

FALLBACK STRATEGY AND TOOL USE:  
FLORISTIC COMPOSITION IN THE *CAATINGA* FOREST AND *CERRADO* AND  
ITS IMPACT ON DIET AND TOOL-USING BEHAVIOR OF CAPUCHIN MONKEYS

A THESIS

SUBMITTED TO THE GRADUATE SCHOOL  
IN PARTIAL FULLFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE

MASTERS OF ARTS

BY

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MUNCIE, INDIANA

MAY 2014

## Abstract

**THESIS:** Fallback Strategy and Tool Use: Floristic Composition in the Caatinga Forest and Cerrado and its Impact on Diet and Tool-Using Behavior of Capuchin Monkeys

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**DEGREE:** Master of Arts

**COLLEGE:** Science and Humanities

**DATE:** May, 2014

**PAGES:** 61

This study examines the effect fallback foods, foods eaten when other, more preferred foods are scarce, have on the tool-using behaviors of capuchin monkeys. In the arid Serra da Capivara National Park in Brazil, black-striped capuchins (*Cebus libidinosus*) use stone tools to dig for underground tubers, a very rare behavior among primates. I test the hypothesis that the capuchins in the Serra da Capivara exploit tubers as a fallback food because palm nuts, an important fallback resource to other groups of capuchins living in arid environments, are either rare or absent there. Studies of floristic analysis at the park and other capuchin sites show that palm nut species recorded to be consumed by capuchins are not found at the Serra da Capivara. Additionally, nutritional analysis of both palm nuts and tubers suggest that tubers could act as a replacement for palm nuts as a fallback food. This may have relevance to human evolution, as several researchers suggest tubers and other underground storage organs were important resources to early hominins.

## Acknowledgements

I would like to thank my committee members, Dr. S. Homes Hogue (Chairperson), Dr. Evelyn Bowers, Dr. Ronald Hicks, and Dr. Kevin Hunt. I'd like to express my gratitude to all my committee members for their invaluable advice and suggestions and especially for working with me long-distance as I experienced several life changes over the past few years. I very much appreciate all of the guidance Dr. Bowers provided once my thesis topic changed focus. I also thank Dr. Hunt for agreeing to be a member on my committee even though I was not one of his students. Dr. Hunt helped me immensely in focusing my thesis topic and his expertise in primatology was very helpful. In addition I'd like to thank the entire Ball State Department of Anthropology for all the support and assistance they've given me throughout the years.

I would also like to thank Dr. James Ratter, Dr. Ary Oliveira-Filho, and Dr. Antonio Moura. Their willingness to respond to my emails and answer all my questions allowed me to find all the data necessary for the completion of this thesis.

Lastly I'd like to thank my loving wife, Amada Rindler. Without her constant support and understanding I would not have been able to complete this project.

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## Chapter 1: Introduction

As do most primates, the capuchin monkeys of Central and South America experience seasonal reductions in the availability of food. What makes capuchins unique is a wide array of complex foraging behaviors, including the use of tools, which has allowed capuchins to adapt to seasonal periods of scarcity and thrive in a vast array of habitats throughout South and Central America (Fragazsy et al., 2004). An animal's population size and range will be limited by its access to the scarcest of nutrients vital to continued survival and reproduction, as illustrated by Liebig's Law of Limits (Liebig, 1843). One strategy to overcome these limitations is "falling back" on foods that are more difficult to access or digest than those which are preferentially consumed during times of plenty. The necessity of these resources, termed fallback foods, can have a profound effect on an animal's behavioral and morphological adaptations and often determine the range of habitats that an organism can occupy. Recent research suggests that fallback foods have played a more important role in primate ecology and evolution than previously realized (Hladik, 1973; Lambert et al., 2004; Marshall and Wrangham, 2007; Constantino and Wright, 2009). In this study I examine the effect of fallback foods on tool use among the black-striped capuchin (*C. libidinosus*) living in the Serra da Capivara National Park in Piauí, Brazil (Moura and Lee, 2004; Mannu and Ottoni, 2009).

Fallback foods, simply defined, are foods eaten when other, more preferred, foods are scarce (Conklin-Brittain et al., 1998; Wrangham et al., 1998; Doran et al., 2002; Marshall and Wrangham, 2007). Preferred foods are those which are eaten by an animal even when other foods are available, and are consumed proportionately more frequently than their abundance in

the environment would suggest (Conklin-Brittain et al., 1998; Doran et al., 2002; Marshall and Wrangham, 2007). Like many animals, primate diet and feeding behavior often change due to seasonal shifts in food availability (Chivers, 1977; Fossey and Harcourt, 1977; Hladik, 1977; Wrangham, 1977). Fallback foods are often of low nutritional value or difficult to access, and thus are rarely eaten when other foods are available. However, when the availability of high quality food is low, the consumption of fallback foods increases (Goodall, 1977; Hladik, 1977; Oates, 1977; Rodman, 1977). Fallback foods may make up only a small portion of an animal's diet and/or be eaten only during certain times of the year. However, they can have a profound effect on an animal's morphology and behavior (Hladik, 1973; Lambert et al., 2004; Marshall and Wrangham, 2007; Constantino and Wright, 2009).

In accord with Optimal Foraging Theory (MacArthur and Pianka, 1966), selective pressures shape an organism's feeding behaviors so that the greatest amount of energy is gained for the least amount of time and energy expended. Foods with a higher net energetic return are preferred over items with a lower net return. Altmann (1998) expressed foraging decisions as solving a 'Packaging Problem' posed by the fact that no one food contains all necessary nutrients in the correct proportions for any animal, and all food items have associated cost in collection, discovery, and consumption. Costs include the digestion and detoxification of secondary compounds, expenditure of time and energy traveling to and processing foods, or exposure to hazards such as predation (Freeland and Janzen, 1974; Altmann, 1998, 2009). Thus animals are expected to prefer foods that provide the most nutrients while presenting the least cost.

However, such foods often are not distributed evenly throughout an environment, and their availability may vary seasonally (Frankie et al., 1974; Terborgh, 1983; van Schaik et al., 1999). In addition, nutritionally rich, easy to access foods are often exploited by a large number of

different animals, creating much competition for such resources (Robinson and Wilson, 1998). Because of this, when preferred foods are unavailable animals must resort to fallback foods that are less nutritious, more costly, or both (van Schaik et al., 1993; Altmann, 1998; Robinson and Wilson, 1998; Marshall and Wrangham, 2007).

This study examines the effect fallback foods have on tool use among the genus *Cebus*, the capuchin monkeys. Capuchins are medium-sized platyrrhines weighing on average between 2.5 and 5.0 kg (Fragazsy et al., 2004). *Cebus* is divided into robust “tufted” and more gracile “untufted” species (Hershkovitz, 1949; Fragaszy et al., 2004; Alfaro et al., 2012). Untufted species include the white-faced capuchin (*Cebus capucinus*), the white-fronted capuchin (*C. albifrons*), the wedge-capped capuchin (*C. olivaceus*), and the Kaapori capuchin (*C. kaapori*). Tufted species include the brown capuchin (*C. apella*), the black-striped capuchin (*C. libidinosus*), the black capuchin (*C. nigritus*), the yellow-breasted capuchin (*C. xanthosternos*), and the blond capuchin (*C. flavius*). Depending on the classification system used, *C. macrocephalus*, *C. cay*, and *C. robustus* are either included as separate species within tufted capuchins or as subspecies of *C. apella*, *C. libidinosus*, and *C. nigritus* respectively (Fragaszy et al., 2004; Alfaro et al., 2012).

Capuchins, especially those species belonging to the “tufted capuchin” group, employ a fallback strategy that focuses on foods embedded in hard or tough coverings or substrates, which other species cannot access (Izawa, 1979; Terborgh, 1983; Wright, 2005). Capuchins have extremely dexterous hands that they can employ in complex manipulative behaviors (Costello and Fragaszy, 1988). They possess robust jaws, teeth with thick enamel, and large canines (Kinzey, 1974; Kay, 1981; Bouvier, 1986; Cole, 1992; Daegling, 1992). This combined with their manipulative abilities allow them to tear and break through hard and tough materials such

as thick nut shells or wood (Izawa, 1979; Terborgh, 1983; Wright, 2005). Capuchins are elective omnivores, able to use their large range of foraging behaviors to adjust to changes in the environment due to climate or seasonal variation. Because of this, capuchins are able to inhabit a vast range of different environments and are among the most widely spread of the New World monkeys. Capuchins inhabit an area ranging from Central America in the north to Paraguay and Northern Argentina in the south and from the Atlantic coastal forest in the east to the lower parts of the Andes in the west (Fragaszy et al., 2004).

Capuchins are highly intelligent monkeys with high brain-to-body mass ratios (Rilling and Insel, 1999). A study by Rilling and Insel (1999) compared the relative brain size of eleven primate species, including humans, based on the encephalization ratio. Encephalization ratios were calculated by dividing the observed average brain volume of a primate species by that species' predicted brain volume based on a best-fit regression line through a plot of the brain vs. body weight of all primate species compared. The brown capuchin (*Cebus apella*) had the highest encephalization ratio of all non-human primates with a quotient of 1.23. Capuchins also had the highest observed neocortex volume compared to body size (Rilling and Insel, 1999).

In order to exploit otherwise difficult to access resources, some tufted capuchin populations employ complex tool-using behavior, such as the use of stone hammers and anvils (Otoni and Mannu, 2001; Fragaszy et al., 2004; Moura and Lee, 2004; Silva et al., 2005; Waga et al., 2006). In this respect capuchins are among a small, but growing, group of organisms observed to use tools (Shumaker et al., 2011). Until fairly recently, it was thought that habitual tool use among non-human primates was restricted to chimpanzees and orangutans (van Schaik et al., 1999). Formerly, use of tools among capuchins had been restricted to laboratory experiments (Visalberghi, 1987; Westergaard and Fragaszy, 1987; Anderson, 1990; Westergaard

and Suomi, 1993; Westergaard and Suomi, 1995) and anecdotal reports of behavior in the wild (Boinski, 1988; Urbani, 1998; Chevalier-Skolnikoff, 1990; Visalberghi, 1990; Fernandes, 1991, Phillips, 1998). More recently many studies have shown nut-cracking among wild capuchin populations in arid environments across central and northeast Brazil (Ottoni and Mannu, 2001; Fragaszy et al., 2004; Moura and Lee, 2004; Silva et al., 2005; Waga et al., 2006; see Ottoni and Izar, 2008 for review).

The use of hammers and anvils is fairly widespread among tufted capuchin populations living in arid environments, but capuchins in the Serra da Capivara National Park in Piau, Brazil, (Fig. 1) exhibit a much larger range of tool-using behaviors than others (Moura and Lee, 2004; Mannu and Ottoni, 2009). Not only do they use stones as tools to crack open fruits and other objects, but they also use stones to cut wood, crush rock, and dig for underground tubers. In addition, capuchins here use sticks or other plant parts as probes to access water, insects, and honey (Moura and Lee, 2004; Mannu and Ottoni, 2009).

Of this expanded tool-using behavior, digging for tubers is of particular interest. Tubers are a type of underground storage organ, plant structures that store water and carbohydrates during adverse environmental conditions such as seasonal dry periods. Other types of underground storage organs include bulbs, corms, and rhizomes (Dominy et al., 2008). Though several species consume underground storage organs, the use of tools to dig for them is extremely rare. *Cebus libidinosus* in the dry forests of the Serra da Capivara National Park in Piau, Brazil, are among the very few primates that have been observed using tools to dig for underground tubers (*Thiloa glaucocarpa*) in the wild (Moura and Lee, 2004; Mannu and Ottoni, 2009). Besides humans and capuchins, tool-aided digging for underground storage organs has only been reported in one instance among wild chimpanzees (Hernandez-Aguilar et al., 2007).

Another reason the exploitation of underground tubers is of interest is because some paleoanthropologists theorize that they may have played an important role in early hominin evolution (Coursey, 1973; Hatley and Kappelman, 1980; Laden and Wrangham, 2005). The leafy herbaceous plants consumed as fallback foods among chimpanzees and gorillas are rare or absent in the dry woodland and savannah environments australopithecines and early *Homo* are thought to have inhabited. Laden and Wrangham (2005) hypothesize that in the absence of leafy vegetation, the underground storage organs of plants provided an abundant and calorie-rich fallback food and may have led to adaptive shifts in early hominins.

In this paper I will test the hypothesis that in the Serra da Capivara National Park, capuchins consume tubers as a fallback food when palm nuts, an important fallback resource for capuchins in other arid environments, are not available. I hypothesize that capuchins in the Serra da Capivara National Park dig for tubers because of the lack of alternative fallback foods, namely palm nuts, available in other environments inhabited by capuchins. Most nut-cracking reports are from sites in the savannah-like *cerrado* environment, where in many locations palm trees fruit year-round (Fragaszy et al., 2004; Silva et al., 2005; Waga et al., 2006). In contrast, Serra da Capivara is in the *caatinga*, or dry woodland (Moura and Lee, 2004; Mannu and Ottoni, 2009). If the palm nuts exploited by other capuchin populations are either rare or absent here, then the capuchins in the Serra da Capivara may have expanded their tool-kit to access other fallback foods. This could have implications for hominin adaptations to arid environments and the development of human tool use.



Fig. 1. Location of the Serra da Capivara National Park (SCNP), in the State of Piauí, Brazil (Mannu and Ottoni, 2009).

## Chapter 2: Literature Review

### Fallback Foods

During the 1970s, long-term ecological studies of many different primate populations and species were conducted in order to understand the effect of ecology on primate social behavior (Clutton-Brock, 1977). These studies revealed that primate diet and feeding behavior often vary with the seasonal availability of different foods (Chivers, 1977; Fossey and Harcourt, 1977; Hladik, 1977; Wrangham, 1977). Studies also showed that most primates carefully select which foods they eat based on factors such as nutritional value, ease of digestion, and amount of toxins (Freeland and Janzen, 1974; Goodall, 1977; Hladik, 1977; Oates, 1977; Rodman, 1977). Because of this, foods that were difficult to procure and gave relatively little energetic yield in return, such as bark, mature leaves, and hard seeds, were “less preferred” than easier to obtain resources such as fruit and young leaves. These less-preferred foods were eaten only rarely by primate, however their consumption would increase when other food sources became scarce (Goodall, 1977; Hladik, 1977; Oates, 1977; Rodman, 1977).

One of the first mentions of the term “fallback food” is found in Tutin and Fernandez (1985), quoting an earlier work by Hladik (1973) that referred to leaves and stems as fallback foods for chimpanzees during times of low fruit availability. Starting in the 1990s, fallback foods were the focus of a number of papers by Wrangham and colleagues, which explored the impact of these foods on primate diet and social structure (Wrangham et al., 1991, 1996, 1998; Malenky and Wrangham, 1994; Conklin-Brittain et al., 1998). More recently, the concept of fallback foods has been applied in paleoanthropology (Marshall and Wrangham, 2005; Grine et

al., 2006; Dominy et al., 2008; Ungar et al., 2008; Rabenold and Pearson, 2011) and in human ecology (Marlowe and Berbesque, 2009). Similarly, many human ecologists have studied the fallback strategies of horticulturalists and agriculturalists when planted crops fail (Wohlt, 1989; Bardhan, 1996; Nascimento et al., 2012).

Preferred and fallback foods place different adaptive pressures on an animal. Due to the ease with which they are harvested and consumed, preferred foods can often be utilized by animals with a large variety of morphological forms. In contrast, fallback foods, though usually abundant in the environment, are often difficult to access and/or hard to digest and may require specialized adaptations to exploit. Because of this, animals are often specialized not for their preferred foods, but for those fallback foods that they exploit in times of scarcity (Robinson and Wilson, 1998; Lambert et al., 2004; Marshall and Wrangham, 2007).

Kinzey (1978) was one of the first to show that primate dental morphology is shaped not only by species' primary source of nutrients, but also by foods that are less often consumed yet may constitute an important part of the diet. Kinzey studied both feeding behavior and molar morphology in the yellow-handed titi (*Callicebus torquatus*) and dusky titi (*Callicebus moloch*) in Peru. He found that while both species spent the majority of their feeding time on fruits, *Callicebus torquatus* devoted the remainder to feeding on insects while *Callicebus moloch* focused more on leaves. Because both leaves and insects are important sources of protein for titi monkeys, Kinzey (1978) suggested that the different feeding behaviors of these two species would be reflected in differing adaptations of the molars. He found that the molars of *Callicebus moloch* possessed higher shearing crests well adapted for tearing and cutting leaves while *Callicebus torquatus* exhibited larger crushing and grinding surfaces for breaking open the chitinous exoskeletons of insects.

Perhaps the best known example of the evolutionary consequences of fallback food choice on morphology was that observed by Boag and Grant (1981) during a drought on the island of Daphne Major in the Galapagos in 1977. Boag and Grant (1981) observed that low rainfall on Daphne Major during the wet season of 1977 severely decreased the amount of soft, small seeds that Darwin's medium ground finch, *Geospiza fortis*, fed on. However, hard, medium and large-sized seeds, eaten only rarely by *G. fortis* before the drought, survived better during the period of low rainfall. Larger finches with larger beaks were able to subsist on these seeds and thus were able to survive and reproduce better than those finches that were only equipped to eat the now-rare small seeds. Because of this, the *G. fortis* population saw a rapid increase in mean overall size and in size of beak (Boag and Grant, 1981).

The relationship between the physical properties of fallback foods and morphological specialization was further highlighted by Robinson and Wilson's (1998) proposed resolution to Liem's Paradox. Liem's Paradox is based on observations of cichlid fish species in Africa's great lakes. The many different species of cichlids possess a wide variety of morphological features seemingly adapted for feeding on certain types of food resources. These range from adaptations designed for consuming other fish and eggs to morphological features adapted solely to eating scales (Robinson and Wilson, 1998). It was observed, however, that some cichlid species only rarely feed on the foods which their morphology suggests they are adapted to. Instead, they subsist primarily on resources eaten in common with other fish, including algae, zooplankton, and aquatic insects (Liem, 1990). This led Karel Liem (1990), an ichthyologist and evolutionary biologist, to conclude that competition for resources could not be the evolutionary force behind the vast variety in cichlid morphology. Instead he proposed that the ease with which it is possible to consume different items in an aquatic environment, due to the force of

suction, allowed a variety of morphological forms to persist because they were adaptively neutral (Liem, 1990).

Robinson and Wilson (1998) proposed a different solution to Liem's Paradox. They highlighted the fact that, according to Optimal Foraging Theory, animals should prefer foods which are easy to consume while providing high amounts of energy (MacArthur and Pianka, 1966). Since only a limited number of foods have these qualities, the same foods will be exploited by many different species. When these preferred foods are scarce, competition will increase and the cichlids will be forced to move on to less desirable, harder to consume foods. An animal with specialized morphological adaptations will be able to access foods unavailable to other species and will thus have an adaptive advantage during times of scarcity. However, specialized morphologies do not prohibit cichlid species from continuing to exploit preferred resources when available. Thus in this model, species can act as ecological generalists the majority of the time while still exhibiting phenotypical adaptations for dietary specialization (Robinson and Wilson, 1998).

For arboreally adapted primates the net return on fruits is high and thus fruits are preferentially consumed by many different primates in tropical environments. However, during periods of low fruit abundance different species of sympatric primates exploit different fallback foods in order to reduce competition. Lambert et al. (2004) reported that the majority of the diet for two sympatric catarrhine species, gray-cheeked mangabeys (*Lophocebus albigena*) and red-tailed guenons (*Cercopithecus ascanius*), in Western Uganda, consists of soft, ripe fruits. However, the grey-cheeked mangabeys possessed extremely thick dental enamel, which also allowed them to consume hard seeds and bark. Though these resources comprised a relatively small portion of the grey-cheeked mangabeys' diet, they became an important resource during

times when fruits were unavailable. Terborgh (1983) observed that fruits made up the majority of the diet for five sympatric platyrrhine species, and many of the same fruits were consumed by several different primates. However, during the dry season when fruit became scarcer, the different species adopted more specialized diets focusing on a narrower range of resources. For example, *Cebus apella* and *Cebus albifrons* focused to different degrees on palm nuts while the closely related squirrel monkey (*Saimiri sciureus*) concentrated on widely dispersed fig trees and exploited insects more heavily than did the capuchins (Terborgh, 1983).

### Capuchins and Fallback Foods

The capuchin diet consists mainly of fruit and insects (Izawa, 1979; Fragaszy et al., 2004). Though a wide range of fruits are eaten, capuchins prefer soft and pulpy fruits that are consumed by a number of other species of New World monkey (Terborgh, 1983). However, in tropical environments the availability of fruit may be highly seasonal (Terborgh, 1983; Janson, 1985). This can be especially true for arid environments such as the *cerrado* and *caatinga* of South America, which can experience extended periods of drought (Peres, 1994; Fragaszy et al., 2004). During these times primates must adapt by either changing their ranging patterns, turning to alternative sources of nutrition, or a combination of both (Altmann, 2009).

Capuchins exhibit a wide variety of fallback strategies in a range of environments with different climates and differing degrees of seasonality. In a study of wedge-capped capuchins (*Cebus olivaceus*) in Venezuela, capuchins increased their consumption of invertebrates and palm pith during the dry season. Additionally, the dry, hard fruit of *Guazuma tomentos* was available throughout the year but only exploited heavily when other ripe fruits were unavailable (Robinson, 1986). At El Ray National Park in Argentina, *C. albifrons* increases its consumption

of bromeliads during the dry season (Brown and Zunino, 1990). In his study, Terborgh (1983) observed that the nuts, inflorescences, and pith of the palm *Astrocaryum* became a vital resource for brown capuchins (*C. apella*) in Cochu Cashu, Peru, during the dry season. Brown capuchins were the only species able to access these resources, and this allowed them to maintain relatively smaller home ranges compared to other primates in the area, which had to range farther for dispersed resources (Terborgh, 1983). Palm nuts and pith also comprised a significant portion of the diet of brown capuchins at Manu, Argentina, during the dry season (Janson, 1985). Similarly, Peres (1994) observed that during periods of low fruit availability a greater portion of the capuchins' diet consisted of palm nuts as well as seeds of other plants. Here the palm species *Oenocarpus bataua* fruits asynchronously throughout the year and thus provides a source of food throughout the dry season.

According to my hypothesis, tubers replace palm nuts as a fallback food for capuchins in Serra da Capivara. Therefore, it has to be determined if both palm nuts and tubers are consumed as fallbacks. As shown above, many wild populations of tufted capuchins increase the rate at which they feed on palm nuts during the dry season, when preferred foods like ripe fruits and invertebrates are often scarce (Terborgh, 1983; Janson and Boinski, 1992; Peres, 1994). However, the role of palm nuts as a fallback food may vary between capuchin groups depending on climate and degree of seasonality in the environment. Spagnoletti et al. (2012) found that nut-cracking activity by capuchins at Fazenda Boa Vista did not correspond with increases or decreases in the availability of fruit. Nut-cracking became more frequent during periods of high nut availability. It must be noted, however, that the authors also recorded that the availability of fruit did not change significantly with seasonal variations in the climate at this site (Spagnoletti et al., 2012).

Because the consumption of tubers is rare in capuchins, there are fewer examples to draw upon to determine tubers' status as a fallback food. Other primates, such as baboons, commonly exploit tubers and other underground storage organs during times of scarcity (Altmann, 2009).

*C. libidinusus* in the Serra da Capivara National Park consumes the tubers of *Thiloa glaucocarpa* throughout the year. Moura (2004) reported that more structural plant parts, such as pith, tubers, and roots, were eaten during the dry season. In addition, though capuchins engaged in digging consistently throughout the year, overall instances of high-energy foraging, which included digging and any foraging that required the breaking apart of wood, stone, soil or other hard substrates, increased during the dry season (Moura, 2004). Based on the evidence presented, I conclude that, as stated in my hypothesis, both palm nuts in certain arid *cerrado* sites and tubers at the Serra da Capivara National Park act as fallback foods for the respective capuchin populations there. However, more study at a variety of different sites is needed to determine exact relationships between the consumption of palm nuts and tubers and the availability of preferred foods such as fruit and insects.

From the above it is apparent that palm nuts are an important resource for many capuchin populations. Palms are woody, monocot plants with a distinctive crown of leaves. They are widely distributed throughout the tropical regions of the world (Jones, 1995). Water availability is an important factor in the distribution of palm species. Most species are found in warm, humid areas such as rain forests with a marked decrease in palm species' richness in more arid areas (Fernandes, 1994; Balslev et al., 2011). In extremely arid environments palms are only able to grow where the water table is high enough for their roots to access it (Fernandes, 1994; Jones, 1995). A survey conducted by Balslev et al. (2011) found that palm community richness was lower in highly seasonal habitats. This may be due to most palms' inability to become

dormant. Several species of palm are common in the *cerrado*, including species of the genera *Acrocomia*, *Allagoptera*, *Astrocaryum*, *Attalea*, *Butia*, and *Syagrus*. Many of these species have short or subterranean trunks, also known as acaulescent trunks (Henderson et al., 1995). This may be an adaptation to arid and seasonal environments (Balslev et al., 2011). Palms are rare in the *caatinga*, but a few species, including the genera *Syagrus* and *Attalea*, are present (Henderson et al., 1995).

The tufted variety of capuchin, including *C. apella* and *C. libidinosus*, exhibit many specialized morphological features of the teeth and jaws, including large anterior and posterior teeth, thick enamel, a wide and deep mandible, thick mandibular cortical bone, and large chewing muscles. These adaptations allow tufted capuchins to chew hard foods and to bite and tear through tough husks and other materials (Wright, 2005). In a comparison among 37 extant primate species conducted by Kay (1981), *C. apella* had the thickest enamel. In a review of catarhine and platyrrhine dental and mandibular morphology, Kinzey (1974) identified several features of *C. apella* that were associated with hard-object feeding. These included a wide zygomatic arch, deep post-orbital constriction, and a sagittal crest in some specimens. This is the result of a large temporalis muscle, which is set more anteriorly in *C. apella* than in other *Cebus*. In addition, the mandible of *C. apella* exhibits a vertical ascending ramus and high condyles (Kinzey, 1974). Bouvier (1986) described *C. apella* as having a short, wide mandible, with a more robust symphysis compared to *C. capuchinus*, and *C. albifrons*. In a comparative study between the mandibular morphology of *C. apella* and that of *C. capuchinus* Daegling (1992) found that the mandible of *C. apella* had a larger cross section due to hypertrophy of the cortical bone. Daegling (1992) concluded that the increased hypertrophy found in *C. apella* was a developmental response to mechanical stresses produced by biting and chewing hard foods. In

another comparative study of *Cebus* mandibles, Cole (1992) found that *C. apella* had greater relative depth and thickness at the mandibular symphysis and greater thickness at the first molar when compared to *C. albifrons*. This allowed the mandible of *C. apella* to resist greater forces during chewing or tearing of hard and tough foods (Cole, 1992; Daegling, 1992). These differences were present even in very young individuals, suggesting they developed prenatally (Cole, 1992). The above two studies show that adaptations for feeding on hard objects are both innate and develop in response to external forces among tufted capuchins.

Depending on the environment, extremely tough or hard foods may make up only a small portion of a tufted capuchin's diet (Wright et al., 2009). However, specialized dental and mandibular adaptations, combined with unique foraging behaviors, enable tufted capuchins to exploit a large variety of foods, like palm nuts, not accessible to other primates (Izawa, 1979; Terborgh, 1983). Terborgh (1983) noted that *C. apella* was able to feed on *Astrocaryum* nuts much more quickly than was the more gracile *C. albifrons*, which focused more on foraging for insects and highly-dispersed figs during the dry season. The ability to exploit hard-to-access foods has allowed tufted capuchins to inhabit many different environments and become among the widest ranging and most ubiquitous of the New-World monkeys (Fragaszy et al., 2004; Wright, 2005).

In order to test the effects of fallback foraging on morphology, Wright et al. (2009) compared the robusticity of the teeth and jaws in capuchin species to the toughness of foods in their diet. Three species were examined, the gracile *C. olivaceus* and two robust tufted species, *C. apella* and *C. libidinosus*. *C. olivaceus* had the lowest dietary toughness and as expected had the lowest mandibular robusticity. *C. libidinosus* had the toughest foods among its diet which led the authors to predict that it would also show the most robust mandible. However, *C. apella*

exhibited the highest robusticity. The authors concluded that this discrepancy was due to the fact *C. libidinosus* often uses stone tools to crack through hard and tough husks surrounding foods while *C. appella* relies solely on its jaws and teeth. This behavioral adaptation may have thus reduced the selective pressure for a large and robust chewing apparatus in *C. libidinosus* (Wright et al., 2009).

As with morphological adaptations, the use of tools is a behavioral adaptation to access fallback foods among several primate species. In addition to the use of stone tools to access palm nuts among *C. libidinosus*, Moura and Lee (2004) attributed the expanded tool kit of capuchins in the Serra da Capivara National Park to the frequent periods of extended food shortage there. Among other primates, Yamakoshi (1998) observed that many of the fallback foods of the chimpanzees at Bossou could only be exploited through the use of tools. Tools also enable orangutans in Sumatra, to access highly nutritious embedded seeds at times of fruit scarcity (van Schaik and Knott, 2001).

### Capuchin Tool Use

Initially, knowledge of tool use among capuchins was restricted to anecdotal reports and experiments in laboratory settings (Ottoni and Izar, 2008). There have long been anecdotal reports of tool use by *Cebus*. Perhaps the earliest written account of capuchin tool use, reported by Urbani (1998), was by Gonzalo Fernández de Oviedo y Valdés in “Chronicler of the Indies,” published in 1526. Here he describes capuchin monkeys smashing nuts with a stone after observing humans perform the same action. Another early report, summarized by Visalberghi (1990), by Erasmus Darwin in 1794, describes a captive capuchin cracking a nut with a stone. More recently, a wide variety of tool-using behavior has been reported in the literature including

the use of a branch to club a venomous snake (Boinski, 1988), the use of a stick to probe for insects (Chevalier-Skolnikoff, 1990), the use of a piece of oyster shell to crack open another oyster (Fernandes, 1991), and the use of leaves as cups to gather water from wood cavities (Phillips, 1998). *C. apella* has been observed habitually cracking open palm nuts by smashing them against the trunk or branch of a tree (Izawa and Mizuno, 1977; Struhsaker and Leland, 1977). After positioning the palm nut on a branch, the capuchin would strike the nut forcefully against the branch or adjoining tree trunk several times in rapid succession. In one case one nut was used to strike against another (Struhsaker and Leland, 1977). After pounding the nut several times, the monkey would then use its teeth to bite at and tear at any cracks or openings it had made in order to widen them. The capuchin would then strike the palm nut against the surface again, repeating the process until the hard husk of the nut was cracked wide enough to allow access to the sweet liquid or coco within.

Experimental studies showed capuchins capable of using a wide variety of tool-types, including hammers (Visalberghi, 1987; Anderson, 1990; Westergaard and Suomi, 1993), probes (Westergaard and Fragaszy, 1987; Westergaard and Suomi, 1993), sponges made of paper and other materials (Westergaard and Fragaszy, 1987), and digging sticks (Westergaard and Suomi, 1995). In these experiments potential tools were placed with foods that offered a challenge, such as hard-shelled nuts or syrup-filled containers with narrow openings. Once presented with the problem and a tool capable of solving it, individual capuchins learned tool-using behavior after repeated trials. Capuchins showed advanced tool-using behavior in experimental conditions, including tool modification (Westergaard and Fragaszy, 1987; Westergaard and Suomi, 1995), and sequential use of multiple tools for a single objective (Westergaard and Suomi, 1993). In an experiment conducted by Westergaard and Fragaszy (1987), capuchins modified stick probes by

stripping of twigs and leaves, and paper towels by modifying their shape, in order to more easily access syrup or juice present in containers with small openings. Westergaard and Suomi (1995) observed capuchins breaking sticks and stripping off bark and leaves to produce digging sticks. In an example of sequential tool use, capuchins in an experiment by Westergaard and Suomi (1993), first used stones to break open walnuts in an apparatus and then used sticks as probes to pry out the meat contained within the shells. As the use of a particular tool spread throughout a group, juveniles learned the behavior by observing older, more competent tool users (Westergaard and Fragaszy, 1987; Anderson, 1990). Tool use exhibited by capuchin monkeys was often compared to similar behaviors by great apes (Westergaard and Fragaszy, 1987; Westergaard and Suomi, 1993). In addition, Westergaard and Suomi (1995) compared the method capuchins used for the construction and operation of digging sticks to that employed by !Kung hunter-gathers and hypothesized that *Homo habilis* may have produced similar tools.

Early indirect evidence for the use of hammer and anvil stones to crack nuts in the wild was reported near Desterro do Malta in Brazil (Langguth and Alonso, 1997). During a drought the authors observed pitted anvil rocks with palm nut shells on them and stones that exhibited signs of pounding nearby. One of the first direct scientific observations of nut cracking was reported by Ottoni and Mannu (2001) at Tiete Ecological Park in Brazil. Since these initial observations, many more examples of stone tool use have been reported throughout the *cerrado* and *caatinga* environments of central and north-eastern Brazil (Fragaszy et al., 2004; Moura and Lee, 2004; Silva et al., 2005; Waga et al., 2006; see Ottoni and Izar, 2008 for review).

Capuchins crack palm nuts by carefully placing the nut on a large, flat rock, lifting a hammer stone with both arms to roughly the level of their heads, and then forcefully bringing the hammer down upon the nut. During this process the capuchin's long tail is held flat against the

ground for extra stability (Ottoni and Mannu, 2001; Frigaszy et al., 2004). Hammer stones are carefully selected and may be transported long distances, along with palm nuts, to the sites of suitable anvils (Fragaszy et al., 2004; Visalberghi et al., 2007). In an experimental study on wild capuchins, Visalberghi et al. (2009) found that when given the a choice between multiple potential hammer stones, capuchins will consistently choose the most effective tool based on the weight and material of the object. Hammer stones can be quite heavy, sometimes exceeding half the weight of the capuchins themselves (Fragaszy et al., 2004; Visalberghi et al., 2007).

Adult males are the most successful nut crackers and tend to engage in tool-using activities more often than females (Ottoni and Mannu, 2001; Ottoni and Izar, 2008; Moura and Lee, 2010; Spagnoletti et al., 2011). This may be due to the fact that male capuchins are much larger than females. The body mass of males at Fazenda Boa Vista averaged 64 percent larger than that of females (Spagnoletti et al., 2011). This causes them to have higher energy requirements but also allows them to use heavier tools that are more efficient at cracking nuts (Spagnoletti et al., 2011). Alternatively, the high energy cost of tool-use may make it too risky for reproductive females to engage in as frequently as males (Moura and Lee, 2010). Juvenile monkeys begin attempting to crack palm nuts with stones at one year of age but don't become proficient at the technique until three (Ottoni and Izar, 2008). Infants and juveniles show much interest in the nut-cracking activity of others, especially dominant males. Observers are tolerated and are often able to "scrounge" food from successful nut crackers. This may increase the chances for observational learning of tool-using behavior (Ottoni and Mannu, 2001; Ottoni and Izar, 2008).

The majority of tool use reports have been for the tufted capuchin *C. libidinosus*. However, hybridization among many of the semi-free ranging populations where tool use has

been observed as well as experimental studies indicate that variation in tool use between capuchin populations cannot be explained by genetic differences alone (Ottoni and Izar, 2008). Rather, tool use among *C. libidinosus* has been attributed to environmental factors (Visalberghi et al., 2005).

The use of stone tools to crack open encased fruits or nuts has been observed in nearly every tufted capuchin population observed living in arid environments (Ottoni and Izar, 2008). However, *C. libidinosus* in the Serra da Capivara National Park show a much expanded tool-kit, both in the various ways in which they employ stone tools and in the use of sticks as probes. Stones are not only used to crack open fruits and seeds, but also to cut open wood to access insects inside, to pry smaller stones from conglomerate rock, to dig for tubers, and to pound quartz stones into powder. The resulting powder from smashing the quartz rocks is sniffed, licked, and rubbed on the face, body, and hands by the capuchins, though the purpose of this is unknown (Mannu and Ottoni, 2009). In addition, sticks and twigs are used to probe into crevices and access insects, water, and honey (Moura and Lee, 2004; Mannu and Ottoni, 2009).

Though all of these behaviors are of interest to primatologists and anthropologists, the focus of this paper is tuber digging. Digging was the most common type of tool-using activity at Serra da Capivara and was performed consistently throughout the year (Moura, 2004; Moura and Lee, 2010). Moura and Lee (2010) found no significant differences in the overall duration of digging between the wet and dry seasons. However, when the result of digging was a food reward, the duration of digging bouts was significantly greater during the dry season (Moura, 2004; Moura and Lee, 2010).

During tuber digging, a capuchin will typically hold the stone in one hand, hitting the ground in order to loosen it, while scooping soil away with the other hand. After striking the

ground several times, the capuchin may then drop the stone and begin digging with both hands. In another method, the capuchin may hold a stone in both hands while striking the ground rapidly, then release the stone to dig with both hands (Mannu and Ottoni, 2009; Moura and Lee, 2010). In some cases stones were also use as a “hoe” to scoop dirt away (Mannu and Ottoni, 2009).

Males engaged in the majority of all types of tool use, including digging, at Serra da Capivara (Moura, 2004; Moura and Lee, 2010). This concurs with other observations of sex-based differences in capuchin tool use at other sites and in laboratory settings (Ottoni and Mannu, 2001; Ottoni and Izar 2008, Spagnoletti et al., 2011). In Moura and Lee’s (2010) study the alpha male of the focal group had the highest recorded individual instances of tool use, followed by the second-ranking male, who used a tool only half as often. The success rates for tool use at Serra da Capivara were relatively low; only 36.6 percent of overall tool-using events resulted in the acquisition of a food item and 40.8 percent for digging events alone. One hypothesis is that these overall low returns, plus the energy expended in tool use, made tool-using behavior too risky for females and juveniles to engage in regularly (Moura and Lee, 2010). The foraging activities of the adult males, especially the alpha, were of great interest to adult females and juveniles. When the alpha male engaged in tool-using activity, adult females and juveniles were found in closer proximity to him than subordinate males (Moura and Lee, 2010). When males are able to attain a reward from tool-use activity, females and juveniles are often able to “scrounge” some of the food. According to Moura tool use may thus allow dominant males to socially signal paternal ability by providing food to potential mates and offspring, increasing reproductive success (Moura, 2004; Moura and Lee, 2010).

Other primates also dig for and consume underground storage organs, including baboons

(Norton et al., 1987; Altmann, 1998), Japanese macaques (Iguchi and Izawa, 1990), and chimpanzees (Hernandez-Aguilar et al., 2007; Hockings et al., 2010). All of these species are catarrhines, and, similar to the platyrrhine *C. libidinous*, are all fairly terrestrial. However, other than humans and tufted capuchins, the only other primates that have been observed using *tools* to dig underground storage organs has been a population of chimpanzees at Ugalla, Tanzania (Hernandez-Aguilar et al., 2007). Though the actual tool use was not observed, many tuber-digging sites were recorded. The sites were associated with numerous sticks, pieces of bark, and other pieces of wood that had been used as digging tools. Digging tools were identified based on the adherence of dirt on one end and microscopic analysis. Unlike capuchins at Serra da Capivara, the chimpanzees at Ugalla appear to have dug for underground storage organs only during the wet season. One possible explanation for this is that soil at Ugalla may have become too hard and compact to dig through during the dry season but was softened by moisture during the rainy season.

The catalyst for the development of tool-using behaviors among tufted capuchins is debated. Moura and Lee (2004) attributed the expanded tool kit of capuchins in the Serra da Capivara National Park to the frequent periods of extended food shortage there. They concluded that tool use was a means of accessing otherwise inaccessible or hard-to-access resources in ‘energy bottlenecks’ created by periods of food scarcity in a harsh environment. This is termed the necessity hypothesis. This claim was contested by Visalberghi et al. (2005), who stated that it was the degree of terrestriality in some populations of tufted capuchin, and not lack of resources, that encouraged the use of tools. In support of their claim, they cited many capuchin populations which go through energy bottlenecks yet do not exhibit tool use (Fragaszy et al., 2004). They also highlight the fact that many observations of spontaneous tool use have occurred among

captive, semi-free, or provisioned capuchin groups (Moura, 2004; Ottoni and Izar, 2008). They proposed that terrestriality and foraging on the ground increase the opportunities to interact with potential tools and food items together and thus increase the chances of developing tool-using behavior (Visalberghi et al., 2005). This is termed the opportunity hypothesis. In response to this article, Moura (2005) cited studies of capuchins that spend much time on the ground yet do not use tools. DeFler (1979) did not observe any tool use among *Cebus albifrons* in Columbia, though both stone and palm nuts were common and available and the monkeys spent up to 50 percent of their time on the ground. It should be noted though that *C. albifrons* is not one of the species in which the habitual use of stone tools has been observed at other sites. Moura also noted the presence of tool use in non-provisioned populations (Fragaszy et al., 2004). According to my hypothesis, capuchins at Serra Da Capivara dig for tubers because of a scarcity or absence of palm nuts in the area. If this is correct, it may provide support for the necessity hypothesis. The lack of calories and other nutrients provided by palm nuts create an energy bottleneck at Serra da Capivara, which has resulted in an expansion of the capuchin toolkit to include stone digging implements and possibly probes in order to access additional resources.

Two recent studies have tested whether capuchin tool use can be attributed to the necessity hypothesis or the opportunity hypothesis. In an article written by Spagnoletti et al. (2012) the authors studied food availability and tool use among two capuchin populations, one provisioned and one not, over several months in Fazenda Boa Vista, Piaui, Brazil. They found that the availability of fruit did not change significantly in this area from the wet to the dry season. Overall tool use did not vary with season or between the provisioned and non-provisioned group. Males used tools more often in the dry season, which corresponded with greater availability of catule palm nuts. There was no correlation between tool use and any other

food in this study. From this the authors concluded that tool use, specifically nut cracking, was associated with opportunistic exploitation of available foods and not energetic necessity (Spagnoletti et al., 2012).

In a study conducted by Emidio and Ferreira (2012), two capuchin populations living in different habitats within the *caatinga* biome, one wetter and one more arid, were compared. Based on the number of active nut-cracking sites and the mass of discarded shells, the authors found a large increase in nut cracking among the dry-habitat capuchins during the dry season. Nut cracking did not vary significantly between seasons among the wet-habitat capuchins, nor did the different capuchin groups vary between each other during the wet season. The authors determined that this evidence supported the necessity hypothesis for tool use. In contrast, they also found that the energetic gains from nut cracking among the dry-habitat group were low, which would support a more opportunistic feeding strategy. However, palm nuts might also provide important nutrients, such as vitamin C, not otherwise available to capuchins during the dry season (Emidio and Ferreira, 2012). Emidio and Ferreira (2012) used the energetic requirements of adult capuchins in their estimates. However, this does not account for the energetic benefits infant and juvenile capuchins gain by “scrounging” from the nut-cracking activities of adult males. Infant, juvenile, and female capuchins all have lower caloric requirements than the much larger adult males and incur little-to-no energetic cost from consuming palm nuts when scrounging. Thus palm nuts may be an important additional food source for certain demographic groups within a capuchin population and may thus increase fecundity and decrease mortality among the group as a whole.

The above studies test the validity of the necessity hypothesis by seeking to determine if there is a relationship between the frequency of tool use and differences in food availability due

to different environmental factors or seasonal variability. If there is no correlation, then the authors of the above studies assume the evidence supports the opportunity hypothesis, however, the opportunity hypothesis itself is not tested. The opportunity hypothesis states that certain capuchin groups use tools because the large amounts of time they spend on the ground gives them the opportunity to interact with both encased food items and potential tools for their extraction (Visalberghi et al., 2005). However, according to the necessity hypothesis, a high degree of terrestriality would instead be a reflection of the need to exploit encased foods on the ground due to energy bottlenecks (Moura and Lee, 2004). Visalberghi and colleagues (2005) did not show any quantitative correlations between terrestriality and tool use, they simply highlighted the fact that habitual tool use is most often seen in capuchin populations in open woodland or savannah-like environments in the *cerrado* or *caatinga*. However, Moura and Lee (2010) recorded a mean of 22.5 percent of time spent on the ground among capuchins at Serra da Capivara, with significantly more time spent on the ground during the dry season. This would seem to support the necessity hypothesis prediction that terrestriality would be greater during periods of low food availability. To better understand any possible correlations between terrestriality and tool use, it should be determined what proportion of the time spent on the ground by highly terrestrial capuchins is devoted to tool use, and how much time is spent in other types of foraging, moving between arboreal resources, and other activities.

### USOs and Human Evolution

This rare tool-using behavior may have implications for early hominin evolution. Hatley and Kappelman (1980) noted similarities between the postcanine dentition of pigs, bears, and early hominins. These similarities include wide, bunodont molars and premolars. They propose

that the evolution of this dentition in all three mammals is the result of an omnivorous diet with significant portions of underground storage organs such as roots and tubers. The authors further propose that the nonretractable claws in bears, cartilaginous snout and tusks in pigs, and the development of digging sticks in hominins are functionally equivalent adaptations for gathering underground resources (Hatley and Kappelman, 1980). Laden and Wrangham (2005) have proposed that exploiting underground storage organs was a critical step for hominins inhabiting dry, savannah-like environments. The authors note that many of the herbaceous leafy plants exploited by chimpanzees and gorillas as fallback foods are absent in the open and arid environments that australopithecines and early *Homo* inhabited. Early hominins thus had to find an alternative source of nutrition accessible during times of scarcity. Underground storage organs could fill this role nicely as they are relatively abundant, available throughout the year, and provide a good source of carbohydrates and other nutrients. Laden and Wrangham note that the presence of underground storage organs in plants is an adaptation to store nutrients and water during seasonal changes in the environment, and thus is more prevalent in savannah-like environments than in rainforests. As an indicator that underground storage organs were present in early hominin habitats, the authors show that many hominin sites also contain fossils of mole rats, a mammal that specializes in the consumption of underground storage organs. Laden and Wrangham propose that this shift began during the late Miocene, after ancestral hominins split with the last common ancestor with chimpanzees, and allowed hominins to colonize expanding savannah-like environments during the Plio- Pleistocene (Laden and Wrangham, 2005). Like Hatley and Kappelman, Laden and Wrangham (2005) suggest the masticatory adaptations common to australopithecines, including large mandibles, large chewing muscles, large molars and premolars, thick enamel, and wide, flat chewing surfaces, may have been adaptations to

chewing of hard, abrasive underground storage organs. They further suggest that the set of masticatory adaptations seen among robust australopithecines may indicate a greater reliance on underground storage organs as a staple fallback food (Laden and Wrangham, 2005).

I propose that capuchins in Serra da Capivara turned to tubers in an environment where other fallback foods, such as palm nuts, were unavailable. If early hominins did in fact consume underground storage organs as a fallback food, then the capuchins at Serra da Capivara may provide an important analogy to help us understand a vital stage of human evolution.

### Chapter 3: Materials and Methodology

My hypothesis states that capuchins in Serra da Capivara exhibit the behavior of tuber-digging because of an ecological factor, the lack of palm trees. Ecological analysis in bioanthropology was first conducted in the study of human groups (Birdsell, 1953). Focus on the ecological context of primate studies began after World War II. During this time Sherwood Washburn and his students collected much data on the societies of many different species of primate in order to develop comparative studies of human and nonhuman primate behavior and functional anatomy, especially in relation to environmental factors and evolutionary relationships (Washburn and DeVore, 1961). Starting with the work of Crook and Gartlan (1966), systematic classification systems were developed for primate social systems in an ecological context. At the same time, sampling methods became standardized and much emphasis was placed on the rigorous, scientific collection of both behavioral and ecological quantitative data (Altmann, 1974). This allowed for the examination of the evolutionary developments of primates' social systems based on ecological factors, giving rise to the incorporation of sociobiology in primatology (Wilson, 1975; Harcourt, 1998). Sociobiology later led to the study of behavioral ecology, where primate behaviors are viewed as phenotypes, shaped by both genetic and ecological components and adapted to the primate's environment (Krebs and Davies, 1993).

#### Environment

Many sites where *C. libidinosus* have been studied fall within the *cerrado* biome. *Cerrado* is one of the largest environment types in Brazil, second only to Amazonian Forest. At

2 million km<sup>2</sup> the *cerrado* covers 23 percent of the land surface in Brazil (Ratter et al., 1997). *Cerrado* is located mainly in central Brazil, extending to the Amazon forest in the north, the *caatinga* in the northeast, the Atlantic forest in the east, and the states of Sao Paulo and Parana in the south (Bridgewater et al., 2004). The *cerrado* biome is characterized by highly seasonal rainfall, low soil fertility, and a high degree of fire disturbance (Oliveira-Filho and Ratter, 2002). Rainfall averages 800mm-2000mm per year with a pronounced dry season from April to September (Ratter et al., 1997). Typically, *cerrado* soils are basic with low pH values, low magnesium and calcium, and high aluminum (Oliveira-Filho and Ratter, 2002). The *cerrado* has highly diverse vegetation types, including open grassland, bushland with shrubs and small trees, and dense woodland. Deciduous and mixed forests are present in the *cerrado* in areas of higher soil fertility, and bodies of water can host riverine or gallery forest along their banks (Oliveira-Filho and Ratter, 2002). Significant for this study, several species of palms are common in the *cerrado*, ranging 1.5m-2.0m tall (Eiten, 1972).

The Serra da Capivara National Park is located in the *caatinga* dry forest biome. The *caatinga* encompasses much of northeastern Brazil, bounded by the Amazon forest to the west, the Atlantic forest to the east, and the *cerrado* in the south. The average annual rainfall ranges from 240mm to 1500mm with 50 percent of the *caatinga* receiving less than 750mm a year (Leal, 2005). Geologically, the *caatinga* sits over the eroded Proterozoic crystalline basement and the Paleozoic and Mesozoic sedimentary rock basins (Sampaio, 1995). Soil varies considerably between these geologic formations. Crystalline rock soils tend to be rich in clay, shallow, and rocky, while those on sedimentary rock are often sandy and deep. *Caatinga* soils tend to be low in organic material but richer in nutrients compared to *cerrado* soils (Daly and Mitchell, 2000). The *cerrado* terrain is mainly flat, 300-500m in elevation and interrupted by higher mountains

and plateaus. The windward faces of these areas of raised elevation are often moister than the surrounding area, creating microclimates termed brejos (Sampaio, 1995). The variation in soils and climate produce a mosaic of vegetation in the *catingaa*. The most common types of vegetation are trees and spiny shrubs. Vegetation in the *catingaa* is xerophytic, meaning they are adapted to a lack of water in the environment. One of the most common adaptations among woody flora is the loss of leaves during the dry season (Sampaio, 1995).

Serra da Capivara receives an average of 800mm of rain annually, with very high variability in rainfall from year to year. There is dry season from May to mid-October with occasional extended periods of drought. This causes fruit production to be highly seasonal (Moura and Lee, 2004). In addition, Moura (2004) noted that a lower percentage of the flora produce fruit throughout the year compared to other neotropical forests. Moura (2004) describes four different topographical zones in Serra da Capivara; plateaus, cliffs, canyons, and plains. The canyons remain moist even during the dry season, and trees fruit there throughout the year. However cliffs, where capuchins are more abundant, show a marked decrease in fruit production during the dry season (Moura, 2007).

## Flora

In order to test the hypothesis that capuchins in the Serra da Capivara National Park dig for tubers because palm nuts are scarce, the presence or absence of palm tree species reported to be consumed by capuchins must be compared between the Serra da Capivara and other capuchin sites. Both a list of sites where capuchins engaged in habitual tool use (Table 3-1) as well as a list of palm species consumed by capuchins (Table 3-2) were compiled from the literature. Floristic data for each site were then searched for any of the palm species listed. Habitual tool

use in the wild is seen among both *C. libidinosus* and *C. xanthosternos*. Because of this, sites containing both species are considered. In some studies, certain palm nuts had only the genus described and did not give the species name. Because of this, in addition to searching floristic lists for specific species, species of the same genera as those consumed by capuchins were also noted.

**Table 1. Capuchin Nut Cracking and Tuber Digging Sites**

Location	State	Coordinates	References
Arthur Thomas Mun. Park, Londrina	Paraná	23°23'S, 51°08'W	Rocha et al., 1998
Brasilia Nat. Park	Distrito Federal	15°43'S, 47°55'W	Waga et al., 2006
Fazenda Barbados, Contendas do Sincorá	Bahia	13°46'S, 41°10'W	Canale et al., 2009
Fazenda Boa Vista	Piauí	09°39'S, 45°25'W	Fragaszy et al., 2004
Fazenda Dos Matos, Montes Claros	Minas Gerais	16°18'S, 48°53'W	Canale et al., 2009
Fazenda Serra Grande, Varzelândia	Minas Gerais	15°32'S, 43°57'W	Canale et al., 2009
Jaragua State Park	São Paulo	23°27'S, 46°46'W	Silva et al., 2005
Lagoa comprida, Itiúba	Bahia	10°28'S, 39°49'W	Canale et al., 2009
Luis Gomes	Rio Grande do Norte	06°23'S, 38°23'W	Emidio and Ferreira, 2012
Morro do Muquém, Matina	Bahia	13°55'S, 42°48'W	Canale et al., 2009
RPPN Pé de Serra, Ibotirama	Bahia	12°07'S, 43°03'W	Canale et al., 2009
Serra da Capivara	Piauí	08°40'S, 42°32'W	Moura and Lee, 2004
Serra das Ponteiros, Belo Monte	Alagoas	09°39'S, 37°24'W	Canale et al., 2009
Serra do Estreito, Jucurutu	Rio Grande do Norte	06°12'S, 37°02'W	Emidio and Ferreira, 2012
Tiete Ecological Park	São Paulo	23°29'S, 46°31'W	Otoni and Mannu, 2001

<b>Table 2. Palm Species Consumed by Capuchins</b>	
<b>Species</b>	<b>Reference</b>
<i>Syagrus romanzoffiana</i>	Otoni and Mannu, 2001
	Rocha et al., 1998
<i>Astrocaryum sp.</i>	Fragaszy et al., 2004
<i>Attalea sp.</i>	Canale et al., 2009
	Fragaszy et al., 2004
	Visalberghi et al., 2008
<i>Acrocomia aculeata</i>	Waga, 2006
<i>Syagrus coronata</i>	Canale et al., 2009
	Canale et al., 2009
	Canale et al., 2009
<i>Attalea seabrensis</i>	Canale et al., 2009
<i>Syagrus oleracea</i>	Canale et al., 2009
	Canale et al., 2009
	Langguth and Alonso, 1997
<i>Astrocaryum campestre</i>	Visalberghi et al., 2008
<i>Attalea barreirensis</i>	Visalberghi et al., 2008

The method in which the floristic surveys were conducted varied with each study. Most commonly several plots of uniform size in an area were chosen at random and all of the woody species within were recorded. However, the number and size of plots depended on the study. Most surveys also included or excluded specimens based on limitations in size and basal circumference (Felfili and Silva, 1993; Ratter et al., 2003). Though the surveys vary slightly in method, Ratter and colleagues (2003) concluded that the various floristic lists provided a reasonable base for comparison. To ensure that the floristic composition of each capuchin site is adequately represented, multiple surveys from an area were used where possible (see Table 3-2).

## Sites

Of the sites where capuchin tool use has been observed, four, including the Serra da Capivara National Park, also had corresponding floristic data appropriate for this study. In total this represents data gathered from 18 floristic surveys. Two of these sites are attributed to the *cerrado* biome, one is attributed to the *caatinga*, and one is Atlantic semi-deciduous forest. One site is inhabited by *C. xanthosternos*, two contain *C. libidinosus*, and one has the species listed as *C. apella*. The sites are listed on Table 3-3.

**Table 3. Site Location, Biome, and Capuchin Species Data**

Site name	Location	Biome	<i>Cebus</i> Species	References
Arthur Thomas Mun. Park	23°15'-23°30'S, 51°00'-51°15'W	Atlantic semi-deciduous forest	<i>C. apella</i> *	Soares-Silva and Barroso, 1992; Soares-Silva et al., 2001; Bianchini et al., 2003; Cotarelli et al., 2008;
Brasilia Nat. Park	15° 43'S, 47° 55'W	<i>Cerrado</i>	<i>C. libidinosus</i>	Pereira et al., 1985; Ramos, 1989, 1994, 1995; Felfili 1990, 1993; Felfili and Silva Junior, 1993
Montes Claros	16°18'S, 48°53'W	<i>Cerrado</i>	<i>C. xanthosternos</i>	Soares-Silva et al., 2001; Araújo, 1994; Brandão et al., 1995
Serra da Capivara	8°26'–8°54'S, 42° 19'–42°45 W	<i>Catingaa</i>	<i>C. libidinosus</i>	Empaire, 1987; Lemos and Rodal, 2002; Lemos, 2004; Moura, 2004

\* This may refer to *C. libidinosus* or another tufted species, as until fairly recently, all tufted capuchins were considered sub-species of *C. apella*.

## Nutritional Value

To understand if underground storage organs can act as replacements for palm nuts as a fallback food in the capuchin diet, it is also necessary to examine the nutritional value of these

foods. From the literature, the percentages of protein, lipids, and total carbohydrates, including fiber, were obtained for five species of palm nut consumed by capuchins (Crepaldi et al., 2001; Coimbra and Jorge, 2011; Nascimento et al., 2011). The nutritional value of *Thiloa glaucocarpa*, the species of tuber consumed by capuchins at Serra da Capivara, has not been found. Instead, the values of several varieties of roots and tubers used during times of famine by human populations living in the *caatinga* were used for comparison (Nascimento et al., 2012). Nutritional values are listed on Table 3-4. The results of these comparisons are considered in the next chapter.

**Table 4. Nutritional Value of Palm Nuts and Underground Storage Organs (USOs)**

<b>Palm Nut Species</b>	<b>Moisture (%)</b>	<b>Protein (%)</b>	<b>Ash (%)</b>	<b>Lipids (%)</b>	<b>Total Carbs (%)</b>
<i>Syagrus romanzoffiana</i>	3.94	23.98	1.72	56.37	14
<i>Acrocomia aculeata</i>	4.97	28.61	2.08	46.06	18.3
<i>Syagrus coronata</i>	28.6	11.5	1.2	49.2	9.7
<i>Syagrus oleracea</i>	4.83	15.46	1.52	45.17	33.06
<i>Syagrus cearensis</i>	2.96	8.95	1.75	69.33	17.01
<b>USO Species</b>					
<i>Dioscorea coronata</i>	81.3	0.9	0.7	0.3	16.8
<i>Mandevilla tenuifolia</i>	85	0.7	0.5	1.1	12.7
<i>Manihot dichotoma Ule</i>	73.6	0.1	0.8	0.4	24.2
<i>Manihot glaziovii</i>	79.6	1.01	0.8	0.2	18.3

Chapter 4: Results

Palm Tree Data

This paper tests the hypothesis that capuchin monkeys in the Serra da Capivara dig for and consume underground storage organs because palm nuts, an important fallback food at other capuchin sites, are absent or very rare in the *caatinga* environment that these monkeys inhabit. These underground storage organs were hypothesized to replace palm nuts as a fallback food in the capuchin diet. Three palm species cracked and consumed by capuchins were recorded among the study sites with sufficient floristic data available. These include *Syagrus romanzoffiana*, *Acrocomia aculeate*, and *Syagrus oleracea*. In addition, two other species belonging to genera consumed by capuchins are present, *Attalea speciosa*, and *Syagrus comosa*. (Table 4-1).

**Table 5. Presence of Palm Species Consumed by the Capuchins Studied**

Site name	Palm Species Consumed by <i>Cebus</i>	Other Palm Species
Arthur Thomas Mun. Park	<i>Syagrus romanzoffiana</i>	<i>None reported</i>
Brasilia Nat. Park	<i>Acrocomia aculeate</i> , <i>Syagrus oleracea</i>	<i>Attalea speciosa</i>
Montes Claros	<i>Acrocomia aculeate</i>	<i>Syagrus comosa</i>
Serra da Capivara	<i>None</i>	<i>None reported</i>

Consistent with my hypothesis, none of the four floristic surveys conducted in the Serra da Capivara show any of the palm species reported to be consumed by *C. libidinosus* or *C. xanthosternos*, as shown in Table 4-1.

## Nutritional Value

In order for underground storage organs to act as a replacement fallback food for palm nuts, capuchins must be able to derive comparable nutritional value from both. The nutritional values of several species of palm nut consumed by capuchins as well as several species of plant underground storage organs are listed in Table 5-2. In palm nuts, protein values range from 8.95 percent in *Syagrus cearensis* to 28.61 percent in *Syagrus coronate*. In underground storage organs protein ranges from 0.10 percent in *Manihot dichotoma* to 1.01 percent in *Manihot glaziovii*. Lipids ranged from 45.17 percent (*Syagrus oleracea*) to 69.33 percent (*Syagrus cearensis*) in palm nuts and 0.20 percent (*Manihot glaziovii*) to 1.10 percent (*Mandevilla tenuifolia*) among underground storage organs. Carbohydrates, including fiber, ranged from 9.70 percent (*Syagrus coronate*) to 33.06 percent (*Syagrus oleracea*) in palm nuts and from 12.70 percent (*Mandevilla tenuifolia*) to 24.20 percent (*Manihot dichotoma*). Where given (Nascimento et al., 2011; 2012), total caloric content (TCC) was taken from the literature. When not given (Crepaldi et al., 2001; Coimbra and Jorge, 2011), TCC was calculated using the total protein, lipids, and total carbohydrates following the Atwater System (Merrill and Watt, 1973). This ranges from 527.30kcal/100g (*Syagrus coronata*) to 727.81kcal/100g (*Syagrus cearensis*) in palm nuts and from 63.2kcal/100g (*Mandevilla tenuifolia*) to 104.2kcal/100g (*Manihot dichotoma*) in underground storage organs (See Table 4-2).

**Table 6. Total Caloric Content of (TTC) Palm Nuts and USOs**

Species	Plant Organ	TCC (kcal/100g)
<i>Syagrus romanzoffiana</i>	Nut (Palm)	659.25
<i>Acrocomia aculeata</i>	Nut (Palm)	602.18
<i>Syagrus coronata</i>	Nut (Palm)	527.3
<i>Syagrus oleracea</i>	Nut (Palm)	600.584
<i>Syagrus cearensis</i>	Nut (Palm)	727.81
<i>Dioscorea coronata</i>	OSU (Tuber)	73.6
<i>Mandevilla tenuifolia</i>	OSU (Tuber)	63.2
<i>Manihot dichotoma Ule</i>	OSU (Root)	104.2
<i>Manihot glaziovii</i>	OSU (Root)	79.5

#### Palm Nuts and Tubers as Fallback Foods

The above shows that 1) palm species consumed by capuchins at many sites are absent in Serra da Capivara; 2) tubers have a nutritional value that is comparable to that of palm nuts; and 3) both palm nuts and tubers are consumed as fallback foods by capuchins. This supports my hypothesis that tubers are consumed by capuchins at the Serra da Capivara National Park as a replacement fallback food because the palm nuts consumed by other capuchin populations as a fallback food are rare or absent there.

## Chapter 5: Discussion and Conclusion

### Discussion

According to the TreeAtlas database, a large database containing biogeographical and environmental information on tropical and subtropical environments throughout South America, the *cerrado* contains 41 different species of palms, while the *caatinga* contains only 11 (Oliveira-Filho, 2010). This indicates that the *caatinga* contains a lesser overall diversity in palm species than does the *cerrado*. Palm species commonly consumed by tufted capuchins are absent in floristic surveys of the Serra da Capivara National Park, where capuchins routinely use tools to extract tubers from the ground (Moura, 2004). Moura (2004) found a total of only three palm trees over 5,000 ha of the park. These trees were of the genus *Copernicia*, which has not been reported to be consumed by capuchins. Thus, consistent with my hypothesis, palm nuts are extremely scarce at the Serra da Capivara, prompting capuchins there to seek alternative sources of fallback foods.

At first glance, the high amounts of protein and lipids found in palm nuts as well as the overall higher amounts of energy they contain might make them appear to be the superior resource when compared to underground storage organs. However, several other factors must be taken into account. First, the numbers given for caloric value are approximate values. When calculating the caloric value of a food, it is important to distinguish between carbohydrates and fiber from the total amount of carbohydrates. This is because fiber varies in its ability to be digested by organisms, thus may provide lower amounts of energy. However, because not all of the literature distinguished fiber from other carbohydrates, it was necessary to use the value of

total carbohydrates for comparison. Though the amount of fiber was not recorded for any of the underground storage organs, where it was recorded for palm nuts, fiber comprised large portions of their total carbohydrates (Coimbra and Jorge, 2011).

Another consideration is the “package” foods come in. Underground storage organs may be larger than a palm nut, and, once taken out of the ground, do not require a hard shell to be breached in order to access them. For instance, the nut of *Syagrus cearensis* consists of 5g of kernel surrounded by 7g of hard shell, compared to a *Thiloa glaucocarpa* tuber weighing an average of 13.9g and lacking mechanical defenses. Another factor is the energy expenditure required to access a certain food. Emidio and Ferreira (2012) calculated that individual capuchins spent on average of 17 calories per month in the dry season and 25 calories in the wet season cracking *Syagrus cearensis* nuts in Jucurutu, a capuchin site in a shrub-arboreal *caatinga* environment. Individual capuchins gained 821 and 1,175 calories from *Syagrus cearensis* nuts during the dry and wet seasons respectively. The energetics of digging have not been calculated, however, digging stones used in Serra da Capivara, weigh much less, 165.1g on average, than the stones used to crack nuts at Jucurutu, which weigh an average of 612 grams (Moura, 2004; Emidio and Ferreira, 2012). Hammer stones at other capuchins sites can be even heavier, with an average 1,460 grams at Fazenda Boa Vista (Lui et al., 2009). This shows that, consistent with my hypothesis, tubers have nutritional value comparable to that of palm nuts and may fulfill a similar role as a fallback food at Serra da Capivara as palm nuts do in other capuchin populations.

The findings of this paper appear to support the necessity hypothesis for the cause of tool use among capuchins. The absence of palm nuts at Serra da Capivara created a nutritional bottleneck that initiated an expansion in the capuchin tool-kit in order to exploit tubers and other

additional resources. However, proponents of the opportunity hypothesis might argue that the unique tool-using behaviors found at Serra da Capivara are simply a matter of the potential tools and resources available there, and not an increased need for additional food sources. Instead of hammer stones and palm nuts, the capuchins at Serra da Capivara come in contact with tubers and stones suitable for digging. There is little data pertaining to the distribution of USOs at capuchin sites. None of the floristic surveys of nut-cracking sites examined in this paper list *Thiloa glaucocarpa* among the species found there. However, USOs are usually abundant in dry, savannah-like environments such as the *cerrado* where most instances of capuchin palm-nut cracking have been observed (Dominy et al., 2008). Therefore it is likely that sites where capuchins consume palm nuts also contain some edible USOs. Because the motions for both nut-cracking and tuber-digging are similar (Fragaszy et al., 2004; Mannu and Ottoni, 2009; Moura and Lee, 2010; Ottoni and Mannu, 2001) it seems that capuchins at nut-cracking sites have the opportunity to dig for tubers, but do not. Few capuchin studies record the consumption of USOs, but for sites where the consumption of both OSUs and palm nuts have been observed, roots and tubers are eaten much less frequently than palm nuts and other hard fruits and seeds (Galetti and Fernando, 1994; Robinson, 1986). Thus the absence of palm nuts at Serra da Capivara may have caused capuchins there to expand their tool-kit in order to exploit a more abundant, and perhaps less desirable, fallback food.

Palm nuts are high in protein and lipids, in addition to other nutrients, and their absence at Serra da Capivara may affect the distribution of capuchins there. Capuchins are most prevalent on the cliff habitats within the park, even though there is more fruit available within the canyons, and many trees within the canyons continue to fruit through the dry season. However, according to surveys conducted by Moura (2004) the cliffs are more abundant in invertebrate

resources than the canyons. The cliffs are also rich in *Thiloa glaucocarpa*. Capuchins obtain most of their protein requirements through the consumption of insects and other invertebrates, but tufted capuchins often gain much protein through plant tissues as well (Terborgh, 1983; Janson and Boinski, 1992). The lack of protein from plant resources such as palm nuts and piths may cause capuchins at Serra da Capivara to live in the cliff habitats in order to exploit the greater invertebrate resources there. However, seasonal dips in the availability of fruit may make underground storage organs like *Thiloa glaucocarpa* an alternative source of carbohydrates. The question of the necessity hypothesis vs. the opportunity hypothesis may be somewhat of a ‘chicken or the egg’ problem. A species with sufficient intelligence, manual dexterity, and flexible foraging habits may develop tool use opportunistically in certain environments. The new resources made available through tool use may then allow the species to expand into new environments that could otherwise not sustain it. Energy bottlenecks and other challenges present in these environments may increase selective pressures to develop new tools, which would allow expansion into new areas and so on. This ratchet effect may partially explain why tufted capuchins have been able to spread across such a vast area and into so many different environments. It may also give insight into the development of tool use, increased cognitive abilities, and geographical spread of hominins.

In recent years, studies of the dental microwear have changed views on hominin diet. The thick enamel, wide molars, and large, thick jaws of australopithecines, especially robust australopithecines, has long been seen as indicators of a diet specializing in hard, brittle foods (Kay, 1981; Grine and Kay, 1988; Teaford and Ungar, 2000; Lambert et al., 2004). However, microwear analysis of early hominin dentition revealed that none of the gracile or robust australopithecines exhibit the extreme pitting or complexity of dental enamel shown in hard-

object feeders (Ungar and Sponheimer, 2011). South African *Australopithecus africanus* and *A. robustus* show more complexity and more pitting than their East African gracile and robust counterparts, indicating they had diets consisting of more hard foods (Grine and Kay, 1988; Scott et al., 2005; Ungar and Sponheimer, 2011). However, there is much variability and overlap in dental microwear patterns within early South African hominins, indicating variability in diet (Scott et al., 2005). East African hominins, such as *A. anamensis*, *A. afarensis*, and *A. boisei*, show low pitting and complexity in tooth enamel (Grine et al., 2006; Ungar et al., 2008; 2010; 2011). In addition, they show very consistent microwear patterns across species and throughout time, which may indicate a similarity in diet across time and taxa (Grine et al., 2006; Ungar and Sponheimer, 2011). Like australopithecines, the cranial and mandibular features of tufted capuchins have been considered adaptations to consuming hard foods. However, tufted capuchins eat a wide variety of foods including many tough and/or abrasive plant materials such as pith, bromeliads, and underground storage organs. Examining the dental microwear patterns of capuchins with known diets may provide greater insight into australopithecine dietary variability.

Stable isotope analysis has also provided insight into hominin diet. By comparing the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  in bone or enamel, it can be determined if an organism ate plants, or other organisms which ate plants, utilizing the  $\text{C}_3$  or  $\text{C}_4$  photosynthetic pathway. *A. boisei* exhibits a diet consisting of 75-80 percent  $\text{C}_4$  foods, which include many tropical grasses and sedges. This proportion is similar to extant grazers in tropical climates (Cerling et al., 2011). However, *A. boisei* does not exhibit a dentition with high shearing crests common in other organisms that consume tough foods like grasses. In order to explain this apparent contradiction, some scholars have proposed that *A. boisei* relied heavily on the pith and/or rhizomes of wetland sedges like

papyrus (Wrangham et al., 2009; Rabenold and Pearson, 2011). In an examination of mechanical properties of underground storage organs, Dominy et al. (2008) postulated that the rhizomes of underwater plants could have caused some of the microwear patterns seen in early hominin dentition. Macho (2014) determined through a comparative study of baboon diet that *A. boisei* could derive a large portion of its nutritional requirements through the consumption of the corms of C<sub>4</sub> grasses and that feeding on corms is consistent with *A. boisei* morphology and dental microwear patterns.

Shallow water wetlands contain abundant amounts of plants with underground storage organs throughout the year. Baboons exploit underground storage organs in the Okavango delta during periods of low fruit availability (Wrangham et al., 2009). As evidence that early hominins may have used these habitats, Wrangham and colleagues (2009) gave examples of many early hominin sites shown through paleoenvironmental data to be near areas with shallow water. Some scholars even suggest bipedalism evolved as an adaptation for wading and harvesting underground storage organs, or other resources, in shallow water (Jolly, 1970, Ellis, 1993; Niemitz, 2002; Verhaegen et al., 2002; Kingdon, 2003). Capuchins at Serra da Capivara primarily inhabit the cliff habitat within the park. This is likely due to the complex relationship of the availability of fruit, invertebrates, and tubers in this location. These same considerations would have affected early hominid's choice of habitat. Similar to capuchins, underground storage organs may have been an important fallback resource when early hominids began to colonize new, harsher environments.

Like capuchins, early hominins may have used tools to provide better access to underground storage organs. The capuchins at Serra da Capivara use unmodified stones as hammers to loosen the soil above tubers and allow easier digging with their hands. Chimpanzees

(Hernandez-Aguilar et al., 2007) and modern hunter-gatherers (Marlowe and Berbesque, 2009) both use pieces of wood or wooden digging sticks. Additionally, capuchins have created wooden digging tools during experimental studies in captivity (Westergaard and Suomi, 1995). It seems likely then that australopithecines were capable of using wood and other organic materials as digging implements, however, such tools are unlikely to survive in archaeological contexts. Bone tools, however, are more likely to be found in archaeological sites. One of the earliest claims for bone tool use among early hominins was Dart's proposed "Osteodontokeratic culture" at Makapansgat and other South African sites (Dart, 1949, 1957). According to Dart, the faunal assemblage at Makapansgat provided evidence that *A. africanus* made and hunted with bone tools (Dart, 1949). Though Dart mainly focused on hunting among *A. africanus*, digging was also mentioned as a possible use for some bone tools (Dart, 1960, 1962). However, later authors showed that features of the Makapansgat bones which Dart ascribed to intentional modifications made by *A. africanus* were actually the result of natural taphonomic processes (Klein, 1975; Shipman and Phillips, 1976; Brain, 1981; Maguire et al., 1980).

Brain and Shipman (2003) analyzed the wear patterns on a collection of proposed bone tools from Swartkrans and Sterkfontein in South Africa dating between 1.8 million and 1.1 million years ago. The study showed that markings on the rounded tips of these bones were caused by wear from their use as tools and not simply taphonomic processes. This led Brain and Shipman to conclude that these bones were used as digging sticks due to the lack of trees in the area (Brain and Shipman, 2003; Shipman, 2001). Reanalysis of the material done by Backwell and d'Errico (2001) compared the wear-use patterns of the bones from Swartkrans and Sterkfontein to bones weathered by known taphonomic processes as well as experimentally produced bone tools used in a variety of task. The comparative analysis confirmed that the

Swartkrans and Sterkfontein bones were used as tools. However, instead of being used to unearth tubers as proposed by Brain and Shipman (2004), the wear patterns of these bones most closely resembled the experimental bone tools used to dig into termite mounds (Backwell and d'Errico, 2001). In Sterkfontein bone tools are found in members 1-3. Both the remains of *A. robustus* and *H. erectus* have been found in members 1 and 2, but only *A. robustus* is present in member 3. This may indicate that *A. robustus* is the hominin responsible for the creation and use of the bone tools. This suggested to Backwell and d'Errico (2001) that termites were an important part in the diet of *A. robustus* and may be the cause of the relatively high level of C<sub>4</sub> foods indicated by stable isotope analysis (Lee-Thorp et al., 1994). It seems that *A. robustus* and perhaps other robust australopithecines were capable of forming and using tools for the digging of underground resources, however more data is required to determine if these tools were used to access underground storage organs. However, no matter what resources were exploited, the use of tools may have allowed early hominins to spread across new environments, and, like capuchins in the Serra da Capivara, these new environments may have then caused expansion in their tool-kits. Some researchers argue the Acheulean tool industry allowed *Homo erectus* to exploit USOs and this resource in turn allowed them to spread out of Africa (O'Connell et al., 1999).

### Conclusion

The capuchins at the Serra da Capivara National Park are well adapted to the harsh and highly seasonal environment that they inhabit. Some of these adaptations may include an expanded tool kit and the exploitation of underground tubers. Tubers are most likely used as a fallback food, much like the palm nuts exploited prevalently in other tufted capuchin habitats. In

this way the capuchins in the Serra da Capivara may face similar adaptive challenges to those of early hominins venturing out into open, arid, and variable environments. However, caution must be taken not to focus too highly on any one resource when studying hominin diet and ecology. Tufted capuchins live in a vast range of habitats, ranging from tropical range forest to savannah and dry woodland. Though tufted capuchins exhibit a similarity in morphological traits, they show much variability in diet, especially in the types of fallback foods they utilize and the degree to which they rely on them. Based upon the growing amount of information we have on hominin dental microwear and stable isotope composition, it seems that they also exhibited much dietary variability across time and geographic location.

Capuchins are highly intelligent primates that have employed a large variety of advanced behaviors, including tool use, to adapt to and thrive in a vast range of different, challenging environments. In this way I believe they provide an important analogue to early hominin evolution. This paper demonstrates that palm trees are nearly absent at the Serra da Capivara National Park, and no species recorded to be consumed by capuchins are present there. Palm nuts may provide significant nutritional benefits to capuchins and are an important part of the diet for many *C. libidinosus* and other tufted capuchin groups living in arid environments. This supports my hypothesis that tubers are consumed by capuchins at the Serra da Capivara National Park as a replacement for palm nuts as a fallback food.

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