geotectonics, Institute of Geosciences, University of São Paulo, CEP 05508-080 São Paulo, Brazil*

KEY WORDS tool use; *Cebus libidinosus*; anvil; hammer; geology; archeology; human evolution

ABSTRACT Capuchins living in Boa Vista (Piauì, Brazil) crack open hard palm nuts on hard, level surfaces (anvils) using stones (hammers) as percussive tools. This activity leaves diagnostic physical remains: distinctive shallow depressions (pits) on the surface of the anvil, cracked shells, and stone hammers on the anvil. To initiate comparison of percussive stone tool use and interpretation of the artifacts it produces across capuchins, chimpanzees, and hominins, we describe a sample of the anvils and hammer stones used by capuchin monkeys at our site. Anvils (boulders and logs) were located predominantly in the transition zone between the flat open woodland and ridges, in locations that offered some overhead coverage, and with a tree nearby, but not necessarily near palm trees. Anvils contained shallow, hemispherical pits with smooth interiors. Hammers represent a diverse assemblage of ancient rocks that are much harder than the prevailing sedimentary rock out of which they eroded. Hard stones large enough to serve as hammers were more abundant on the anvils than in the surrounding area, indicating that capuchins transport them to the anvils. Capuchins use hammers weighing on average more than 1 kg, a weight that is equivalent to 25–40% of the average body weight for adult males and females. Our findings indicate that capuchins select stones to use as hammers and transport stones and nuts to anvil sites. Wild capuchins provide a new reference point for interpreting early percussive stone tool use in hominins, and a point of comparison with chimpanzees cracking nuts. Am J Phys Anthropol 132:426–444, 2007.

Contemporary humans around the world crack nuts using stone tools (de Beaune, 2000). Nuts are a rich source of proteins and lipids and figure prominently in the diet of hunter-gatherers, for example, native North Americans (Driver, 1961). Cracking nuts with stone tools can leave characteristic use-wear pitted depressions on anvils and hammer stones (Goren-Inbar et al., 2002). Pitted stones have been found at several archeological sites dating from African Early stone age eras (e.g., Leakey, 1971). Pitted stones may reflect the production of bipolar stone flakes (Jones, 1994), and some pitted stones may also be the product of cracking nuts (Goren-Inbar et al., 2002). The latter argument was supported by taphonomic data and experimental efforts to knap flakes using the prevailing basalt stone at Gesher Benot Ya'aqov (Israel). Goren-Inbar et al. (2002) found fossil nuts of several species, including wild almonds (*Amygdalus communis*, which has a very tough shell) together with pitted hammers[1] and anvils in the Middle Pleistocene sequence of the Gesher Benot Ya'aqov site. When the authors experimentally flaked stones using basalt cobbles from this site, they produced shallow pits with rough interior surfaces. Some of the pitted stones from their site had this appearance, but others had deeper, rounder, and smoother pits. Goren-Inbar et al. (2002) argued that the latter pits were not likely the result of knapping stone flakes, but were likely the result of pounding nuts on an anvil surface. Thus, they concluded, the inhabitants of Gesher Benot Ya'aqov probably used stone tools for both activities, and perhaps others as well (see also Spears, 1975, cited by Goren-Inbar et al., 2002).

[1]To indicate the stone used for the pounding action we will use the term "hammer", and "hammering" to indicate the pounding action. Our use of these terms is consistent with their use in the paleo-anthropological literature. However, we consider these words potentially misleading. According to Webster's Dictionary, a hammer is "a hand tool consisting of a solid head set crosswise on a handle." and "to hammer" is "to strike blows, especially repeatedly, with, or as if with, a hammer". Therefore, stones are not hammers; using a stone to pound is not hammering. True hammering, with a head piece mounted on a shaft, requires less energy to apply the same force than pounding with that same stone held in the hand.

Grant sponsor: MIUR and CNR, Italy; Grant sponsor: EU Analogy Project; Grant number: 029088; Grant sponsor: National Science Foundation, USA; Grant number: BCS 0125486; Grant sponsors: CNPq, Brasil, CAPES São Paulo, Leakey Foundation and National Geographic Society.

*Correspondence to: Dr. Elisabetta Visalberghi, Consiglio Nazionale delle Ricerche, Istituto di Scienze e Tecnologie della Cognizione, Unità di Primatologia Cognitiva, Via Ulisse Aldrovandi 16/B 00197 Roma, Italy. E-mail: elisabetta.visalberghi@istc.cnr.it

Received 5 October 2006; accepted 7 November 2006

DOI 10.1002/ajpa.20546
Published online 18 December 2007 in Wiley InterScience (www.interscience.wiley.com).

Fig. 1. Shells of the nuts of different palm species belonging to the genus *Attalea* (Lorenzi et al., 2004) cracked open by capuchins. These thick shells were collected after we observed capuchins crack them open (Photographs by E. Visalberghi).

Two species of nonhuman primates, chimpanzees (Sugiyama and Koman, 1979; Anderson et al., 1983; Kortlandt, 1986; Kortlandt and Holzhaus, 1987; Boesch and Boesch-Achermann, 2000; Matsuzawa, 2001; see McGrew et al., 1997 for review) and bearded capuchins monkeys (*Cebus libidinosus*, Moura and Lee, 2004; Fragaszy et al., 2004b) use unmodified stones as percussive tools in natural environments to crack open nuts on stone and log anvils. Goren-Inbar et al. (2002) argued that the anvils and hammer stones they observed at Gesher Benot Ya'aqov display use wear pits similar to those used by chimpanzees (Boesch and Boesch-Achermann, 1983, 2000): rounded shallow depressions with a smooth interior. These pits are diagnostic of hammer and anvil use in cracking nuts.

Observational study of chimpanzees' tools, including stone and wood hammers and anvils to crack nuts has expanded our knowledge about simple tool use in hominids prior to the advent of flaking and other modification technologies (McGrew, 1992; Boesch and Boesch-Achermann, 2000; Matsuzawa, 2001). Such studies illustrate the range of behaviors chimpanzees adopt in the course of using tools. For example, chimpanzees crack nuts of several species over long periods of the year, transport hammers and nuts to anvil sites, collect tools from areas out of view of anvils, and use the same anvil sites over long periods (Boesch and Boesch-Achermann, 1983, 2000). According to Boesch and Boesch-Achermann (1983), chimpanzees predominantly use granite hammers for harder species of nuts, such as *Panda oleosa*, and wood hammers (termed clubs) for softer species of nuts, such as *Coula edulis*. Hammers can weigh more than 9 kg and may be carried more than 500 m. Most anvils used by chimpanzees in the Taï Forest, where Boesch and Boesch-Achermann conduct their research, are exposed tree roots, but the chimpanzees also use rock anvils. Chimpanzees at Bossou frequently use larger loose stones as anvils and smaller loose stones as hammers (Sakura and Matsuzawa, 1991).

Wild bearded capuchin monkeys (*Cebus libidinosus*), although they weigh much less than chimpanzees (2.5–3.7 kg as adults, Fragaszy et al., 2004a, vs. 44.6–46.3 kg for adult chimpanzees, Fleagle, 1999), crack open tough palm nuts of roughly the same sizes (3–6 cm in length) as those opened by chimpanzees. In 2003, we discovered a population of capuchin monkeys that, like chimpanzees, use stone hammers to pound palm nuts on stone and log anvils (see Figs. 1 and 2) (Fragaszy et al., 2004b). We observed that nut cracking by capuchin monkeys, as in chimpanzees, resulted in distinctive enduring remains: pitted depressions on the surface of the anvil, and large hammer stones and cracked shells on or near the anvil (Fragaszy et al., 2004b). Thus it is possible to identify sites used as anvils by monkeys. In a survey made in January and February 2005, we located 42 anvils used within the previous year and 71 others that showed signs of having been used in the more distant past. Continuing work at this site has confirmed that capuchin monkeys from several groups use the anvils we noted as active, as well as many other anvils that we did not locate in our 2005 census.

Here we report the results of our first study of anvils and hammer stones used by capuchins monkeys in the Boa Vista area, based upon the sample of anvils located and evaluated in January 2005. The aims of this report are 1) to provide a thorough description of the anvils

Fig. 2. An adult male capuchin monkey uses a stone tool to crack open a nut (Photograph by E. Visalberghi).

and hammers used by the capuchins, to support comparisons with the anvils and hammers used by chimpanzees and early hominids, and 2) to test a series of hypotheses (see below) concerning the properties governing the selection and use of hammers and anvils by the monkeys. Our hypotheses were generated from a consideration of the properties of hammers and anvils that would make them convenient, efficient and safe to use, drawn from ecological and biomechanical perspectives.

Our first hypothesis was that capuchin monkeys, as proficient and practiced tool users, would selectively use appropriate surfaces to crack nuts. It is easier to crack a nut on a flat, hard surface than on an inclined or soft surface (as suggested also by Marchant and McGrew, 2005) and chimpanzees use hard, flat surfaces (Boesch and Boesch-Achermann, 1983, 2000). We predicted that anvils used by capuchins would have similar properties. Second, we predicted that anvils would be located near trees or boulders providing visual coverage, arboreal access, and escape routes. The loud noise produced by a monkey using a stone to crack a nut increases the risk of predation or usurpation by other monkeys. A human can locate a monkey cracking a nut from many hundreds of meters away; so also can a predator or a conspecific. Thus, we hypothesized that escape routes and visual cover are both important features guiding selection of anvil sites. Third, we hypothesized that monkeys would use anvils that are within sight of the nuts they encounter, minimizing transport costs and reducing the need to plan ahead. Thus, we predicted that anvils would be located near a palm tree. We also predicted that hammer stones would be found in higher density on the anvil than in the surrounding area, reflecting transport of nearby stones to the anvils by the monkeys.

Finally, we evaluated the properties and number of pits on anvil surfaces, and their distribution on anvil surfaces. Specifically, we wanted to confirm that pits are hemispherical, shallow, and have a smooth interior, as do anvils used by chimpanzees and by humans (Boesch and Boesch-Achermann, 1983; Goren-Inbar et al., 2002).

Frequency of pits reflects long-term use, and distribution of pits may indicate choice of specific locations on a larger boulder.

On the basis of our preliminary study (Fragaszy et al., 2004b) and subsequent observations of the monkeys cracking nuts with stone hammers, we expected that stones found on the anvils would have an adequate shape, size, and hardness to serve as effective hammers. Here we sought normative data concerning these properties, and whether the hammer stones were composed of the prevailing sandstone, or had other origins. If the hammer stones were not of the prevailing sandstone, we were concerned to identify where in the local region they might have originated, again to understand how far they might have been transported. In this regard, we looked for evidence that anvils were near ephemeral streams because, if the stones were washed down from the ridges above, they would be found in the lower reaches of these stream beds. Anvils located near streams would thus be close to a potential source of hammer stones, and transport distances from stream bed to anvils could be relatively short.

To summarize, the aims of this study are to provide a thorough description of the anvils and stones used by the capuchins in Boa Vista to crack nuts, and to test a series of hypotheses concerning the properties of anvils and hammers. The findings allow us to compare capuchins' artifacts with those of chimpanzees and early hominids known or thought to be the result of percussive tool use to crack nuts. Study of the artifacts associated with stone tool use, coupled with direct observations of capuchin monkeys at this site, provide a new comparative reference point in discussions about ecological, social, physical, and cognitive correlates of nut-cracking with stone tools. Clear description of such sites supports further targeted research on tool sites and tool-using behavior, and provides a guide for the search for other populations of capuchin monkeys that use percussive stone tools.

METHODS

Site

Our site is located at Fazenda Boa Vista and adjacent lands (hereafter, Boa Vista) in the southern Parnaíba Basin (9°39′ S, 45°25′ W) in Piauí, Brazil. Boa Vista is a flat open woodland (altitude 420 m asl) punctuated by sandstone ridges, pinnacles, and mesas rising steeply to 20–100 m above it. Sedimentary rocks of two formations occur in the southern Parnaíba Basin: Sambaíba Formation (age Triassic, 250–200 Ma) covers the Pedra de Fogo Formation (age Permian, 250–300 Ma) (DNPM, 1973). The Sambaíba Formation comprises white to reddish fine-grained sandstones with abundant cross-beddings. The lowermost part of the Sambaíba Formation, which is in contact with the Pedra do Fogo Formation, is marked by a conglomeratic level with pebbles of siliceous rocks. The Pedra de Fogo Formation comprises interbedded sandstones, siltstones, and shales; sandstones are white to yellowish, fine-grained, while siltstones are reddish to purple. There are some beds of limestone and anhydrite toward the top of the formation. The sandstone ridges are heavily eroded and at the lower elevations are cut by small water courses that have running water only after rainfall. The flat open woodland is dissected in areas by gullies that can reach 5 m in depth. The sandstone escarpments often have vertical faces with fields of boulders at the foot, evidence of occasional shearing failure of the rock face.

The area is lightly populated by humans, and contains cultivated areas, wetlands, private lands where cattle graze and some less disturbed woodland areas, including a biological reserve (Green Wing Valley – Serra de Água Branca) owned and managed by the Fundação BioBrasil. The flat areas (even where grazed) are open woodland; the ridges are more heavily wooded. Palms are abundant in the open woodland. Local practice is to burn grazing lands at intervals; the woodlands reflect frequent irregular burning. The climate is seasonally dry (annual rainfall 1,156.00 mm, total rainfall during dry season, April to September 230.00 mm, data from 1971–1990, source: Embrapa).

Anvils sampled

We located our sample of anvils in January and February, 2005, during the wet season. Some anvils were identified by observers following a group of capuchin monkeys. Some were known previously to one of the authors (M.O.), and some were discovered by a team of three researchers walking through a transect 13.8 km long × 20 m wide along pre-existing paths (that were around the three ridges or that connected them), covering an area of 27.7 ha, and looking at likely boulders and logs for evidence of use. Only one anvil in this sample was included in the sample of anvils described by Fragaszy et al. (2004b). Our sample includes anvils along three ridges (30 m or more of elevation) in which at least three different groups of bearded capuchins range (personal observation), and through open woodland between the ridges. We aimed to include approximately equal numbers of anvils in each of the three ridges; our sample is representative, not exhaustive. Continuing work at this site has confirmed that many more anvils exist in the areas we sampled than are included in the data reported here. For descriptive and comparative purposes, we measured the size of each anvil and counted the number of pits present on its surface.

Anvils were identified on the basis of our previous experience at this site (see Fragaszy et al., 2004b) by the joint presence of two of the following three elements: a) a potential hammer stone (hard stone weighing 150 g or more) on the putative anvil or nearby, b) distinctive shallow pitted depressions (1–2 cm deep) on the upper surface of the anvil that derive from cracking nuts with stones (hereafter, pits; Fig. 3), and c) the presence of cracked palm shells on or near the anvil (see Fig. 4). We previously observed that when capuchin monkeys pound open palm nuts, they produce shell fragments with jagged angles. In contrast, rodents access the kernels by gnawing a hole in the otherwise intact shell. Thus fragmented shells are diagnostic of activity by capuchins.

In this study, we identified both abandoned anvils and anvils in current use. The abandoned anvils had shells with a gray interior and hard gray exterior judged to be older than 1 year. Anvils containing only old shells, or without shells, were categorized as abandoned. The anvils in current use had recently cracked shells (i.e., brown interior and/or fibrous outer layer). This criterion overestimates the number of abandoned anvils, but makes the identification of the anvils in current use certain. Our estimation that an anvil was in current use

Fig. 3. Stone anvil MM30. Nut shells and other debris have been removed from the anvil and to aid in counting the number of pitted depressions one white bean has been placed in each of them. This anvil had 43 pits. The two stone hammers were found on the anvil and marked. The stone on the left was judged to have low sphericity and angularity 0.4 according to Power's (1953) scale. The stone on the right was judged to have low sphericity and angularity 0.2. The picture was taken at the time we measured the anvil. (Photograph by E. Visalberghi).

Fig. 4. An anvil in use is characterized by the presence of relatively fresh nut shells. This anvil has a number of hemispherical pits, with smooth interiors, and a hammer, together with fresh nut shells. The picture was taken before starting the measurement protocol. (Photograph by E. Visalberghi).

was subsequently confirmed either a) by directly observing monkeys using hammers on these anvils; or b) indirectly by the similarity between the remains found on the anvil judged in current use and those found on other anvils where we observed capuchins cracking open palm nuts; or c) subsequently, by monthly census of the anvils, checking for new cracked shells or repositioning of the hammer stones, which we took as evidence of recent use. The monthly census data will be presented elsewhere. We located the coordinates of each anvil using global positioning (GPS, Garmin, eTrex Summit model).

Measures taken on the anvils in current use

We collected extensive data on the anvils judged in current use and their hammer stones. First, we identified use-wear pits at least 1 cm deep using a hemispherical object with depths marked along one circumference. We counted the number of such pits on each anvil, and noted their general condition. Where a large boulder contained separate distinctive areas with pits (for example, one area at the top of a boulder and another area at its base), we counted the complex anvil as one anvil and took measurements in the area that appeared to us to have been used most recently. The pits were judged to be old if they were covered with moss/lichen or if they were filled with sand or organic debris.

To test the prediction that capuchins use horizontal hard rock surfaces as anvils and to assess whether they select the hardest horizontal (or almost horizontal) surface area of the anvil to crack open nuts, we measured inclination (in degrees) in the center of the area where pits are present using a level and protractor, and we determined the hardness of the anvil surface in the area where pits were present and in an area of similar inclination, if present. For this purpose we used a sclerometer, or Schmidt hammer (SEB corporation) to measure elastic rebound. This measure is related to the material's compressive strength, expressed as kg/cm^2, adopting a mean density value for the anvil of 2.3 g/cm^3. The area was first leveled using a hand grinding wheel. The sclerometer was positioned perpendicular to the surface to be tested. Failures (due to fracture of the surface by the action of the sclerometer) were noted and the test repeated until 10 values were accumulated. We collected 10 values per location and averaged the values.

To test the prediction that anvils are located near trees or boulders providing visual coverage and escape routes, we measured the distance from the center of the region with pits to the nearest tree trunk (i.e., a potential escape route) with a DBH (Diameter at Breast Height) of at least 8 cm was measured (this size corresponds to an average DBH of the trees in this habitat; Rodal et al., 1998; Farias and Castro, 2004). When multiple branches or trunks were present at breast height, we measured each limb and added the values. The height of this tree was measured using a tangent height gauge (Kager Inc., Lunenburg, MA, USA). We also measured the distance of the nearest tree to any edge of the anvil surface, and the DBH of the largest tree within 3 m from any edge of the anvil. We rated the overhead visual coverage provided to the anvil by features of the landscape (e.g., rock) or forest canopy above the area of the anvil in which pits were concentrated. For this purpose we used a 4-point scale, from no coverage to full coverage.

To test the prediction that the boulders or logs used as anvils are nearby a water course (where hard stones could be found), the distance to the nearest ephemeral water course within 10 m of any edge of the anvil were noted. To test the prediction that anvils should be located near palms, we noted the presence of one or more palms within 3 m from any edge of the anvil. Finally, we estimated the height of the anvil surface above the ground surface to evaluate the prediction that the monkeys use low boulders as anvils. This prediction follows from the hypothesis that the monkeys minimize the energetic cost of transporting stones.

Measures taken on potential hammer stones

Potential hammer stones were identified as loose stones more than 150 g that were hard enough to resist a moderate strike with the pointed end of a geological hammer. This method was adopted because we noted previously that stones of the predominant sandstone shattered when we struck palm nuts with them, and the nuts did not crack when struck with such stones. The designation of hammer stones as stones that withstood striking by the geological hammer restricted this classification to stones that were hard enough to crack open nuts. Hammer stones were described by their location (on the anvil, 0–30 cm from the anvil, or between 30 cm and 3 m from the anvil; areas A, B, and C in Fig. 5a). We weighed the stones to the nearest 20 g using a spring scale (Pesola, Switzerland), except for one stone weighing more than 2.5 kg for which we used a scale with a resolution of 25 g. We measured the volume of each hammer stone as the difference between the level of the water in a marked beaker, with a resolution of 25 ml, with the stone submerged and without the stone. Density was derived by dividing weight by volume. When possible, a flake was taken from the hammer stone for later mineral analysis. When we could not take a flake from the hammer stone, we collected a smaller stone in the vicinity that appeared similar in color and texture. Thin sections of 14 flakes from hammer stones and 17 pebbles that were judged to be similar to hammer stones were analyzed under a polarizing binocular microscope (Olympus BX50) for mineral composition and petrographic classification.

The three-dimensional sphericity and angularity of the hammer stone was estimated using a scale adapted from Powers (1953). The scale recognizes two levels of sphericity (high and low), and within each level, 6 levels of angularity, from 0.1–1.0, where 0.1 is jagged and 1.0 is round (see Figs. 3, 7, and 9 for illustrations).

To evaluate if monkeys transport hammer stones to anvils, we tested the prediction that hammer stones were distributed unevenly, with more found on the anvil than in its vicinity. In particular, we compared the number of hammers per square meter present in the anvil area (area A, see Fig. 5a), in the corona ranging 30 cm around the anvil (area B, where a hammer might have fallen after having been used on the anvil) and in the corona, ranging from 31 cm to 3 m around the anvil (area C). The surface of these three areas was estimated for stone anvils and for log anvils in the following ways.

The area of each stone anvil was estimated from its perimeter and diagonals in the following way. We calculated the perimeters and the areas of the largest (rectangle) and smallest (rhomb) convex geometrical figures whose diagonals (rhomb), or axes (rectangle) were the

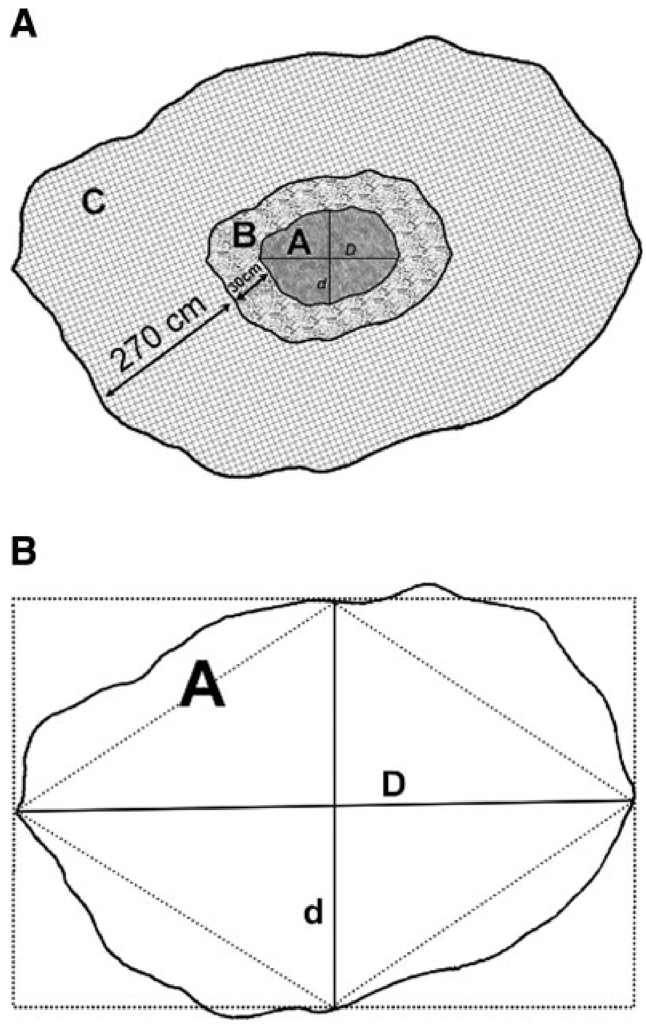

Fig. 5. **(a)** Schematic representation of the areas of the anvil (area A, with diagonals D and d), of the area B and of the area C. The areas are not to scale. **(b)** Areas of the rhomb and of the rectangle having the same diagonals as the anvil A. (Drawing by Alessandro Garramone).

measured diagonals of the anvil (Fig. 5b). Then, the difference between the perimeter of each anvil and the perimeter of the corresponding rhomb was expressed as percentage of the difference between the perimeters of the corresponding rectangular and rhomb. At this point, the area of each anvil (area A) was estimated by adding the area of the rhomb to the area obtained by multiplying the difference between the areas of the corresponding rectangle and rhomb as calculated earlier. In similar ways, we estimated the area of [A + B] and of the area of [A + B + C]. Finally, by subtracting as required we obtained the areas of the coronas B and C.

For log anvils, the area A was estimated as the rectangle with the axes of the length of the log and the diameter of the log; the area of the "corona" B as the rectangle formed by the length of the log + 60 cm and the diameter of the log + 60 cm, minus area A; and the area of the corona C as the rectangle formed with sides of the length of the log + 300 cm and the diameter of the log + 300 cm, minus areas A and corona B.

Our calculations of the probability of encountering a hammer stone within 3 m of an anvil are underestimates, because monkeys might have removed hammers from this area to transport them to the anvil. To compensate for the potential removal of hammer stones from corona B and C to the anvils, we re-calculated the relative density of hammer stones in corona B and C (summed together) assuming that every hammer stone on an anvil should be counted as collected from corona B or C. When this value was compared with the density of hammer stones found on the anvils, the difference was still statistically significant. As the results do not change, we report our first calculations as given earlier.

Statistical analyses

All data were collated by area and by type of anvil (stone or log). Parametric and nonparametric statistical techniques were used to compare data across areas and types of anvils. Nonparametric statistics were used when the assumptions of parametric statistics were not met. To assess whether the stone anvils present in the three areas surveyed (ML, MS, and MM) differ in hardness, their rebound was compared across areas by means of the Kruskal–Wallis analysis and between areas with the Mann–Whitney U test. The average rebound of the used area (with pit) and the control area (when present) were compared with the Student *t*-test for dependent samples. The frequencies of hammer stones in the areas A, B, and C were compared with a MANOVA and the Tukey Test was used for *post hoc* comparisons between areas. Pooled data are reported for those variables for which no differences emerged across areas or type of anvil.

RESULTS

Distribution of anvils

As shown in Map 1 (see Fig. 6), we surveyed three areas 0.5–3 km apart from one another at their closest points. A total of 119 anvils were encountered; we encountered an anvil every 332.1 $\pm$ 193.9 m, on average (1.82 $\pm$ 0.82 anvils/ha). Four times we encountered a cluster of anvils within a few meters; in these cases we measured one of the anvil that appeared to have been used the most recently. We judged 46 anvils to be in current use and 71 as abandoned. The use status of two additional anvils was judged ambiguous. The anvils in current use for which we report data below were distributed across the three areas as follows: 11 in ML (10 stone anvils, 1 log anvil in 2.6 km of walking surveyed); 14 in MS (all stone anvils in 7.8 km surveyed); and 17 in MM (12 stone and 5 log anvils in 3.5 km surveyed).

Description of anvils

For each anvil, Table 1 provides values on perimeter, estimated area, inclination, distance from the closest stream, height of the nearest tree, distance of the nearest tree, DBH of the nearest tree and of the largest tree within 3 m, and number of pits. Table 1 also provides summary descriptive statistics (average, median, and SD).

Stone anvils are made up of relatively soft sedimentary rocks, mostly siltstones and fine-grained sandstones, with relatively high amounts of iron oxides as cementing material. These are the most abundant rock types in the region, and due to their strongly layered structure they can easily provide large horizontal surfaces which are useful as anvils. Their relative softness also leads to the

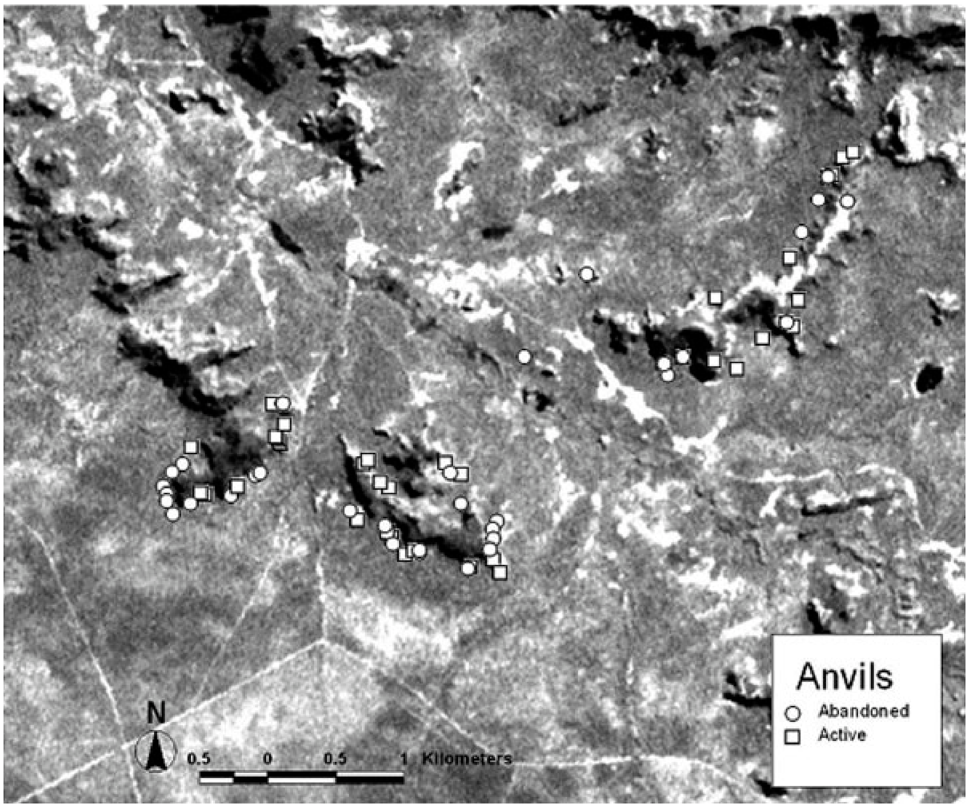

Fig. 6. Satellite image of the study area showing the location of censused anvils. The shading in the image depicts vegetation; white is absence of vegetation, darker gray to black is heavy vegetation. Note that the anvils occur predominantly at the interface between the less vegetated (flat) region and the more heavily vegetated ridges. Note that a symbol may indicate more than one anvil when the anvils are close to each other. Image courtesy of the Center for Remote Sensing and Mapping, University of Georgia.

formation of pits on their surface if they are struck with harder stones and palm nuts.

The average estimated area of the stone anvils was 1.89 m^2 (range 0.2–11.9); on average they contained 7.1 pits (range 0–43). Twenty-three anvils (55%) contained pits that had not been used recently; in all others, all the pits had been used recently. The average estimated area of the log anvils was 1.9 m^2 (range 0.9–3.6). Following Lorenzi (1992), the log anvils were identified as two *candeia* trees (*Piptocarpha rotundifolia*, Compositae, see Fig. 7), the wood of which is moderately heavy (density 0.65 g/cm^3), hard, moderately durable, and having thick/rough texture and good mechanical resistance; two *jatobá* trees (*Hymenaea sp*, Leguminosae-Caesalpinoideae, Caesalpinaceae) the wood of which is heavy (density 0.90–0.96 g/cm^3), very hard, and moderately durable; one *sucupira* tree (*Pterodon emarginatus*, Leguminosae-Papilionoidae, Fabaceae) the wood of which is heavy (density 0.94 g/cm^3), compact, tough and difficult to crack, and very durable even if exposed to weather; and one *folha larga* tree of unknown species. The pits were located on largely horizontal flat surfaces of the logs. The average circumference of the area where the pits were found on log anvils was 93 cm. On average log anvils contained 2.5 pits (range 1–4).

Several variables characterized anvils in current use, although no single element was ubiquitous or diagnostic. First, they were most often found at the transition zone between the sloping ridge and the flat open woodland, a few meters above the level of the woodland (see Fig. 8). Only nine anvils were found in the open woodland, six of which were logs (all the log anvils). Second, anvils were often found near an ephemeral water course. Heavy rains result in many small water courses along the slopes of the ridges that contain running water for a matter of hours. Such ephemeral water courses are identifiable as small eroded gullies with exposed tree roots and stone, pooled sand, and loose pebbles. Most anvils (33 out of 42; i.e. 79%) were within 10 m of an ephemeral water course. The average distance to a water course for these 33 anvils was 3.4 m. Eight of them were closer than 1 m to a water course.

Four other variables characterized most anvils. They were relatively low to the ground, possessed a flat, horizontal surface, and fairly good visual coverage overhead, and were close to at least one tree. The average height above ground of the upper surface of the anvils was 83 cm ($N = 34$). As shown in Table 1, the average inclination of the area where nuts were broken was 6.4° ($N = 42$; range 0–20°). Twenty-seven of 42 (64%) anvils had full or nearly full overhead coverage; 11 (26%) had less coverage, and 4 (10%) had none. A tree with DBH $\geq$ 8 cm was on average 0.93 m from an edge of the anvil, and only four anvils lacked a tree within 3 m. These four anvils were close to woody bushes that, although dense, did not meet our criteria as trees. The average DBH of the nearest tree was 0.19 m, the average DBH of the largest tree within 10 m was 0.26 m.

We found no differences across stone anvils in the three ridges in the variables measured (Table 1), except

TABLE 1. Anvils estimated in current use

Anvil	Perimeter	Estimated area	Inclination (degrees)	Ephemeral water course (distance)	Height of the nearest tree	Distance of the nearest tree	DBH of the nearest tree	DBH of the largest tree	Number of pitted depressions
Stone anvils									
ML 1	5.7	2.15	5	8	5	1	0.16	0.21	4
ML 2	4	1.03	0	6	9	0.4	0.36	0.36	3
ML 3	4.6	1.41	4	1.5	3	0.4	0.14	0.16	24
ML 4	6.5	2.65	5	1	6	0.0	0.24	0.24	4
ML 6	13.8	11.85	15	6	13.8	2.45	0.18	0.18	21
ML 7	1.9	0.23	0	1.2	8	1.9	0.19	0.32	3
ML 8	4.3	1.12	0	2.9	6	1.1	0.09	0.25	2
ML 9	3.4	0.73	5	1	10	0.22	0.21	0.21	5
ML 10	3.1	0.62	15	2.1	4	0.61	0.09	0.25	12
ML 13	3.2	0.64	10	0	4	1.45	0.19	0.19	8
MS 1	2.8	0.49	8	3.8	12	0.15	0.08	0.17	5
MS 2	12	9.00	0	0	5	0.2	0.26	0.26	22
MS 3	3.5	0.68	5	0	12	1	0.31	0.31	1
MS 4	4	1.25	10	9.2	5.5	1.5	0.14	0.14	2
MS 5	6.2	2.76	5	1	5.5	2.1	0.19	0.19	5
MS 6	3.2	0.65	15	6.3	Bush	Bush	Bush	Bush	1
MS 7	6.1	2.35	5	2.8	21	0.9	0.19	0.19	3
MS 8	6.3	3.06	20	2.2	7.1	1.4	0.15	0.15	4
MS 9	3.2	0.65	15	10	Bush	Bush	Bush	Bush	1
MS 10	3.2	0.69	11	No	16	1.38	0.41	0.41	2
MS 11	6.6	2.82	0	4.2	12.4	0.6	0.31	0.31	5
MS 12	2.8	0.50	15	No	Bush	Bush	Bush	Bush	2
MS 13	7.8	3.92	0	No	14.8	0.8	0.21	0.21	11
MS 14	4.8	1.46	6	7.6	10	0.13	0.11	0.11	15
MM 20	5	1.53	10	No	7	0.22	0.08	0.29	0
MM 21	4.8	1.45	0	No	11	1.56	0.09	0.16	10
MM 22	3.7	0.85	15	0	6.5	0.23	0.09	0.24	3
MM 23	4.1	1.06	0	8.6	13.8	2.54	0.54	0.54	33
MM 24	5.4	1.84	12	1.4	6	2.23	0.11	0.11	3
MM 25	6.8	2.91	0	No	11.5	0.36	0.11	0.60	5
MM 26	4.9	1.46	7.5	9.7	4	0.2	0.19	0.37	3
MM 27	3.5	0.78	7.5	5.2	9.2	1.3	0.24	0.24	3
MM 28	2.6	0.43	14	No	4.5	0.35	0.17	0.17	3
MM 29	4.5	1.60	5	0	4	0.56	0.14	0.25	6
MM 30	4	0.99	9	0.3	10.1	0.15	0.17	0.17	43
MM 31	2.9	0.54	0	5	4	1.45	0.18	0.18	5
Total	175.2	68.15	254	107	281.7	31.34	6.31	8.14	282
N	36	36	36	29	33	33	33	33	36
Average	4.9	1.89	7.1	3.7	8.5	0.95	0.19	0.25	15.2
Median	4.2	1.19	5.5	2.8	7.1	0.8	0.18	0.21	4
SD	2.4	2.31	5.9	3.3	4.3	0.73	0.1	0.11	9.6
Wood anvils									
MM 11[a]	24.6	3.55	7	0	8	0	0.14	0.14	2
MM 12[b]	10.5	1.24	0	2.4	9	2.5	0.21	0.21	1
ML 5[a]	17.1	2.11	3	4	Bush	Bush	Bush	Bush	3
MM 14[c]	14.8	2.04	0	No	10.5	0.57	0.33	0.48	4
MM 15[c]	9.0	1.61	0	0	8.1	0.4	0.33	0.29	3
MM 16[d]	6.4	0.88	5	No	9.2	0.52	0.17	0.48	2
Total	82.3	11.43	15	6.4	44.8	3.99	1.11	1.6	15
N	6	6	6	4	5	5	5	5	6
Average	13.7	1.91	2.5	1.6	9	0.80	0.24	0.32	2.5
Median	12.6	1.83	1.5	1.2	9	0.52	0.21	0.29	1
SD	6.6	0.93	3	2	1	0.98	0.09	0.16	2.5
Stone and wood anvils									
Total	257.5	79.58	269	113.4	326.1	35.33	7.48	9.74	297
N	42	42	42	33	38	38	38	38	42
Average	6.1	1.88	6.4	3.4	8.6	0.93	0.2	0.26	7.1
Median	4.8	1.25	5	2.4	8.1	0.61	0.18	0.22	3.5
SD	4.5	2.13	5.8	3.2	4	0.75	0.1	0.12	9.1

For each anvil perimeter, estimated area, inclination, distance from the closest ephemeral water course, height of the nearest tree, diameter at breast height (DBH) of the nearest and of the largest tree, and number pitted depressions are reported (for details on how these measures were taken see the Methods section). The apex letters indicate wooden anvils ([a]candeia, [b]sucupira, [c]jatobá, and [d]folha larga). Measures are expressed in meters.

Fig. 7. Wood anvil ML5 (*Piptocarpha rotundifolia*). This anvil has three pits. The arrow points toward the first pit, the second pit is between the first and the hammer stone, and the third is covered by the stone. The hammer stone was judged to have high sphericity and angularity 0.6, according to Power's scale. (Photograph by E. Visalberghi).

hardness. The stone anvils were siltstone or sandstone with an average Rx value of rebound in the used area of 27.9 (Table 2). In particular the ML stone anvils had a Rx of 22.2, the MS stone anvils 30.5, and the MM stone anvils 29.6. The log anvils had a rebound of 30.8. The Kruskal–Wallis analysis showed that these values are statistically different (H (3, $N = 42$) = 10.4, $P < 0.02$). Pair-wise tests showed that the ML anvils were softer than all the other anvil groups (ML vs. log, $z = -2.3$, $N_1 = 10$, $N_2 = 14$, $P < 0.03$; ML vs. MS, $z = -2.6$, $N_1 = 10$, $N_2 = 14$, $P < 0.01$; ML vs. MM, $z = -2.8$, $N_1 = 12$, $N_2 = 14$, $P < 0.01$). In contrast, no difference was found between the other three groups (log vs. MS, $z = 0.5$, $N_1 = 6$, $N_2 = 14$; log vs. MM, $z = 0.6$, $N_1 = 6$, $N_2 = 12$; MS vs. MM, $z = 0.7$, $N_1 = 14$, $N_2 = 12$). In general, the anvils in a given area reflected the hardness of the prevailing sedimentary rock.

The average rebound of the pitted areas on the stone anvils was 28.3 ($N = 42$), and that of the control (unpitted) areas was 28.1 ($N = 35$). For the 35 anvils in which there were both pitted and control areas, their rebound values did not differ (Student t for dependent samples, $N = 35$, df = 34; $t_{34} = -0.13$). This indicates that these anvils had at least one other area with similar hardness to that selected by the monkeys to crack open nuts.

Many anvils (19 of 42; 45%) were more than 3 m away from the nearest palm, indicating that transporting palm nuts for distances of several meters is common. Only 4 anvils (10%) had palms within 3 m distance bearing nuts.

Description of hammer stones

As shown in Table 3, hammer stones were found on every anvil in current use except one, and this anvil had a hammer stone in the B area (i.e., within 30 cm from the anvil). The stones found on the anvils (area A) weighed on average 1168 g (SD = 488.8, range 250–2530, $N = 46$; Fig. 9); those found in the B area weighed on average 600 g (SD = 242.4, range 220–850, $N = 7$). Overall, hammer stones and potential hammer stones across all three zones averaged 1096 g Abandoned anvils frequently lacked a hammer stone (38 of 70 cases, data missing for two cases). Although stones in all sizes of the prevailing siltstone and fine-grained sandstone were abundant in the transition zone where stone anvils occur, potential hammer stones (that resisted striking by the geological hammer) were not (see Table 3). In fact, 28 anvils (66.7%) did not have any hard stone in the C zone (between 0.3 and 3 m from the anvil). Seven (16.7%) had one stone and seven (16.7%) had more than one stone in the C zone. The average area of the anvils ($N = 42$) was 1.9 m^2 (SD = 2.2), the average area of B zone was 1.8 m^2 (SD = 1.4) and the average area of C zone was 37.8 m^2 (SD = 17.3). The average frequencies of potential hammer stones per square meter in the area A were 1.1 (SD = 0.9), in the area B were 0.2 (SD = 0.3), and in the area C were 0.03 (SD = 0.09). The frequencies of potential hammer stones per square meter in the three areas were statistically different (MANOVA, df 2, 82, $F = 46.2$, $P < 0.0001$); in particular, the frequency of stones in the areas A were significantly higher than in areas B (Tukey Test, $P < 0.0001$) and areas C (Tukey Test, $P < 0.0001$). No significant difference emerged between areas B and C (Tukey Test, $P = 0.53$).

There was a trend for the stones found on the anvils to be heavier than those found in the C area. For those anvils in which we found stones on the anvil and stones on the area C, the average weight of the heaviest stones found on the anvils was 1193.3 g (SD = 421.0, range 560–1990, median = 1225, $N = 12$) whereas that of the

Fig. 8. Stone anvil MM30. This anvil, like most, is located in the transition zone between the sloping ridge and the flat open woodland, and a stream bed is visible on its right. Note two whitish hammer stones on the anvil. (Photograph by E. Visalberghi).

heaviest stones found in the C area was 802.5 g (SD = 661.1, range 150–2400, median = 600, N = 12). The comparison between these values yields $T = 17$, $N = 12$; $P = 0.084$.

In sum, in the vicinity of the anvils, hard stones that make durable, effective hammers are present but rare, and potential hammer stones are not randomly distributed in space. Instead, they are more abundant on the anvils than in the area nearby. These findings suggest that capuchins transport hammer stones to the anvils.

The stones found on the anvils or within 30 cm exhibited considerable variation in weight, volume, sphericity, and angularity (see Table 3). Density averaged 2.4 g/cm^3 (SD = 0.4, range 1.2–3.0, median = 2.5, N = 42). By comparison, the density of sandstone ranges between 1.8 and 2.7 g/cm^3, and that of basalt between 2.8 and 3.1 g/cm^3. None of the hammer stones contained a clear hemispherical use-wear pit.

Petrographic description of hammer stones

Hammers were predominantly sandstone and quartzite, the latter being a sandstone that underwent metamorphism under higher temperature and pressure, becoming harder and less porous than sandstone. Quartzite, the hardest rock in the area, occurs only as pebbles in conglomerate beds, probably in the lowermost portion of the Sambaíba Formation. When the conglomerate beds are weathered and eroded, the quartzite pebbles become loosened from the surrounding rock matrix, and thus available to the capuchins. As the sedimentary beds, including the conglomerate beds, are close to horizontal, conglomerates and therefore loosened quartzite pebbles cover a large area. Thus potential hammer stones are likely to be widely distributed, even if sparse, across the region in which we censused anvils. Other potential hammers are fragments of quartz veins, which also occur as rounded pebbles in conglomerates. Siltstone and ironstone hammers were also found. Together with sandstones, these are the most abundant rock types in the area, but because they are relatively soft rocks, they will have a shorter use as hammers. A short petrographic description of the hammers found at the anvils obtained through the analysis of flakes taken from the hammers or of stones of similar appearance is reported in Table 4.

DISCUSSION

Our findings confirm our suggestion (Fragaszy et al., 2004b) that nut cracking with tools, namely hammers and anvils, is a routine activity among the wild bearded capuchin monkeys in Boa Vista. We show here that the monkeys crack nuts in many places and have done so over long periods of time. Phylogeny does not predict this pattern: this Neotropical species last shared a common ancestor with Catarrhini about 35 million years ago (Schrago and Russo, 2003). No other species of monkey, in the New or Old World, is known to use tools routinely for foraging, or any other purpose. Thus, nut-cracking in capuchins likely arose independently of similar behaviors in Hominoidea. Nut-cracking in capuchins offers a valuable opportunity to consider the behavioral and ecological correlates of stone tool use. Study of the lithic remains of their tool-using activities is one way to understand how capuchins manage this activity. Below we address several notable features of the monkeys' anvil sites, and compare them to anvils and hammers used by wild chimpanzees and ancient hominins.

Anvil and hammer stones

Anvils are widespread in Boa Vista and are relatively easy to find in the transition zone between flat open woodland and ridge, where anvil surfaces and hammer stones are in proximity to each other and to palms. We found areas with several anvils in current use within a few meters of each other, areas with used and abandoned anvils close to each other, and finally, areas with only abandoned anvils for long stretches. Boesch and Boesch-Achermann (1983) report finding more than 1,000 anvil sites ("ateliers") at their site in Taï Forest, Ivory Coast in a one-year period. We do not yet have an estimate of the number of anvil sites in Boa Vista, nor their density. At this point, we can say that anvils are far more numerous than the few we surveyed in January 2005 and that those constitute the basis for the present report. Developing a more comprehensive survey of anvils at Boa Vista is underway.

Some of the capuchins' anvils had large quantities of accumulated broken shells and all except one contained use-wear pits on their surfaces, indicating that in the right circumstances, an anvil may be used for years (see Fig. 3). This is also the case for some anvils used by

TABLE 2. *Average rebound values and number of failures for the used and the control areas of each anvil*

	Rebound				
Anvil	Used	No. of failures		Control	No. of failures
Stone anvils 1					
ML 1	20.7	0		27.8	0
ML 2	24.7	0		16.4	27
ML 3	16.3	8		23.5	3
ML 4	19.4	2			
ML 6	27.2	2		28.5	0
ML 7	21.2	2		18	2
ML 8	22.5	0		22.1	0
ML 9	17.7	8		18.6	5
ML 10	20.4	0		22.6	7
ML 13	31.5	0		21	0
Total (N = 10)	221.6	22	Total (N = 9)	198.4	44
Average	22.2	2.2	Average	22	4.9
Median	21	1	Median	22.1	2
SD	4.6	3.2	SD	4.2	8.7
Stone anvils 2					
MS 1	32.2	0		31.3	0
MS 2	29.8	0			
MS 3	30.9	0		40.5	0
MS 4	46.8	0		36.6	0
MS 5	36.6	0			
MS 6	29.7	1		28.1	0
MS 7	14.4	10		18.2	10
MS 8	32.7	0		31.1	0
MS 9	33.1	0		31.5	0
MS 10	29.7	0		32.2	1
MS 11	29.5	0			
MS 12	15.5	9		16.4	5
MS 13	37	0		38.4	0
MS 14	29.4	0		27.6	0
Total (N = 14)	427.4	20	Total (N = 11)	331.8	16
Average	30.5	1.4	Average	30.2	1.5
Median	30.4	0	Median	31.3	0
SD	8.1	3.4	SD	7.5	3.2
Stone anvils 3					
MM 20	33	0			
MM 21	23.3	0		29.4	0
MM 22	26.7	0		27.1	0
MM 23	24.9	0		29.2	0
MM 24	32.3	1		29.4	0
MM 25	28.2	0		30.4	0
MM 26	28.8	0		30.1	0
MM 27	32.3	0		34	0
MM 28	33	0		34.4	0
MM 29	43.3	0		30.5	0
MM 30	18.6	2		23.4	2
MM 31	30.3	0			
Total (N = 12)	354.7	3	Total (N = 10)	297.9	2
Average	29.6	0.3	Average	29.8	0.2
Median	29.6	0	Median	29.8	0
SD	6.2	0.6	SD	3.1	0.6
Stone anvils					
Total (N = 36)	1003.6	45	Total (N = 30)	828.3	62
Average	27.9	1.3	Average	27.6	2.1
Median	29.5	0	Median	28.9	0
SD	7.4	2.8	SD	6.4	5.3
Wood anvils					
MM 11	20.7	0		24.5	0
MM 12	37.6	0		35.8	0
ML 5	30.5	0			
MM 14	33.5	0		30.8	0
MM 15	39.6	0		36.6	0
MM 16	22.9	0		27.8	0
Total (N = 6)	184.9	0	Total (N = 5)	155.4	0
Average	30.8	0	Average	31.1	0
Median	32		Median	30.8	
SD	7.7		SD	5.2	
Stone and wood anvils					
Total (N = 42)	1188.4	45	Total (N = 35)	983.8	62
Average	28.3	1.1	Average	28.1	1.8
Median	29.6	0	Median	29.2	0
SD	7.4	2.6	SD	6.3	5

For details on how these measures were taken, see the Methods section.

TABLE 3. Hammers

Anvil	Hammer 1					Hammer 2					Other stones in area C		
	Loc	W (g)	Dens	Sph	Ang	Loc	W (g)	Dens	Sph	Ang	No.	W 1 (g)	W 2 (g)
Stone anvils 1 (Area ML)													
ML 1	A	1,600	1.21	l	0.5	B	700	2.33	l	0.5	2	1,390	300
ML 2	A	1,200	2.4	l	0.3	B	700	2.59	l	0.4	1	2,400	
ML 3	A	1,200	1.32	l	0.85						0		
ML 4	A	400	2.5	l	0.6						0		
ML 6	A	1,600	2.72	l	0.25						0		
ML 7	A	1,300	2.5	h	0.5						1		
ML 8	A	1,550	2.14	h	0.35						1	250	
ML 9	A	2,530	2.85	l	0.5						0		
ML 10	A	1,300	2.6	l	0.5						0		
ML 13	A	1,200	2.57	h	0.4	B	700	2.2	l	0.25	0		
Total (N = 10)		13,880	22.54										
Average		1,388	2.25										
Median		1,300	1,300										
SD		528.94	0.54										
Stone anvils 2 (Area MS)													
MS 1	A	1,100	2.75	h	0.8						0		
MS 2	A	500	2.5	l	0.6						0		
MS 3	A	1,450	2.64	l	0.45	A	250	2.5	h	0.7	1	700	
MS 4	A	950	3.02	l	0.3						0		
MS 5	A	1,400	2.46	l	0.2						0		
MS 6	A	300	2.14	h	0.75						0		
MS 7	A	1,000	2.94	h	0.4						1	500	
MS 8	A	1,250	2.5	l	0.35	B	290	2.5	l	0.35	2	980	200
MS 9	A	870	2.07	l	0.35						0		
MS 10	A	1,350	2.7	l	0.7						0		
MS 11	A	1,300	2.52	l	0.4						0		
MS 12	A	1,320	2.44	l	0.35						2	150	140
MS 13	A	740	2.6	h	0.6						0		
MS 14	A	850	2.33	l	0.4	A	480	2.67	l	0.2	2	950	190
Total (N = 14)		14,380	35.61										
Average		1027.14	2.54										
Median		1,050	2.51										
SD		349.62	0.27										
Stone anvils 3 (Area MM)													
MM 20	A	910	2.56	l	0.35						0		
MM 21	A	800	2.58	l	0.5						0		
MM 22	A	1,420	2.56	l	0.3	A	1,180	2.57	h	0.25	>20[a]		
MM 23	A	950	1.3	l	0.4						0		
MM 24	A	650	2.5	l	0.4						4	430	330
MM 25	A	1,990	2.4	h	0.35	A	400	2.5	l	0.25	1	150	
MM 26	A	620	2.48	l	0.8						0		
MM 27	A	900	2.57	l	0.4	B	850	2.46	l	0.4	3	1,340	200
MM 28	A	1,240	2.34	l	0.5						0		
MM 29	A	560	2.24	l	0.5						1	390	
MM 30	A	740	2.55	l	0.4	A	290	2.64	l	0.2	0		
MM 31	A	665	1.41	h	0.35						0		

(continued)

TABLE 3. (Continued)

	Hammer 1					Hammer 2					Other stones in area C		
Anvil	Loc	W (g)	Dens	Sph	Ang	Loc	W (g)	Dens	Sph	Ang	No.	W 1 (g)	W 2 (g)
Total ($N = 12$)		11,445	27.51										
Average		953.8	2.29										
Median		850	2.49										
SD		414.44	0.45										
Stone anvils													
Total ($N = 36$)		39,975	85.91										
Average		1110.42	2.39										
Median		1,150	2.5										
SD		478.03	0.43										
Wood anvils													
MM 11	A	900	2.57	h	0.4						0		
MM 12	A	850	2.02	l	0.5						0		
ML 5	A	2,200	2.93	h	0.6						0		
MM 14	A	950	2.53	l	0.35						0		
MM 15	A	700	2.33	h	0.2						0		
MM 16	B	740	2.55	l	0.4	B	220	2.16	l	0.25	0		
Total ($N = 6$)		6,340	14.95										
Average		1056.67	2.49										
Median		875	2.54										
SD		568.04	0.3										
Stone and wood anvils													
Total ($N = 42$)		46,045	97.99										
Average		1096.31	2.33										
Median		1,100	2.5										
SD		462.78	0.42										

For each hammer, the location (A = on anvil; B = 0–30 cm from the anvil; C = 30–300 cm from the anvil), weight (in grams), density, sphericity (h = high sphericity; l = low sphericity), and angularity of the hammers present on the anvil, and the number of other stones (potential hammers) and the weight of the two heaviest one found in the area C are reported (for details on how these measures were taken see the Methods section).
[a] River bed

Fig. 9. Stone anvil ML9 with a quartzite stone, the heaviest hammer (2,530 g) found during the survey. This stone was judged to have low sphericity and angularity 0.5, according to Power's (1953) scale. The ruler is scaled in centimeters. (Photograph by E. Visalberghi).

chimpanzees in the Taï National Park where their pounding activities result in large quantities of stone and plant refuse accumulating in specific *loci* (Mercader et al., 2002) and for those of early hominids discovered by Goren-Inbar et al. (2002). As seen in chimpanzees' anvils (Boesch and Boesch-Achermann, 1983), the pits on capuchins' anvils were hemispherical, shallow (<2 cm), and had smooth interiors.

Although fallen logs were also abundant and as hard as the stone anvils (as measured by elastic rebound) in our site, we found many fewer log anvils than stone anvils. The lack of a wide horizontal surface, and the low overhead coverage provided by the open woodland where log anvils were typically found, may limit the suitability of many logs for use as anvils. Another factor limiting the use of logs as anvils in the open woodland could be the scarcity of potential hammer stones nearby. These stones are probably washed to the foot of the ridge in ephemeral water courses during heavy rains. Logs far from the ridge would likely also be far from potential hammer stones.

Capuchins' anvils had an area of nearly 2 m^2 on the upper surface; large enough for a capuchin to stand on while cracking and to leave the hammer stone on the anvil after using it. On average the anvil surface was about 80 cm above ground. Chimpanzees in both Taï Forest, Ivory Coast and at Bossou, Guinea crack nuts sitting on the ground nearby, rather than on the anvil surface directly, and they leave their hammer stones near, not on, the anvils (Boesch and Boesch-Achermann, 1983, 2000; Sakura and Matsuzawa, 1991).

Capuchins' stone anvils contained on average 7 pits 1–2 cm deep; log anvils contained about one third as many (2.5 pits, average). The anvils used by chimpanzees at Taï are usually tree roots at ground level, with a smaller exposed surface area than the stone anvils used by the capuchins (Boesch and Boesch-Achermann, 1983). Data on average number of pits per anvil for chimpanzees at Taï has not been presented yet to our knowledge, but pictures provided by Boesch and Boesch-Achermann (1983) suggest that most anvils had one to three. Thus, capuchins' and chimpanzees' wood anvils at Taï appear to have a similar number of pits, but capuchins' stone anvils have a larger number of pits.

Anvils with a larger surface area could support a larger number of pits (see Sakura and Matsuzawa, 1991 for a similar suggestion), and capuchins' anvils are considerably larger than chimpanzees'. Anvils used by chimpanzees at Bossou have a higher number of use-wear pits than do the (smaller) hammer stones at that site; hammers have 1–3 depressions, and anvils have up to eight (Sakura and Matsuzawa, 1991). Additionally, some of the capuchins' stone anvils were softer (as measured by elastic rebound) than their log anvils, and thus pits would develop more easily on stone anvils than on log anvils at Boa Vista. Relative hardness of the anvils and of the nuts and hammer stones struck against them will of course influence how readily pits form, and we do not yet have adequate data to compare these variables across anvils used by capuchins and chimpanzees at various sites.

Anvils used by capuchins and chimpanzees at Taï are similarly nearly horizontal, and the pits are of equivalent depth, 1–2 cm (cf. Boesch and Boesch-Achermann, 1983). It seems likely that deeper holes would impede cracking nuts, as little surface area of the nut would be

TABLE 4. Petrographic classification of the hammers found in each anvil site

	Rock type	Remark
Samples collected at stone anvils		
Anvil site		
ML 1	Siltstone: well-cemented, reddish brown due to the presence of Fe-oxide	Actual hammer
ML 2	Siltstone: well-cemented, reddish brown due to the presence of Fe-oxide	Actual hammer
ML 3	Quartzite: composed by quartz and minor amounts of muscovite and Fe-oxides; quartz with evidence of deformation and recrystallization	Actual hammer
ML 4	Quartzite: fine-grained; pores originated by dissolution of felspars; Fe-oxides give a dark brown color to the rock	Actual hammer
ML 6	Sandstone: light-colored, strongly silicified	Actual hammer
ML 7	Quartz: rounded pebble (diameter ~ 2 cm) from a vein	Similar to hammer
ML 8	Sandstone: light-colored, strongly silicified	Actual hammer
ML 9	Quartzite: light brown pebble (diameter ~ 3 cm)	Similar to hammer
ML 10	Quartz: milky, rounded pebble (diameter ~ 2 cm) from a vein	Similar to hammer
ML 13, H1	Quartz: colorless, fragment of a larger pebble from a vein	Similar to hammer
ML 13, H2	Siltstone/sandstone: reddish brown, interbedded sedimentary rock	Similar to hammer
MS 2	Sandstone (ironstone): dark brown to black, with abundant ferruginous cement	Similar to hammer
MS 3, H1	Quartzite: strongly silicified, light-colored, with low porosity, microscopic evidence of deformation in quartz	Actual hammer
MS 3, H2	Quartz: milky, rounded pebbles (diameter ~ 2 cm) from a vein	Similar to hammer
MS 4	Sandstone (ironstone): dark brown to black, with abundant ferruginous cement	Actual hammer
MS 5	Sandstone: light-colored, strongly silicified	Actual hammer
MS 6	Quartzite: 2 pebbles (one with ~ 10cm diameter); brown in the surface due to Fe-oxides, almost white inside	Similar to hammer
MS 7	Sandstone: light-colored, strongly silicified	Actual hammer
MS 8	Sandstone (ironstone): with abundant ferruginous cement, dark brown to black; Fe-oxide coat the rounded quartz grains; relatively low density due to high porosity	Actual hammer
MS 9	Sandstone: light-colored, strongly silicified	Actual hammer
MS 10	Sandstone: weathered	Actual hammer
MS 11	Sandstone: yellowish, coarse-grained, weathered	Actual hammer
MS 12	Sandstone (ironstone): dark brown to black, very porous, with abundant ferruginous cement	Actual hammer
MS 13	Sandstone: light-colored, strongly silicified	Actual hammer
MS 14	Sandstone: red-colored, fine-grained, with Fe-oxide cement	Actual hammer
MM 20	Sandstone: light-colored, slightly weathered	Actual hammer
MM 21	Quartzite: pebbles (diameter ~ 5 cm), with pores due to dissolution of felspar	Similar to hammer
MM 22	Siltstone: reddish brown, strongly silicified, containing acicular microfossils	Similar to hammer
MM 23	Sandstone: reddish due to Fe-oxides, fine-grained	Actual hammer
MM 24	Siltstone: reddish brown, strongly silicified, containing thin beds of sand; evidence of brittle deformation; presence of some idiomorphic quartz grains	Similar to hammer
MM 25	Quartzite: fine-grained, porosity due to dissolution of felspars. Fine-grained Fe-oxides give a dark brown color to the rock.	Similar to hammer
MM 25	Microbreccia: with fragments of reddish brown siltstone	Similar to hammer
MM 26	Quartzite: pebble (diameter ~ 5 cm), light-colored	Similar to hammer
MM 27	Quartz: milky, pebble of from quartz vein (diameter < 2 cm)	Similar to hammer
MM 29	Microbreccia: comprising yellowish sandstone and reddish brown siltstone	Actual hammer
MM 30	Quartzite: light-colored	Actual hammer
MM 31	Quartzite: pebble (diameter ~ 2 cm), light-colored	Similar to hammer
Samples collected at wood anvils		
Hammer number	Microbreccia: comprising yellowish sandstone and reddish brown siltstone	Actual hammer
MM 12	Sandstone: light-colored, slightly weathered	Actual hammer
ML 5	Quartzite: light brown, very homogeneous, with quartz and minor muscovite	Similar to hammer
MM 14	Sandstone: light-colored, slightly weathered	Actual hammer
MM 15	Sandstone: fine-grained, yellowish to reddish brown, weathered	Actual hammer

As noted in the remark column, flakes were taken from the hammer(s) present at the anvil (actual hammer), or from a stone collected at the same anvil site and similar to the hammer (similar to hammer). When two or more hammers were present at an anvil, we indicate whether the sample comes from (H1 = hammer1; H2 = hammer 2, etc.).

exposed to the blows of the hammer. Thus in terms of the presence of pits, their shape and depth, and the horizontal plane of the anvil surface, chimpanzees at Taï and capuchins use similar anvils.

In other respects, however, capuchins' anvils differed from chimpanzees' anvils. As we predicted, capuchins' anvils had several properties that make them convenient and relatively safe to use for monkeys that face aerial and terrestrial predators: most had good overhead visual cover and on average a tree was less than a meter away, which facilitates arboreal access and departure. Capuchins' anvils are in most cases not close to palm trees; in contrast, the anvils of the chimpanzees living in the primary forest at Taï are usually close to the tree providing nuts to crack (Boesch and Boesch-Achermann, 1983). When choosing where on the anvil to pound, capuchins do not need to be extremely selective since most of the anvils had more than one equivalently hard, horizontal area. Chimpanzees at Taï and at Bossou have less choice of where to pound on a smaller anvil. Chimpanzees at Taï sometimes transported nuts more than 30 m to a stone anvil, however, suggesting that hardness does factor into their choice of anvil (Boesch and Boesch-Achermann, 1983, 1984).

Although we do not yet have quantitative measures of the toughness of the nuts in our site, we judged this property by trying to crack the nuts ourselves. Like the monkeys (see Fig. 2), we have to select heavy stones (800–1000 g) for this purpose, position the nut on a hard surface and crack the nuts with repeated blunt strikes of a stone held firmly in both hands. A heavy stone provides greater force for this purpose than a lighter stone, and a hard stone withstands the impact with the nut. Most sandstone, siltstone and ironstone fragments simply shatter when struck against the palm nuts. In fact, all of the hammer stones that we found on anvils in current use are sufficiently hard to be difficult to flake with a geological hammer. Sufficient weight and hardness appear to be very important requirements for hammer stones; a specific shape is not. Hammer stones used by capuchins varied widely in angularity and sphericity.

Hammer stones used by chimpanzees apparently also vary in shape (as shown for example by photos provided by Boesch and Boesch-Achermann, 1983 and Sakura and Matsuzawa, 1991). Some hammer stones used by chimpanzees and by early hominins in Gesher Benot Ya'aqov show evidence of pitting, in the same manner as anvils (Boesch and Boesch-Achermann, 1983; Sakura and Matsuzawa, 1991; Goren-Inbar et al., 2002). Use-wear pits were produced by capuchins on the surface of anvils but not in their hammers. This difference could be due to 1) a higher turnover in the use of anvil and hammer stones, perhaps arising from the frequent fires typical of the *Cerrado* habitat resulting in the abandonment of an anvil or fracturing of the hammer stone, or 2) to the lesser density of siltstone and quartzite, and therefore shorter use before breaking, compared with the granitic stones used by the chimpanzees in Taï or the basalt stones used by humans at Gesher Benot Ya'aqov (Boesch and Boesch-Achermann, 1983; Goren-Inbar et al., 2002). It can also be due to the lesser forces on the hammer stones produced by capuchins compared with chimpanzees and humans that weigh at least 10 times more than capuchins.

Capuchins' hammer stones were much heavier than we expected on the basis of our preliminary work (Fragaszy et al., 2004b). We previously reported an average weight of about 500 g for potential hammer stones on or near anvils, whereas in this study they weighed on average 1,096 g. The difference in weights of hammers between the two studies reflects the operational definition of hammers in this study to stones hard enough to withstand striking by the geological hammer. In our previous study, we accepted as hammers some stones that, in retrospect, would likely be excluded with the more restrictive operational definition used here.

Comparing the hammer stones used by capuchins with those used by chimpanzees provides appreciation of the motor skills and strength involved. The chimpanzees of the Taï National Park typically use wooden (club) hammers (that are more abundant in the forest than stone hammers) to crack open *Coula edulis* nuts and stone hammers to crack open the harder *Panda oleosa* nuts (Boesch and Boesch-Achermann, 1983). The typical club hammers weighed less than 2 kg in 77% of the cases and 2–4 kg in 16% of the cases. The stone hammers used for *Panda* were heavier: 15% weighed more than 9 kg (one weighed 10 kg), 42% between 3 and 8.9 kg, 23% between 1 and 2.9 kg, and only 19% less than 1 kg. Sakura and Matsuzawa (1991) report that chimpanzees at Bossou, Guinea, use hammer stones that weigh on average 0.7 kg. Adult chimpanzees only rarely use hammers that weigh one third of their body weight (see Introduction), whereas capuchins use hammers that are on average one third of their body weight and that sometimes weigh more than one half of their body weight.

The finding that most of the anvils were near an ephemeral water course supports the hypothesis that water courses are possible sources of hammer stones. Future work should establish the provenance of hammer stones by mapping the distribution of the conglomerate bed(s) in the field, locating more precisely its stratigraphic position in the Sambaíba and Pedra do Fogo formations, and also evaluate the distribution and abundance of suitable hammer stones washed to the foot of the ridge compared with their availability elsewhere.

Implications: Transport, traditions, and transition zones

Transportation of nuts and stones to anvil sites encompasses various degrees of planning. Indirect evidence shows that hominins carried raw material, hammers, and manuports as well as the flakes produced by knapping to and from anvil sites (Davidson & McGrew, 2005). Boesch and Boesch-Achermann (1984, 2000) report that when chimpanzees in Taï National Park, Ivory Coast, crack open *Panda* nuts, they often transport a hammer to the anvil site (average transport distance = 120 m). Good stone hammers and good anvil sites are apparently rarer in Taï National Park than in our site (Visalberghi, personal observations), and thus transport distances may be greater, although we have no quantitative data to make a specific comparison. At Boa Vista, the scarcity of stones suitable for use as hammers in the vicinity of the anvils and the fact that most anvils are more than 3 m from any palm tell us that capuchins must also look for stones suitable as hammers and for palm nuts and transport them several meters at least. Falotico (2006) showed that semi-free capuchin monkeys would transport stone tools 10 m to anvils in experiments in Tiête Ecological Reserve, São Paulo; this was the greatest distance he placed hammer stones from the anvils. On the basis of informal observations at Boa Vista, we expect that monkeys carry hammer stones to an anvil and from one anvil to another across a range of distances, including to anvils that are out of sight of the start point of transport. We are currently collecting data to evaluate the cognitive demands posed by searching for, selecting and transporting hammer stones and nuts.

Wild chimpanzees crack open nuts with tools only in some parts of their natural range (i.e. in western Africa, Boesch and Boesch-Achermann, 2000) although the ecological conditions elsewhere seem equally suitable for this activity (McGrew et al., 1997). The discrepancy in behavior across populations has led many to propose that nut-cracking is a tradition of specific populations (e.g. Whiten et al., 2001). Matsuzawa et al. (2001) and

Inoue-Nakamura and Matsuzawa (1997) provide developmental data that confirm that social context supports young chimpanzees learning this skill (as prescribed by Fragaszy and Perry, 2003 to claim a behavior as a tradition), thus confirming that nut-cracking is a tradition in Bossou. Boesch and Boesch-Achermann's (2000) descriptions of the supportive social context during nut-cracking and the acquisition of nut-cracking skills by young chimpanzees in Taï Forest are also congruent with this hypothesis.

The picture for capuchins is similar to that for chimpanzees, both in terms of patchy geographic distribution of the behavior, and, more important for the claim that nut-cracking is a tradition, the social contribution to its acquisition. Primatologists did not report the use of tools by wild capuchins to crack open hard shelled nuts until 2004 (Fragaszy et al., 2004a,b; Moura and Lee, 2004). However, after these two initial reports, several others followed (Ottoni and Izar, submitted[2]; Waga et al., 2006), all concerning populations living in Cerrado habitats. Capuchins living in these deciduous South American habitats overall have been less studied than capuchins living in wetter habitats. Thus nut-cracking appears to occur in only part of the large natural range of *Cebus*. The contribution of social context to the acquisition of nut-cracking by capuchins appears to be considerable, as documented by Ottoni, Resende and colleagues (Resende et al., 2003; Resende, 2004; Ottoni et al., 2005). For example, infant capuchins spend much time near others while the others crack nuts; they are tolerated and permitted to take pieces of nuts cracked by others; they spend a long time in this permissive social setting playing with stones and nuts prior to learning to crack. In these ways, the acquisition of nut-cracking in capuchins appears similar to that of chimpanzees, and in both species social context seems to support the acquisition. Nut-cracking is likely to be a tradition in capuchins, as it is likely to be a tradition in chimpanzees. Additional studies with both species tracking the acquisition of nut-cracking are needed to understand if social context provides the same extent of support for learning to crack nuts in the two genera.

Transition zones between habitat types are areas of enhanced biodiversity (Krebs, 1989; Gaston, 1996). Goren-Inbar et al. (2002) argued that during the Pleistocene era, areas of high biodiversity, given their rich variety of natural resources, might have attracted hominins and might have enhanced their opportunities to develop new skills, such as nut cracking. In the case of the capuchin monkeys in Piauí, it is likely that the juxtaposition of the plant resources of the flat open woodland (the palms) and the geological resources of the ridges (anvils and hammer stones) might have favored the innovation of a technology involving a combination of resources available in the two zones, such as the exploitation of palm nuts with tools. We can examine this hypothesis through documenting the geographic context of nut-cracking in other populations of capuchins. A geographic habitat model developed by Hinely (2006) using data from our site will help us to do this.

By transporting stones to anvil sites and leaving them there, capuchin monkeys (like chimpanzees) alter the site for future users. Similarly, by producing pits in anvils through cracking nuts, the monkeys alter the affordances of the anvil for future nut crackers. In both these ways, the capuchin monkeys "construct" their own and others' niches (*sensu* Odling-Smee et al., 2003) by making the physical environment more supportive for others to acquire the use of tools to crack nuts. Here again, capuchin monkeys, like apes, participate to some degree in a process thought to be critical in the appearance of human societies. This aspect of simple tool technology deserves further consideration.

[2]Ottoni EB and Izar P. submitted. Towards a map of capuchin monkeys' tool use: overview and implications. Evol Anthropol.

CONCLUSIONS

Stone-tool use can no longer be thought of as the province of hominids and hominoids – it belongs dramatically also to Neotropical primates. Our findings show that nut cracking is a robust phenomenon in wild bearded capuchins living in a Cerrado habitat in Brazil. This phenomenon opens up a new reference point for the comparative analysis of tool use. The monkeys transport hard, heavy stones some distance to use them on anvils that show, by their pitted surfaces, evidence of habitual use over long periods. In both of these features, capuchins' anvil sites are like those of chimpanzees, and indeed, like those of humans. Capuchins' anvils reflect stronger bias towards avoidance of predation than do chimpanzees' anvils: they are located near trees and in areas with overhead coverage. The extreme mass of capuchins' hammer stones relative to the mass of the monkeys, compared with those of chimpanzees and humans, suggests that nut-cracking is for these small monkeys an enormously strenuous activity. Determining the distribution of nut-cracking across populations, and within populations, determining the ecological, social, cognitive and physical correlates of nut-cracking will provide new insights into the costs and benefits of tool use in feeding.

ACKNOWLEDGMENTS

Permission to work in Brazil granted by IBAMA and CNPq to DF and EV. Thanks to Fundacão BioBrasil for permission to work at Green Wing Valley Reserve and logistical support. Thanks to Eduardo Darvin Ramos Silva for critical assistance in collecting the census data. Thanks to Drs. Tom Jordan and Marguerite Madden of the Center for Remote Mapping Science, University of Georgia, for providing Figure 6 and other assistance in mapping our site. We also thank Francesca Bozzano, Maria Rosaria Manuel, Francesca Tecce and Valentina Barucci for their help in various phases of the study. We are also grateful to the editor, three anonymous referees, and to Elsa Addessi and Bill McGraw for their comments on the manuscript.

LITERATURE CITED

Anderson JR, Williamson EA, Carter J. 1983. Chimpanzees of Sapo forest, Liberia: density, nests, tools and meat-eating. Primates 24:594–601.

Boesch C, Boesch-Achermann H. 1983. Optimisation of nut-cracking with natural hammers by wild chipanzees. Behaviour 83:265–286.

Boesch C, Boesch-Achermann H. 1984. Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. Primates 25:160–170.

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

Davidson I, McGrew WC. 2005. Stone tools and the uniqueness of human culture. J R Anthropol Inst 11:793–817.

de Beaune SA. 2000. Pour une archeologie du geste. Paris: CNRS Editions.

DNPM. 1973. Parte das folhas SC. 23 Rio São Francisco e SC. 24 Aracaju; geologia, geomorfologia, solos, vegetação e uso potencial da terra (mapa geológico 1:1.000.000). Depto. Nacional de Produção Mineral, Projeto Radam, Rio de Janeiro, Brazil.

Driver HE. 1961. Indians of North America. Chicago, IL: Chicago University Press.

Falotico T. 2006. Estudo experimental do uso de ferramentas para quebra de frutos encapsulados por macacos-prego (Cebus apella) em semi-liberdade. MS dissertation, University of São Paulo.

Farias RRS, Castro AAJF. 2004. Fitossociologia de trechos da vegetação do Complexo de Campo Maior, Campo Maior, PI, Brasil. Acta Bot Brasil 18:949–963.

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

Fragaszy D, Fedigan L, Visalberghi E. 2004a. The complete capuchin. The biology of the genus *Cebus*. Cambridge: Cambridge University Press.

Fragaszy D, Izar P, Visalberghi E, Ottoni E, Gomes de Oliveira M. 2004b. Wild capuchin monkeys (*Cebus libidinousus*) use anvils and stone pounding tools. Am J Primatol 64:359–366.

Fragaszy DM, Perry S. 2003. The biology of traditions. Cambridge: Cambridge Uinversity Press.

Gaston KJ. 1996. Biodiversity: a biology of numbers and difference. Oxford: Blackwell Science.

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

Hinely, A. 2006. GIS-based habitat modeling related to bearded capuchin monkey tool use. MS thesis, University of Georgia.

Inoue-Nakamura N, Matsuzawa T. 1997. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). J Comp Psychol 111:159–173.

Jones PR. 1994. In: Leakey MD, Roe, DA, editors. Olduvai Gorge excavations in bed III, IV and the Masek beds: 1968–1971, Vol. 5. Cambridge: Cambridge University Press. p 254–298.

Kortlandt A. 1986. The use of tools by wild-living chimpanzees and earliest hominids. J Hum Evol 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.

Krebs CJ. 1989. Ecological methodology. New York: Harper and Row.

Leakey MD. 1971. Olduvai Gorge, excavations in beds I and II: 1960–1963. Cambridge: Cambridge University Press.

Lorenzi H. 1992. Árvores Brasileiras. Manual de identificação e cultivo de plantas nativas do Brasil. Nova Odessa, SP: Editora Plantarum, Brasil.

Lorenzi H, Souza HM, Costa JTM, Cerqueria LSC, Ferreira E. 2004. Palmeiras brasileiras e exóticas cultivadas. São Paolo (Brasil): Instituto Plantarum de Estudos da Flora Ltda.

Marchant L, McGrew WC. 2005. Percussive technology: Chimpanzee baobab smashing and the evolutionary modeling of hominin knapping. In: Roux V, Bril B, editors. Stone knapping: the necessary conditions for a uniquely hominid behavior. Cambridge: McDonald Institute for Archaeological Research. p 341–352.

Matsuzawa T. 2001. Primate foundations of human intelligence: a view of tool use in nonhuman primates and fossil hominids. In: Matsuzawa T, editor. Primate origins of human cognition and behavior. Tokyo: Springer. p 3–25.

McGrew WC. 1992. Chimpanzee material culture: implications for human evolution. Cambridge: Cambridge University Press.

McGrew WC, Ham RM, White LJT, Tutin CEG, Fernandez M. 1997. Why don't chimpanzees in Gabon crack nuts? Int J Primatol 8:353–374.

Mercader J, Panger M, Boesch C. 2002. Excavation of a chimpanzee stone tool site in the African rainforest. Science 296:1452–1455.

Moura ACA, Lee PC. 2004. Capuchin stone tool use in Caatinga dry forest. Science 306:1909.

Odling-Smee FJ, Laland KN, Feldman MW. 2003. Monographs in population biology, Vol 37: Niche construction: the neglected process in evolution. Princeton, NJ: Princeton University Press.

Ottoni EB, Resende BD, Izar P. 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. Anim Cogn 8:215–219.

Powers MC. 1953. A new roundness scale for sedimentary particles. J Sediment Res 23:117–119.

Resende BD. 2004. Ontogenia de comportamentos manipulativos em um grupo de macacos-prego (*Cebus apella*) em situação de semiliberdade [Ontogeny of manipulative behavior in a semifree group of tufted capuchin monkeys]. Doctoral dissertation, University of São Paulo, Brazil.

Resende BD, Izar P, Ottoni EB. 2003. Interaction between social play and nut-cracking behavior in semifree tufted capuchin monkeys (*Cebus apella*). Rev Ethol 5:198–199.

Rodal MJN, Andrade KVA, Sales MF, Gomes APS. 1998. Fitossociologia do componente lenhoso de um refugio vegetacional no municipio de Buique, Pernambuco. Rev Brasil Biol 58:517–526.

Sakura O, Matsuzawa T. 1991. Flexibility of wild chimpanzee nut-cracking behavior using stone hammers and anvils: an experimental analysis. Ethology 87:237–248.

Schrago CG, Russo CA. 2003. Timing the origin of new world monkeys. Mol Biol Evol 20:1620–1625.

Spears CS. 1975. In: Baker CM, editor. Arkansas Eastman archaeological project, Vol 6. p 83–116.

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

Waga I, Dacier AK, Pinha PS, Tavares MCH. 2006. Spontaneous tool use by wild capuchin monkeys (*Cebus libidinosus*) in the Cerrado. Folia Primatol 77:337–344.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama T, Tutin CEG, Wrangham RW, Boesch C. 2001. Charting cultural variation in chimpanzees. Behaviour 138: 1481–1516.