

Prehensile Tail Use during Feeding and Foraging of White-faced capuchins, *Cebus capucinus*

A Senior Honors Thesis

Presented in Partial Fulfillment of the Requirements for graduation *with distinction* in Anthropology in the undergraduate colleges of The Ohio State University

by

Ryan Covey

The Ohio State University  
November 2005

Project Advisor: Professor W. Scott McGraw, Department of Anthropology

## **ABSTRACT**

The prehensile tail appears to have evolved at least twice in New World Monkeys, once in Atelines (*Alouatta*, *Ateles*, *Lagothrix*, *Brachyteles*) and once in the genus *Cebus*. Compared to that of Atelines, the prehensile tail in *Cebus* is shorter, fully haired, lacks specialized tactile receptors, and differs in the extent of dorsal and ventral muscle bundle development. Given these morphological differences, it is plausible that the functional roles of prehensile tails differ in these platyrrhine clades. The prehensile tail has been studied extensively in several Ateline species, however little information exists on how members of *Cebus* use this specialized appendage.

In order to address this question, I examined the positional behavior, activity budget, foraging strategies and associated tail use of white-faced capuchins *Cebus capucinus* for three weeks at the La Suerte Biological Field Station in Northeast Costa Rica. I used an instantaneous focal animal sampling method to specifically examine the role the prehensile tail plays during feeding and foraging in a group of 15 habituated individuals.

At La Suerte, white-faced capuchins use their prehensile tail 20.87% of the total observation time. Prehensile tail use occurred during 42.02% of all feeding observations and 28.79% of all foraging observations. The capuchins fed and foraged for insects 51% of the time and fruit 43% of the time. Prehensile tail use occurred more during insect feeding and foraging, occurring 37.5% of the time. The prehensile tail was used during 33.64% of all fruit feeding and foraging observations.

The factors responsible for the parallel development of the prehensile tail in *Cebus* species as well as Atelines are not completely understood. My data support the

argument that *Cebus* evolved a prehensile tail to aid during feeding and foraging since tail grasping was rarely observed during travel. My associated feeding data support Cant's (1977) argument that the prehensile tail evolved as a means to better exploit a frugivorous diet on terminal branches. These findings contrast with data for most Atelines where tail use occurs in similar frequencies during both feeding and traveling. More research is needed to fully understand the function of the prehensile tail in *Cebus capucinus* as well as within the entire *Cebus* genus. Once we understand the role the tail plays in their lives, we can more accurately hypothesize about the evolution of the prehensile tail.

## **INTRODUCTION & BACKGROUND**

Prehensile or grasping tails are specialized appendages that act as a fifth limb enabling an animal to suspend itself below a branch while the tail independently supports the full body weight (Garber and Rehg, 1999). The tail may also be used in conjunction with one or more limbs to suspend the body below a support (Bergeson, 1996). The tail is also used to maintain balance in the trees (Bergeson, 1996; Garber and Rehg, 1999). Figure 1 gives examples of different tail uses in arboreal monkeys.

A grasping tail has evolved independently in at least six distinct mammalian lineages as a solution to a variety of problems faced by animals exploiting an arboreal environment (Garber and Rehg, 1999). The platyrrhine species that possess a prehensile tail use it primarily to assist in feeding behaviors and as an additional support during travel (Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cant, 1986; Lemelin, 1995; Garber and Rehg, 1999).

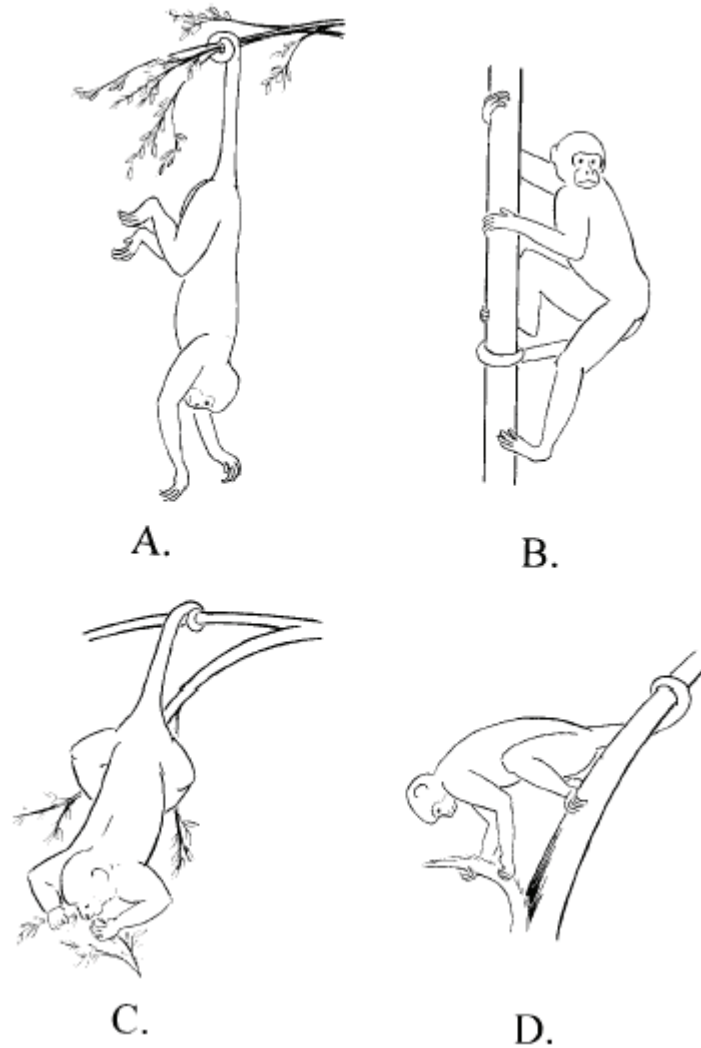


Fig. 1 – Prehensile tail uses by *Cebus capucinus* **A)** Full suspension by prehensile tail; **B)** Wrapping of tail to aid in climbing ; **C)** Tail-assisted use with hindlimbs to bear some body weight, but not all; **D)** Tail used to support body weight in this horizontal tripod position, usually seen during feeding or foraging (Garber and Rehg, 1999).

Several explanations for the evolution of a prehensile tail in platyrrhines have been put forth, including as an adaptation to increased body size (Napier, 1967; Grand, 1972), as a means to better exploit a frugivorous diet (Cant, 1977), to reduce distance and time traveling between feeding patches (Cant, 1986), as a means to enhance the ability to feed in terminal branches (Grand, 1972, 1984; Bergeson, 1996), and to utilize fragile

forest structures (Emmons and Gentry, 1983). It is likely that a combination of factors is responsible for the evolution of prehensile tails since none of these ideas is unique to either Atelines or *Cebus* species (Meldrum, 1998).

A small number of New World monkey possess a prehensile or grasping tail (Garber and Rehg, 1999). Both genetic and anatomical evidence indicates that this specialized appendage has evolved at least twice in these taxa (Rosenberger, 1983; Lemelin, 1995): once in the common ancestor of Atelines (*Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*) and again in the ancestor of all capuchins (*Cebus* species) (Garber and Rehg, 1999). Molecular and paleontological data indicate that Atelines and *Cebus* species last shared a common ancestor approximately 20 million years ago (Schneider and Rosenberger, 1996; Garber and Rehg, 1999). This indicates that the co-occurrence of the prehensile tail in *Cebus* species and Atelines is the product of parallel evolution rather than inheritance from a common ancestor (Rosenberger, 1983; Garber and Rehg, 1999). Lockwood (1999) notes that *Cebus* species are of a similar body mass to Atelines, and their morphology and positional behavior parallel them more than any other platyrrhine.

### **The Anatomy of Prehensile Tails**

In both *Cebus* and Atelines, prehensile tails are characterized by more caudal vertebrae than nonprehensile tails and each caudal element appears to be, on average, shorter relative to overall tail length (Schmitt et al., 2005). This allows for an increased range of flexion and extension in the tail (Schmitt et al., 2005). Prehensile-tailed Atelines also have relatively wider transverse processes on the more distal caudal vertebrae than nonprehensile-tailed species which may reflect the larger loads placed on the tail and the

enhanced tail musculature (Lemelin, 1995; Meldrum, 1998; Schmitt et al., 2005). The Ateline tail is relatively long, possesses a bare area on the distal part of its ventral surface covered with dermatoglyphs, is richly innervated with Meissner's corpuscles, and is characterized by a well developed set of muscles associated with caudal flexion and tail extension (Lemelin, 1995; Garber and Rehg, 1999). In comparison, the prehensile tail of *Cebus* species differs in that it is relatively short, fully haired, lacks specialized tactile receptors, and differs from Atelines in the degree of development of the dorsal and ventral muscle bundles in the tail, and the origin of the transverse processes of the lumbar vertebrae (Bergeson, 1996; Garber and Rehg, 1999).

The tail in *Cebus* shares a few similar traits to the tail morphology in Atelines, while differing from the tails of most other primates (Lemelin, 1995). The tail of *Cebus* has an increased size of the ventral relative to the dorsal muscle mass (Grand, 1977), a smaller number of caudal vertebrae crossed by tendons of the flexor muscles (Lemelin, 1995), caudal vertebrae with wide neural arches, and relatively wide transverse processes in the dorsal region of the tail (German, 1982). Although the differences in capuchin and Ateline tail morphology are well documented, it is not clear whether these two primate groups use their tail in similar fashions (Garber and Rehg, 1999). My study will give a better understanding of the prehensile tail of *Cebus* species, and determine if it fulfills similar ecological roles with the Atelines. Due to the small sample size, I cannot statistically compare my data with other studies on capuchins and Atelines. I am able to make biological suggestions from my data and compare them with the trends found in other studies.

## Capuchin Monkeys

Groves (2001) recognizes eight species of *Cebus*: *C. capucinus*, *C. albifrons*, *C. olivaceus*, *C. kaapori*, *C. apella*, *C. libidinosus*, *C. xathosternos*, and *C. nigrinus*. With the possible exception of *Alouatta*, capuchins likely have the widest geographical distribution of any Neotropical primate genus (Fragaszy et al., 1990). The distribution of *Cebus capucinus* is shown in Fig. 2. Capuchins are found in every type of Neotropical forest, including humid and dry tropical forests, swamp forests, seasonally flooded forests, mangrove forests, gallery forests, and dry deciduous forests where rainfall is absent for 5-6 months a year (Freese and Oppenheimer, 1981; Fragaszy et al., 2004). Their success depends on their flexibility, adaptability, and opportunism (Fragaszy et al., 2004).

*Cebus capucinus* or white-faced capuchins are a sexually dimorphic species. Males are up to 25-35% larger than females and possess larger shoulders, heavier jaws, and longer canines (Oppenheimer, 1968; Fedigan, 1990; Rose, 1994; Fragaszy et al., 2004). White-faced capuchins are a robustly built, small to mid-sized primate, with an average weight of 3.87 kg for males and 2.67 kg for females (Ford and Davis, 1992; Fragaszy et al., 2004). White-faced capuchins live in multimale, multifemale groups of 6 to 35 individuals where the alpha male is dominant over the group (Fedigan et al., 1985; Massey, 1987; Robinson and Janson, 1987; Rose, 1994; Sussman, 2003). Males migrate out of their natal group and females are philopatric (Perry et al., 2003). Like many other New World primates, they are arboreal quadrupeds (Fleagle and Mittermeier, 1980; Gebo, 1992; Johnson and Shapiro, 1998).

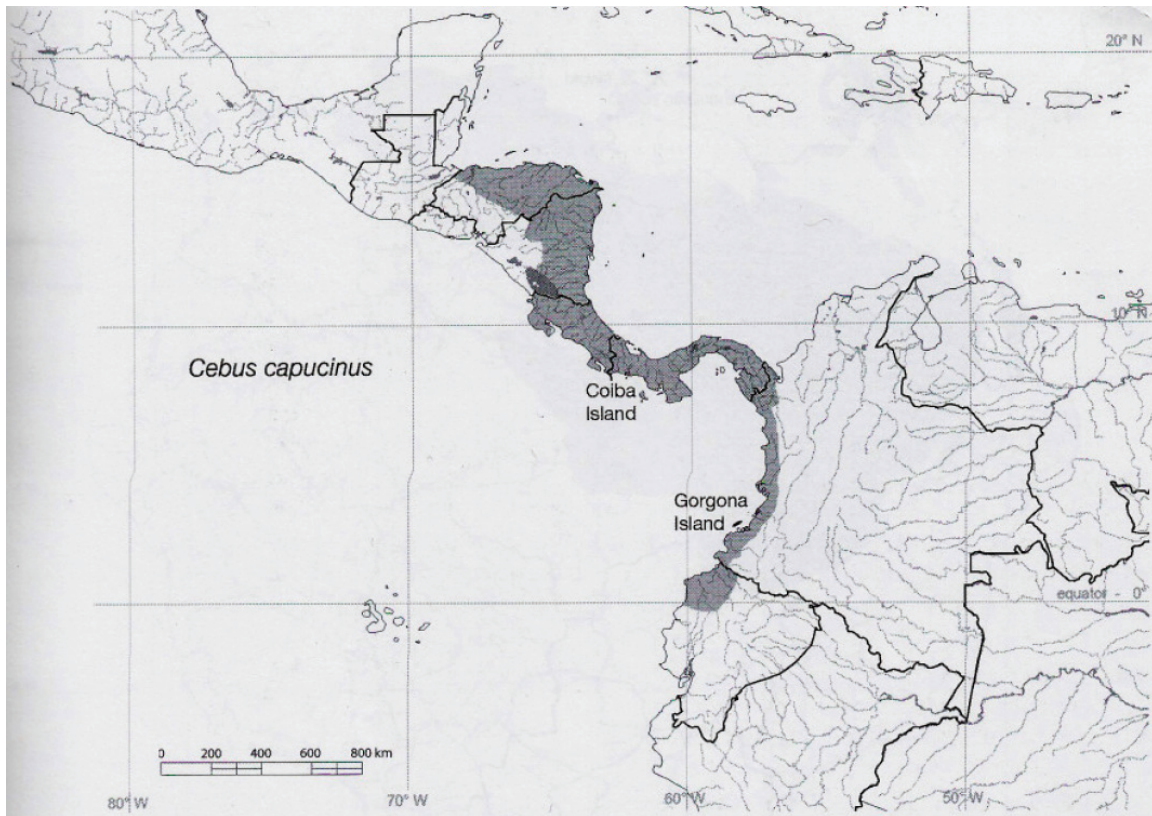


Fig. 2. Distribution of *Cebus capucinus* (Fragaszy et al., 2004).

*Cebus capucinus* are omnivorous monkeys who feed primarily on vertebrates, including lizards, squirrels, birds and their eggs, mice, and coatis; invertebrates, and fruit (Terborgh, 1983; Chapman, 1988; Fedigan, 1990; Janson and Boinski, 1992; Rose, 1997; Bergeson, 1998). Invertebrates consumed by capuchins include ants, termites, wasps, cicadas, grasshoppers, spittle bugs, and some species of Coleoptera (Sussman, 2003). White-faced capuchin males feed more on vertebrates than females (Robinson, 1986; Fedigan, 1990; Rose, 1994, 1997). They are highly opportunistic foragers, able to manipulate a wide range of materials and substrates due to their greatly enhanced manual dexterity (Rose, 1994). Their dietary flexibility allows them to readily switch from accessible foods such as fruit to more inaccessible ones during times of fruit scarcity (Fragaszy et al., 2004). Such flexibility reduces competition with other arboreal animals,



such as spider and squirrel monkeys, coatis, parrots, and ant eaters (Fragaszy et al., 2004). Capuchins have robust mandibles, large canines, and molars with thick enamel, making them well adapted to crushing seeds and tearing open hard fruits and tough substrates (Fragaszy et al. 2004).

*Cebus* monkeys are characterized as highly extractive foragers for their ability to use their size and strength to rip apart portions of trees to reach prey hidden inside the bases of palm fronds, dead twigs, branches, logs, and other parts where invertebrates are located (Freese and Oppenheimer, 1981; Terborgh, 1983; Robinson and Janson, 1987; Chapman and Fedigan, 1990; Perry et al., 2003). *Cebus* does not usually search for mobile prey, most likely because their large size disturbs the prey and causes them to flee (Janson and Boinski, 1992). *Cebus* spends more time searching for prey hidden in tough substrates that require them to use their teeth, pull with their arms or even their whole body (Janson and Boinski, 1992). The reason capuchins spend so much time foraging for protein from invertebrates and vertebrates, as opposed to readily available sources like leaves and seeds, is related to their body size (Fragaszy et al., 2004). Richard (1985) states that larger species tend to be more frugivorous and folivorous, relying more on carbohydrates to meet their nutritional needs, whereas smaller species tend to be more insectivorous, relying on the calories from protein and fat, even though they still consume fruit for ready energy. Extensive behavioral adaptations for capuchin foraging and dietary patterns give them the ability to access food that other monkeys cannot or do not eat, as well as the ability to map their food sources in time and space (King, 1986; Janson and Boinski, 1992). In most primate environments, food is distributed in a patchy fashion, where areas of high food concentration are separated from areas of low concentration

(Oates, 1987). The patchiness of food that primates feed on affects how much time they spend foraging for food.

### **Understanding the Context of Prehensile Tail Use: This Study**

Suspension likely has a high adaptive significance in many primate species, including hylobatids and atelines where it is a relatively frequent positional behavior, particularly during feeding (Bergeson, 1998). Suspension has also been linked with feeding among small branches (Napier, 1967; Fleagle and Mittermeier, 1980; Cant, 1992) and feeding in the periphery of a tree crown (Napier, 1967; Grand, 1972). Typically, foods eaten by primates, i.e., fruits, flowers, and leaves, are found either on the ends of thin, unstable branches, or the insects they are searching for are themselves feeding on the plant materials found on the thin branches (Boinski, 1989). Feeding in terminal branches becomes difficult because trees naturally become more slender towards the periphery. Suspension with a tail is one way to increase the ability to utilize these food sources (Grand, 1972). Increased body size makes it more difficult to feed on terminal branches, thus selecting for suspensory behavior (Napier, 1967; Cant, 1992). The prehensile tail of *Cebus* species allows them to anchor themselves to stronger supports away from the terminal branches, thus enabling them to reach fruits, leaves, or insects on the tree's periphery (Janson and Boinski, 1992).

In this paper, I examine patterns of prehensile tail use within the context of feeding, habitat use, and locomotion in *Cebus capucinus*. The types of foods fed and foraged on will also be important for examining the role of the prehensile tail, as well as the location within the trees of these foods. I tested three hypotheses:

- 1) Prehensile tail use occurs more during feeding/foraging behaviors than traveling
- 2) The prehensile tail is used more during foraging than feeding
- 3) Fruit feeding and foraging causes the capuchins to use their prehensile tail more than insect feeding and foraging

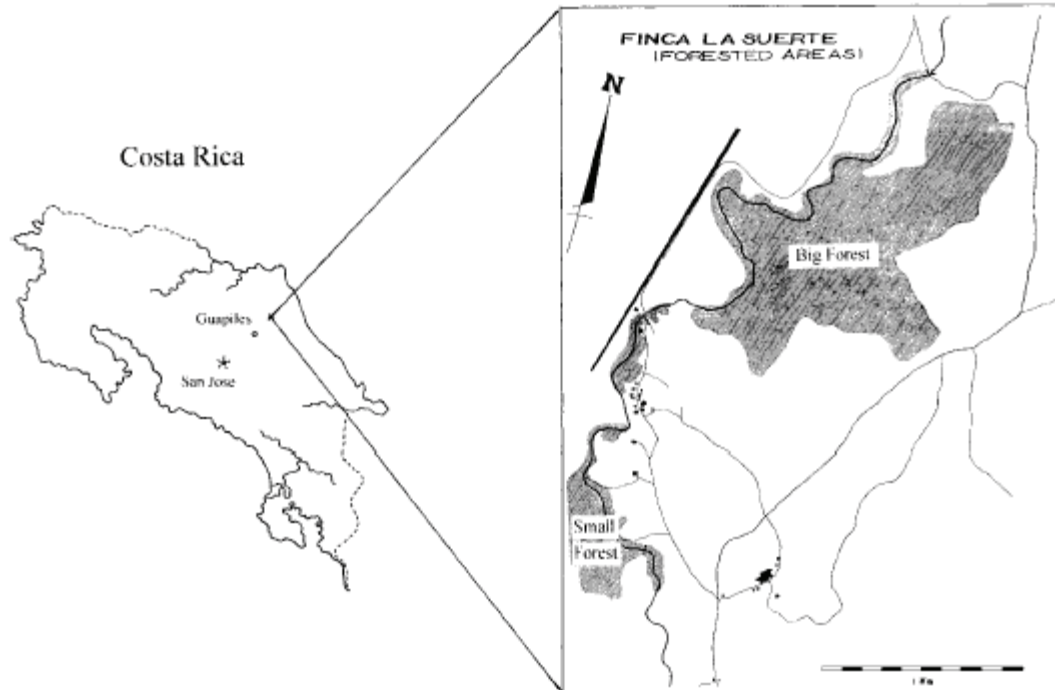


Fig. 3. Map of La Suerte Biological Research Station in northeastern Costa Rica (Garber and Rehg, 1999).

## **MATERIALS AND METHODS**

### **Study Site**

I collected data on a habituated group of 15 white-faced capuchin monkeys from July 19, 2004 to August 14, 2004, at the La Suerte Biological Field Station in Northeast Costa Rica (Fig. 3). The station is located on the Río Suerte and its coordinates are 10°26'N and 83°47' W. The study site is described as a wet tropical lowland rainforest

that averages 3962 mm of rainfall per year, with most of the precipitation occurring during the months of May through December (Sanford & et al, 1994). Secondary forest characterized the study group's home range, which is about 15-20 ha (Garber and Rehg, 1999). Their home range was focused on the area in Fig. 3 known as the "small forest." During my study, the group never traveled into the "large forest," only leaving the "small forest" to go onto adjacent banana plantations. Additional information on the study site can be found in Garber and Rehg (1999). The forest also contains populations of mantled howling monkeys (*Alouatta palliata*) and black-handed spider monkeys (*Ateles geoffroyi*).

The study group was composed of 2 adult males, 5 adult females, 1 adult female with an infant, and 6 juveniles. The capuchins were not marked so I was unable to consistently record data on specific individuals. I was, however, able to recognize the two adult males, the female and her infant, and one of the juveniles. Capuchins move quickly through the canopy during travel and focal animals were often lost after only 1 or 2 samples. In these cases, the next animal sighted became the focal animal. Once an individual was located, it was observed until lost. In only a few instances did I observe an individual for more than 20 minutes. In most cases, an individual was lost after a few observations and the next individual was located. A Chi Square statistical analysis was chosen to test for significance in my data. This test was chosen because my data is based on the frequency in which an observation occurs. The size of my data set however, did not allow me to run many Chi Square analyses with any confidence because there were not enough data points for the particular tests.

## Data Collection

On most days, data were collected between the hours of 6:00 and 13:30. All data were collected using 2 minute intervals of instantaneous focal animal sampling (Altmann, 1974). A total of 503 observations, consisting of 16 hours and 46 minutes, of continuous contact were obtained. During each observation, data on 9 variables were collected: time, focal animal, activity, positional behavior, tail use, food type, branch size, branch angle, and crown level (See Fig. 4 for a sample data sheet). Activity budget categories included feeding, rest, active posture, foraging, travel, and social behavior. The definitions are listed below:

- 1) Active posture - any activity in which it was pausing between movements and was usually characterized by sitting on its ischia
- 2) Rest - any point in which the focal animal was inactive or resting, and usually characterized by laying or sitting in the tree
- 3) Social behavior - interactions with other individuals in the group, such as play or grooming
- 4) Feeding – any behavioral activity associated with handling, biting, or ingesting a potential food item (Garber and Rehg, 1999)
- 5) Foraging – localized movement within the crown of a tree that was associated with the visual inspection or manual manipulation of a potential food bearing substrate (Garber and Rehg, 1999)
- 6) Travel – relatively straight-line progression within the crown of a tree or between the crowns of adjacent trees which did not appear to be food related (Garber and Rehg, 1999)

Table 1 shows the different positional behaviors recorded using definitions provided by Hunt et al. (1996).

Five categories of tail use were recorded: tail hang, tail touch, tail wrap, tail weight-bearing, and tail only. The following definitions are provided:

- 1) Tail hang involved the tail hanging from the body, not making contact with any object.

- 2) Tail touch was recorded when the tail may have been resting on a branch or other object.
- 3) Tail wrap involved the tail wrapped around a branch or object where it was used to maintain balance and did not bear any body weight.
- 4) Tail weight-bearing was used in association with either the hindlimbs or forelimbs, acting as a fifth limb in aiding the other limbs in supporting body weight
- 5) Tail only was used when the capuchin fully suspended itself by its tail with no other limbs holding on to any part of the tree, unless grabbing a branch with food, but not bearing any body weight.

Tail hang and tail touch observations do not use the grasping ability of the tail. Refer back to Figure 1 for examples of the three prehensile tail uses.

I used 5 categories of food type: fruit, flowers, leaves, invertebrate, and vertebrate. When visual contact was obstructed and food type could not be seen, it was recorded as unknown, and any food not categorized in the above 5 types was recorded as other. Different species were not identified for the food types due to time constraints.

The last three types of data recorded all deal with the structure of the tree. The location within the tree, the branch sizes, and branch orientation present arboreal animals with different challenges, including stability, weight support, or movement through the canopy (Fleagle and Mittermeier, 1980; Cant, 1992; Garber and Rehg, 1999). Table 2 gives the definitions for different branch sizes, branch angles, and crown locations. No exact measurements can be given for each level because of the different sizes of trees.

## **RESULTS**

*Cebus capucinus* spent the most time foraging (26.24%) followed by feeding (23.66%), (Table 3). Prehensile tail use occurred during 20.87% of all observations. Of the 3 prehensile tail use positions, tail wrap occurred most frequently (Table 4). *Cebus*

*capucinus* used its prehensile tail during 35.06% of all feeding/foraging behaviors compared to 5.41% of travel (Table 5). Results of the chi-square test reveal a significant relationship between prehensile tail use and feeding/foraging but not between tail use and travel (Chi-square = 129.6376,  $p < .0001$ ). Juvenile capuchins used their prehensile tail more than adults (Table 6).

The La Suerte capuchins fed and foraged more for insects than fruit; insects occupied 51% of their combined feeding and foraging time (Table 7). Fruit was the most commonly *consumed* food item but more time was spent foraging for insects. The prehensile tail was used 33.64% while feeding/foraging for fruit compared to 37.5% while feeding/foraging for insects. Tail wrap was the most frequently employed prehensile tail behavior during fruit feeding/foraging (Table 8). Tail weight-bearing and tail only postures were more common during feeding/foraging for insects. Male capuchins spent more time feeding/foraging for insects than fruit, while females spent the most time feeding/foraging for fruit (Table 9).

The most common positional behavior was sitting (Table 10). Sitting occurs most often during feeding and in 40.51% of all feeding observations (Table 11). Quadrupedal walking was the most frequent locomotor behavior used during travel, accounting for 61.26% of all observations (Table 11). Table 12 provides data on the positions associated with each type of prehensile tail use. Behaviors not or only rarely associated with prehensile tail use are omitted. Fruit and insects were fed and foraged in association with the sitting posture more than any other positional behavior (Table 13).

Overall, capuchins spent most of their time on small, horizontal branches in the lower level of the canopy (Table 14). Feeding and foraging occurred most often on small,

horizontally angled branches at low levels of the forest (Table 15). Prehensile tail use occurred more frequently on small branches (Table 16). These same substrates were used most for obtaining fruit and insects, and most food was acquired from low levels of the forest (Table 17). Quadrupedal walk and sitting were observed at the highest frequencies on small, horizontal branches at low forest levels (Table 18).

## **DISCUSSION**

*Cebus capucinus* at La Suerte uses its prehensile tail 20.87% of the time.

Prehensile tail use occurs more often during feeding and foraging than travel. During feeding, the prehensile tail is used primarily as a stabilizer, while during foraging the main function of the prehensile tail is to support body weight when capuchins suspend themselves while searching for food. Patterns of prehensile tail use during feeding and foraging in the La Suerte capuchins are associated with the types of food items that were selected. Prehensile tail use occurs more often during feeding than foraging because of the association between fruit and tail use. Tail wrap is the most frequently employed behavior during stationary postures, which occurs most during fruit feeding and foraging. Fruit is more visible and easier to locate than insects and once fruit is obtained, capuchins simply wrap their tail around a support for stability during feeding.

Although various studies (Fleagle and Mittermeier, 1980; Fleagle, 1984) found few broad correlations between diet and positional behavior, it is likely that certain positional behaviors are important for the acquisition of specific food resources in at least some primate species (Bergeson, 1998). My data show correlations between the capuchins diet and their positional behavior. Suspensory positional behaviors were much



more common during foraging activities. These positions include horizontal tripod, tail-hindlimb suspend, tail suspend, and vertical tripod (Table 13). Tail weight-bearing and tail only positional behaviors occur at significantly higher rates during insect feeding and foraging compared to feeding and foraging on fruit. The location of the food items is the primary reason behind this. Fruit and insects are found in small branches or clumps where prehensile tail use most often occurs. Fruit tends to be easier to locate than insects, so capuchins are able to grab fruit more easily than insects and return to more stable supports to feed without the use of suspension. During insect foraging, capuchins are likely to suspend themselves for longer periods of time to search under leaves or branches and once invertebrate prey are located, capuchins will usually remain suspended to avoid the chance of prey escaping.

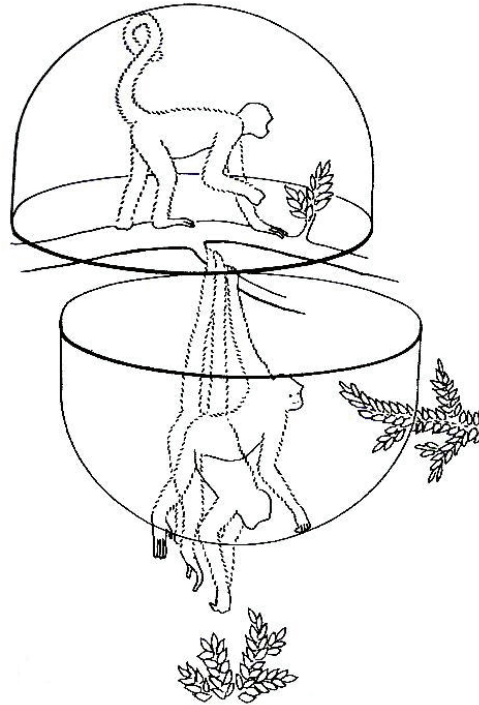
Capuchin foods greatly influence the location of prehensile tail use within the canopy (Bergeson, 1998). *Cebus capucinus* generally preferred small, horizontal supports located between the trunk and the periphery of the tree. The use of small supports by smaller-bodied monkeys is greatly influenced by species-specific foraging and travel strategies. This is due to the location of preferred food items and the avenues chosen for travel from one feeding site to the other (McGraw, 1998). Overall prehensile tail use occurs most on small, horizontal branches, as indicated by the high frequency of tail wrapping. Most capuchin food are located in the outer reaches of a tree's crown, where accessing fruit and insects requires the negotiation of smaller, less stable supports (McGraw, 1998). Among quadrupedal platyrrhines, use of larger supports increases with body size (Fleagle and Mittermeier, 1980). Food items located in clumps were not fed and foraged for as often as food items located on small branches due to the potential

hazards of placing the body weight on thin, unstable branches. The large size of capuchins do not allow the animal to effectively obtain fruit or insects from these clumps without possible risk of injury from falling. A grasping tail allows capuchins to avoid injury and reach these desired food objects. The suspensory positional behaviors employed in clumped and small branches allow capuchins to utilize a more extensive set of small branches from which to feed (Grand, 1972). Feeding and foraging in clumps was primarily for insects, suggesting capuchins were more willing to put themselves at risk to locate invertebrates.

Garber and Rehg (1999) report similar results for prehensile tail use during feeding and foraging in *Cebus capucinus* (40.6%), whereas Bergeson (1996, 1998) reported prehensile tail use 60% of the time during feeding and foraging in the same species. Bergeson's (1995) study of *Cebus capucinus*, *Alouatta palliata*, and *Ateles geoffroyi* revealed that capuchins use their tails much less (36.3%) than howler monkeys (58.3%) and spider monkeys (71.3%). Studies by Youlatos in French Guiana (1994) have also revealed a general decrease in prehensile tail use from spider monkeys, howler monkeys and capuchins. Tail only suspension serves a greater role in the repertoire of howler and spider monkeys than among *Cebus* species (Bergeson, 1998; Youlatos, 2002). The larger body size in Atelines makes it more difficult for these monkeys to feed in the terminal branches of a tree. The prehensile tail allows these monkeys to suspend themselves from stronger supports in the desired feeding sphere. Feeding heavily in the periphery of a tree allows the tail of the Atelines as well as *Cebus* to increase their feeding sphere, up to 150% of that available when sitting or standing (Fig. 5) (Bergeson, 1998). Because *Cebus* is smaller than any Ateline, they do not have to suspend

themselves as frequently in the terminal ends of a tree. The reduced body weight allows them to take up other positional behaviors in the terminal branches without having to suspend themselves on such a frequent basis.

Fig. 5 – Increased feeding sphere with prehensile tail use (Mittermeier and Fleagle, 1976)



Garber and Rehg (1999) found in their study of *Cebus capucinus*, that capuchins also preferred small supports (65.6%). The higher frequency in their study is due to combining small and clumped branches into the same category; I recorded these as separate support structures. In comparison with other *Cebus* species, Youlatos (1998) found *Cebus olivaceus* and *Cebus apella* preferred small substrates during feeding, foraging, and traveling. The *Cebus* species generally prefers small substrates as a result of the location of the preferred food items and avenues for travel.

Travel (22.07%) and feeding (23.66%) occupy similar portions of the La Suerte capuchins activity budget, but the prehensile tail only play's a major role in the latter.

The La Suerte capuchins used their prehensile tail in only 5.41% of all travel observations. The low frequency of prehensile tail use during locomotor behaviors such as quadrupedal walk and vertical climb suggest that in *Cebus* the prehensile tail has not evolved to serve a major role during locomotion. Capuchins spend the majority of their time traveling in the lower canopy where the abundance and proximity of horizontal supports permits them to choose specific routes that are safer and easier to cross. A specialized tail is not needed if capuchins tend to travel by walking quadrupedally within and between trees primarily on connected, arboreal runways.

Other studies have found similarly low frequencies in prehensile tail use during travel for *Cebus* (Garber and Rehg, 1999; Youlatos, 1999). Among Atelines the prehensile tail appears to serve a greater role during traveling as well as feeding compared to that in *Cebus* species. For example, in *Ateles paniscus*, the prehensile tail was used during 61.5% of all travel observations and 88.7% of all feeding observations (Youlatos, 2002). The additional support needed by spider monkeys during travel in the periphery of trees is largely responsible for the increased prehensile tail use during their activity budget. Branches in the periphery are generally characterized as thin and unstable, and for a large-bodied primate like a spider monkey, negotiating these supports can be dangerous. A prehensile tail allows spider monkeys to more effectively bridge between trees, as well as aiding during brachiating.

Our ability to identify these relationships is important in understanding the positional behavior of extant primates, as well as reconstructing the positional behavior of extinct primates (Bergeson, 1998). Once we understand the ecological context of locomotor modes and feeding postures, we may begin addressing questions regarding

their adaptive significance (Fleagle, 1979; Bergeson, 1998). The evolutionary significance of any positional behavior must be examined within a behavioral and ecological context (Fleagle, 1979; Bergeson, 1998). Two examples of significant positional behaviors within an ecological context from my study would be the horizontal tripod and the tail-hindlimb suspend positions – see Table 1 for definitions. In both positions, the tail acts as an anchor to bear additional body weight that the hindlimbs are not supporting. While in these positions, both hands are freed allowing the monkey to feed on fruits in terminal branches or search for invertebrates hidden along the trunks of trees or on leaves within the terminal branches (Fragaszy et al., 2004). 97% of the observations of these two positions were recorded within the context of feeding and foraging. These two positions would not be possible without the aid of a specialized appendage. The prehensile tail allows capuchins to adopt these positions, which increases the potential feeding sphere of capuchins. Based on the frequencies and the ecological context that these positions were observed in *Cebus capucinus*, we can make assumptions about their adaptive significance and have a better chance of reconstructing the positional repertoire of fossil platyrrhines.

### **Implications and Future Work**

In the La Suerte capuchins, the prehensile tail serves many roles during feeding and foraging. These roles include increasing the ability to use suspensory postures for feeding and foraging in the crown periphery, an expansion of the feeding sphere due to suspensory postures, increasing the ability to balance on small branches, and freeing the forelimbs during feeding and foraging activities (Bergeson, 1996). My data further suggest that the prehensile tail plays a very small role during travel in capuchins. More

comparative studies are needed not only on *Cebus capucinus*, but on all prehensile tailed monkeys. In future research, I plan on gathering additional data on *Cebus capucinus*, as well as members of the Atelines for a more detailed analysis of the functional role of the prehensile tail between these species. Once we achieve a better understanding of the adaptive significance of this specialized tail in all primates possessing one, we can make more informed inferences about the ancestors of these primates as well as the evolutionary forces that selected for such a specialized appendage.

## **SUMMARY AND CONCLUSIONS**

- 1) Prehensile tail use occurred more during feeding (42.02%) and foraging (28.79%) than traveling (5.41%).
- 2) Contrary to my predictions, the prehensile tail was used more during feeding than foraging. Prehensile tail use occurred more during feeding due to the high number of tail wrap observations.
- 3) Capuchins used their prehensile tail more during insect feeding/foraging compared to fruit feeding/foraging. Suspension by the prehensile tail was more common for insect feeding/foraging due to the location of the invertebrate prey in the trees.
- 4) The ideas proposed for the parallel evolution of the prehensile tail in Atelines and *Cebus* species are not unique to either group of primates. My results suggest that the tail evolved as a feeding adaptation in *Cebus capucinus*. This is not the case for all *Cebus* species or for Atelines, but it does provide a framework for understanding the parallel evolution of this appendage in these species. A larger sample size will allow me to more confidently compare my results to other studies. In future work I plan to further explore

the relationship between the tail in *Cebus* species as well as Atelines in order to better understand how this specialized limb evolved.

## **ACKNOWLEDGEMENTS**

I would first like to thank Dr. W. Scott McGraw for all the help he has given me with this thesis and as an advisor. This journey started with the first class I had of his and the help he has given me with structuring and editing this thesis has been tremendous and greatly appreciated. Thanks to Dr. Paul Sciuli for his help in analyzing my data and for the use of his statistical program which saved me a lot of valuable time. My appreciation is extended to the staff of La Suerte for allowing me to do my research there as well as keeping me fed. Thank you to Michelle Bezanson for accepting me into her field school and giving me the opportunity for carrying out this research. Finally, thanks to the capuchins for allowing me to follow them through the forest, hopefully disturbing them as little as possible.

## **BIBLIOGRAPHY**

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227-265.
- Bergeson, D. 1995. The ecological role of the platyrrhine prehensile tail. *Am. J. Phys. Anthropol.* (suppl.) 20: 64-65.
- Bergeson, D. 1996. *The Positional Behavior and Prehensile Tail Use of Alouatta palliate, Ateles geoffroyi, and Cebus capucinus*. Ph.D. Thesis. Washington University, St. Louis.
- Bergeson, D. 1998. Patterns of suspensory feeding in *Alouatta palliate, Ateles geoffroyi*, and *Cebus capucinus*. In Strasser E., Fleagle, J., Rosenberger, A., and McHenry, H. (eds.) *Primate Locomotion: Recent Advances*. Plenum Press, New York, pp. 45-60.
- Boinski, S. 1989. The positional behavior and substrate use of squirrel monkeys: ecological implications. *J. Hum. Evol.* 18: 659-677.
- Cant, J.G.H. 1977. *Ecology, locomotion and social organization of spider monkeys (Ateles geoffroyi)*. Ph.D. Dissertation, University of California, Davis.
- Cant, J.G.H. 1986. Locomotion and feeding postures of spider and howling monkeys: Field study and evolutionary interpretation. *Folia Primatol.* 46: 1-14.
- Cant, J.G.H. 1992. Positional behavior and body size of arboreal primates: A theoretical framework for field studies and an illustration of its application. *Am. J. Phys. Anthropol.* 88: 273-283.
- Chapman, C. 1988. Patterns of foraging and range use by three species of neotropical



- primates. *Primates* 29: 177-194.
- Chapman, C., Fedigan, L.M. 1990. Dietary differences between neighboring *Cebus capucinus* groups: Local traditions, food availability or responses to food profitability? *Folia Primatol.* 54: 177-186.
- Emmons, L.H., Gentry, A.H. 1983. Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *Am. Nat.* 121: 513-524.
- Fedigan, L.M. 1990. Vertebrate predation in *Cebus capucinus*: Meat eating in a Neotropical monkey. *Folia Primatol.* 54: 196-205.
- Fedigan, L.M., Fedigan, L., Chapman, C. 1985. A census of *Alouatta palliata* and *Cebus capucinus* monkeys in Santa Rosa National Park, Costa Rica. *Brenesia* 23: 309-322.
- Fleagle, J.G. 1979. Primate positional behavior and anatomy: Naturalistic and experimental approaches. In Morbeck, M.E., Preuschoft, H., and Gomberg, N. (eds.) *Environment, Behavior, and Morphology: Dynamic Interactions in Primates*. Gustav Fischer, New York, pp. 313-325.
- Fleagle, J.G. 1984. Primate locomotion and diet. In Chivers, D., Wood, B., and Bilsborough, A. (eds). *Food Acquisition and Processing in Primates*. Plenum Press, New York, pp. 105-117.
- Fleagle, J.G., Mittermeier, R.A. 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *Am. J. Phys. Anthropol.* 52: 301-314.
- Ford, S.M., Davis, L. 1992. Systematics and body size: implications for feeding adaptations in New World Monkeys. *Am. J. Phys. Anthropol.* 88: 415-468.
- Fragaszy, D.M., Visalberghi, E., Robinson, J.G. 1990. Variability and adaptability in the

- genus *Cebus*. *Folia Primatol.* 54: 114-118.
- Fragaszy, D.M., Visalberghi, E., Fedigan, L.M. 2004. The Complete Capuchin: The biology of the genus *Cebus*. Cambridge University Press, Cambridge.
- Freese, C.H., Oppenheimer, J.R. 1981. The capuchin monkeys, genus *Cebus*. In Coimbra-Filho, A.F., Mittermeier, R.A. (eds.) *Ecology and Behavior of Neotropical Monkeys. Vol. 1*. Academia Brasileira de Ciencias, Rio de Janeiro, pp. 331-390.
- Garber, P.A., Rehg, J.A. 1999. The ecological role of the prehensile tail in white-faced capuchins (*Cebus capucinus*). *Am. J. Phys. Anthropol.* 110: 325-339.
- Gebo, D.L. 1992. Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. *Am. J. Primatol.* 26: 277-290.
- German, R. 1982. The functional morphology of caudal vertebrae in New World monkeys. *Am. J. Phys. Anthropol.* 58: 453-459.
- Grand, T.I. 1972. A mechanical interpretation of terminal branch feeding. *J. Mammol.* 53: 198-201.
- Grand, T.I. 1977. Body weight: Its relation to tissue composition, segment distribution, and motor function. I. Interspecific comparisons. *Am. J. Phys. Anthropol.* 47: 211-240.
- Grand, T.I. 1984. Motion economy within the canopy: Four strategies for mobility. In Rodman, P.S., Cant, J.G.H.(eds.): *Adaptations for Foraging in Nonhuman Primates*. Columbia University Press, New York, pp. 54-72.
- Groves, C.P. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington D.C.
- Hunt, K.D., Cant, J.G.H., Gebo, D.L., Rose, M.D., Walker, S.E., Youlatos, D. 1996.

- Standardized descriptions of primate locomotor and postural modes. *Primates* 37: 363-387.
- Janson, C.H., Boinski, S. 1992. Morphological and behavioral adaptations for foraging in generalist primates: the case of the Cebines. *Am. J. Phys. Anthropol.* 88: 483-498.
- Johnson, S.E., Shapiro, L.J. 1998. Positional behavior and vertebral morphology in Atelines and Cebines. *Am. J. Phys. Anthropol.* 105: 333-354.
- King, B.J. 1986. Extracting, foraging, and the evolution of primate intelligence. *Human Evolution* 4: 361-372.
- Lemelin, P. 1995. Comparative and functional mycology of the prehensile tail in New World monkeys. *J. Morphol.* 224: 351-368.
- Lockwood, C.A. 1999. Homoplasmy and adaptation in the atelid postcranium. *Am. J. Phys. Anthropol.* 108: 459-482.
- Massey, A. 1987. A population survey of *Alouatta palliata*, *Cebus capucinus*, and *Ateles geoffroyi* at Palo Verde, Costa Rica. *Rev. Bio Tropical* 35: 345-347.
- McGraw, W.S. 1998. Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *Am. J. Phys. Anthropol.* 105: 493-510.
- Meldrum, D.J. 1998. Tail-assisted hind limb suspension as a transitional behavior in the evolution of the platyrrhine prehensile tail. In Strasser, E., Fleagle, J., Rosenberger, A., and McHenry, H. (eds.) *Primate Locomotion: Recent Advances*. Plenum Press, New York, pp. 145-156.
- Mittermeier, R.A., Fleagle, J.G. 1976. The locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a reevaluation of the locomotor category semibrachiation. *Am. J. Phys. Anthropol.* 45: 235-256.

- Mittermeier, R.A. 1978. Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus*. *Folia Primatol.* 30: 161-193.
- Napier, J.R. 1967. Evolutionary aspects of primate locomotion. *Am. J. Phys. Anthropol.* 27: 333-342.
- Oates, J.F. 1987. Food distribution and foraging behavior. In Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (eds.) *Primate Societies*. Chicago University Press, Chicago, pp. 197-209.
- Oppenheimer, J.R. 1968. *Behavior and Ecology of the White-faced Monkey, Cebus capucinus, on Barro Colorado Island, C.Z.* Ph.D. Thesis. University of Illinois, Urbana.
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K.C., Manson, J.H., Panger, M., Pyle, K., Rose, L. 2003. Social conventions in wild white-faced capuchin monkeys. Evidence for Traditions in a Neotropical Primate. *Curr. Anthropol.* 44: 241-268.
- Richard, A.F. 1985. *Primates in Nature*. W.H. Freeman and Co., San Francisco.
- Robinson, J.G. 1986. Seasonal variation in use of time and space by the wedge-capped capuchin monkey *Cebus olivaceus*: Implications for foraging theory. *Smith. Contrib. to Zool. No. 431*. Smithsonian Institution Press, Washington D.C.
- Robinson, J.G., Janson, C.H. 1987. Capuchins, squirrel monkeys, and atelines: Socioecological convergence with Old World primates. In Smuts, B. B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (eds.) *Primate Societies*. Chicago University Press, Chicago, pp. 69-82.
- Rose, L.M. 1994. Sex differences in diet and foraging behavior in white-faced capuchins

- (*Cebus capucinus*). *Int. J. Primatol.* 15: 95-114.
- Rose, L.M. 1997. Vertebrate predation and food-sharing in *Cebus* and *Pan*. *Int. J. Primatol.* 15: 727-765.
- Rosenberger, A.L. 1983. Tale of tails: parallelism and prehensibility. *Am. J. Phys. Anthropol.* 60: 103-107.
- Sanford, R.L., Paaby, P., Luvall, J.C., Phillips, E. 1994. Climate, geomorphology, and aquatic systems. In: McDade, L., Bawa, D., Hespdenheide, H., Hartshorn, G. (eds.) *La Selva: Ecology and natural history of a neotropical rain forest*. Chicago University Press, Chicago, pp. 19-33.
- Schmitt, D., Rose, M.D., Turnquist, J.E., Lemelin, P. 2005. Role of the prehensile tail during ateline locomotion: Experimental and osteological evidence. *Am. J. Phys. Anthropol.* 126: 435-446.
- Schneider, H., Rosenberger, A.L. 1996. Molecules, morphology, and platyrrhine systematics. In Norconk, M., Rosenberger, A.L., and Garber, P.A. (eds.) *Adaptive radiations of neotropical primates*. Plenum Press, New York, pp. 19-33.
- Sussman, R.W. 2003. *Primate Ecology and Social Structure: Volume 2: New World Monkeys*. Pearson, Boston.
- Terborgh, J. 1983. *Five New World primates: a study in comparative ecology*. Princeton University Press, Princeton.
- Youlatos, D. 1994. Maitrise de l'espace et acces aux ressources chez le singe hurleur roux (*Alouatta seniculus*). *Folia Primatol.* 61: 144-147.
- Youlatos, D. 1998. Positional behavior of two sympatric guianan capuchin monkeys, the

brown capuchin (*Cebus apella*) and the wedge-capped capuchin (*Cebus olivaceus*). *Mammalia* 62: 351-365.

Youlatos, D. 1999. Comparative locomotion of six sympatric primates in Ecuador. *Ann. Sci. Nat.* 20: 161-168.

Youlatos, D. 2002. Positional behavior of black spider monkeys (*Ateles paniscus*) in French Guiana. *Int. J. Primatol.* 23: 1071-1093.

Fig. 4 – Sample Data Sheet

<b>Time</b>	<b>Focal Animal</b>	<b>Activity</b>	<b>Positional Behavior</b>	<b>Tail Use</b>	<b>Food Type</b>	<b>Branch Size</b>	<b>Branch Angle</b>	<b>Crown Level</b>
6:16	J	Fd	S	Th	L	M	H	L1
6:18	J	T	St	Tw	-	Cl	T	U3
6:20	J	Fo	S	Tw	Fr	Cl	T	U2

Table 1 – Positional behaviors recorded, definitions from Hunt et al. (1996).

<b>Postures</b>	<b>Definitions</b>
<b>Sit</b>	Ischia bears a substantial portion of the body weight
<b>Squat</b>	Body weight is borne solely by the feet/foot, both hip and knee are strongly flexed
<b>Cling</b>	Flexed limb posture most common on vertical-subvertical supports
<b>Stand</b>	Four-limbed standing on horizontal or subhorizontal supports
<b>Bipedal Stand</b>	Standing on the hindlimbs with no significant support from any other body part
<b>Horizontal tripod</b>	Combination of tail hang and bipedal standing in which the animal is partly supported by its tail, anchored to a support above the base of the tail
<b>Vertical Tripod</b>	Flexed bipedal stand in which additional stability is provided by contact between the stiffened tail and the ground
<b>Forelimb-hindlimb suspend</b>	Suspension by a forelimb and a foot with the trunk in a subhorizontal orientation, limbs are typically extended
<b>Quadrumanous suspend</b>	Suspension with the torso pronograde, with all four limbs providing approximately equal support
<b>Tail suspend</b>	Suspension from the tail with no support from the limbs
<b>Tail-hindlimb suspend</b>	Suspension with substantial support from the extended hindlimb(s) and the tail
<b>Tail-forelimb suspend</b>	At least half the body weight is borne by the tail with significant weight borne by the forelimb(s)
<b>Lie</b>	Torso orthograde posture on a relatively horizontal support, body weight borne principally by the torso
<b>Quadrupedal Walk</b>	Locomotion on top of supports angled at $<45^\circ$ ; typically all four limbs contact the support
<b>Tripedal Walk</b>	Same as quadrupedal walk in its various expressions, except one limb is not used in locomotion, the other often being used to grasp a carried object
<b>Quadrupedal Run</b>	Fast locomotion using asymmetrical or irregular gaits and with a period of free flight
<b>Vertical Climb</b>	Ascent on supports angled at $\geq 45^\circ$
<b>Leap</b>	Gap-crossing movement in which the hindlimbs principally are used as propulsors with an extended period of free flight
<b>Tail swing</b>	Pendular movement during tail suspension propels the animal forward to cross a gap



Table 2 – Description of branch sizes, branch angles, and crown locations

	<b>Description</b>
<b>Branch Size</b>	
Small	Branches estimated at $\leq 5$ cm in circumference
Medium	Branches estimated at $> 5$ and $\leq 30$ cm in circumference
Large	Branches estimated at $> 30$ cm in circumference
Clump	Many small branches clumped together, no one branch can be identified as the exact weight-bearing support
<b>Branch Angle</b>	
Horizontal	Branches between $0-15^\circ$
Oblique	Branches between $16-74^\circ$
Vertical	Branches between $75-90^\circ$
Terminal	Mass of small branches oriented at different angles to the ground
<b>Crown Level</b>	
Lower	Bottom area of the tree
Middle	Middle of tree
Upper	Upper crown of tree
1	Area centered around the trunk of the tree
2	Includes middle area between the trunk and the periphery of the tree
3	Periphery of the tree

Table 3 – Distribution of Activity Budget

	Active Posture	Feeding	Foraging	Rest	Social Behavior	Travel
Frequency of activities (%)	11.33	23.66	26.24	12.72	3.98	22.07

Table 4 – Distribution of Tail Positions

	Tail hang	Tail touch	Tail wrap	Tail weight-bearing	Tail only	Total
Frequency	337	61	62	37	6	503
% of Total (%)	67.00	12.13	12.33	7.36	1.19	

Table 5 – Tail Use frequencies recorded during activities

Frequency % Tail Use of each Activity	Tail wrap	Tail weight- bearing	Tail only	Total
Active Posture	7 12.28	0 0.00	0 0.00	67 12.28
Feeding	34 28.57	14 11.76	2 1.68	119 42.01
Foraging	13 9.85	22 16.67	3 2.27	132 28.79
Rest	3 4.69	0 0.00	0 0.00	64 4.69
Social Behavior	1 5.00	0 0.00	0 0.00	20 5.00
Travel	4 3.60	1 0.90	1 0.90	111 5.40

Table 6 – Tail positions of focal animals

Frequency Row % Column %	Tail hang	Tail touch	Tail wrap	Tail weight-bearing	Tail only	Total
Female	39 81.25 11.57	0 0.00 0.00	8 16.67 12.90	1 2.08 2.70	0 0.00 0.00	48
Female with infant	12 75.00 3.56	2 12.50 3.28	1 6.25 1.61	1 6.25 2.70	0 0.00 0.00	16
Juvenile	140 64.81 41.54	18 8.33 29.51	29 13.43 46.77	25 11.57 67.57	4 1.85 66.67	216
Male	146 65.47 43.32	41 18.39 67.21	24 10.76 38.71	10 4.48 27.03	2 0.90 33.33	223
Total	337	61	62	37	6	503

Table 7 – Food types involved with feeding and foraging

	Fruit	Insects	Leaves	Total	%
Feeding	64	41	11	119	47.41
%	53.78	34.45	9.24		
Foraging	43	87	0	132	52.59
%	32.58	65.91	0		
Total	107	128	11	251	
%	42.63	51.00	4.38		

Table 8 – Prehensile tail use with the different food types

Frequency Row % Column %	Tail wrap	Tail weight-bearing	Tail only	Total
Fruit – feed/forage	29 27.10 61.70	6 5.61 16.67	1 0.93 20.00	107
Insects – feed/forage	16 12.50 34.04	28 21.88 77.78	4 3.13 80.00	128
Leaves – feed/forage	2 18.18 4.26	1 9.09 2.78	0 0.00 0.00	11
% Tail use with all food observations	18.73	14.34	1.99	251

Table 9 – Food items fed and foraged by focal animals

Frequency Row % Column %	Female	Female with infant	Juvenile	Male
Fruit	22 20.56 68.75	3 2.80 75.00	44 41.12 37.93	38 35.51 38.38
Insects	7 5.47 21.88	1 0.78 25.00	64 50.00 55.17	56 43.75 56.57
Leaves	2 18.18 6.25	0 0.00 0.00	5 45.45 4.31	4 36.36 4.04



Table 10 – Frequency of positional behaviors

Position	Frequency %
Bipedal stand	0.20
Cling	2.39
Horizontal tripod	3.38
Lie	10.54
Leap	3.98
Quadrupedal run	0.20
Quadrupedal walk	23.46
Sit	31.41
Squat	3.18
Stand	9.94
Tail-hindlimb suspend	3.18
Tail suspend	0.99
Tail swing	0.20
Vertical climb	5.77
Vertical tripod	1.19

Table 11- Most common positional behaviors during feeding, foraging, and traveling

Frequency Row % Column %	Horizontal Tripod	Cling	Quadrupedal Walk	Sit	Squat	Stand	Tail- hindlimb suspend	Tail Suspend	Vertical Climb	Vertical Tripod	Total
Feeding	6 5.04 35.29	4 3.36 33.33	6 5.04 5.08	64 53.78 40.51	13 10.92 81.25	12 10.08 24.00	7 5.88 43.75	2 1.68 40.00	1 0.84 3.45	1 0.84 16.67	119
Foraging	10 7.58 58.82	4 3.03 33.33	43 32.58 36.44	20 15.15 12.66	1 0.76 6.25	19 14.39 38.00	9 6.82 56.26	3 2.27 60.00	15 11.36 51.72	5 3.79 83.33	132
Travel	1 0.90 5.88	1 0.90 8.33	68 61.26 57.63	4 3.60 2.53	0 0.00 0.00	3 2.70 6.00	0 0.00 0.00	0 0.00 0.00	13 11.71 44.83	0 0.00 0.00	111
Total	17	12	118	158	16	50	16	5	29	6	

Table 12 – Prehensile tail use in the most frequent positional behaviors

Frequency Row % Column %	Tail Wrap	Tail weight-bearing	Tail only
Horizontal Tripod	0 0.00 0.00	17 100.00 45.95	0 0.00 0.00
Lie	5 9.43 8.06	0 0.00 0.00	0 0.00 0.00
Quadrupedal Walk	8 6.78 12.90	0 0.00 0.00	0 0.00 0.00
Sit	24 15.19 38.71	0 0.00 0.00	0 0.00 0.00
Squat	7 43.75 11.29	0 0.00 0.00	0 0.00 0.00
Stand	15 30.00 24.19	0 0.00 0.00	0 0.00 0.00
Tail-hindlimb Suspend	0 0.00 0.00	16 100.00 43.24	0 0.00 0.00
Tail Suspend	0 0.00 0.00	0 0.00 0.00	5 100.00 83.33
Vertical Tripod	1 16.67 1.61	4 66.67 10.81	0 0.00 0.00

Table 13 – Positional behavior frequency during feeding and foraging for fruit and insects

Frequency Row % Column %	Cling	Horizontal Tripod	Lie	Quadrupedal Walk	Sit	Squat	Stand	Tail- hindlimb suspend	Tail Suspend	Vertical Climb	Vertical Tripod	Total
Fruit	1 0.93 14.29	2 1.87 12.50	2 1.87 50.00	19 17.76 38.78	46 42.99 59.74	7 6.54 70.00	14 13.08 48.28	4 3.74 28.57	1 0.93 20.00	8 7.48 50.00	1 0.93 16.67	107
Insects	6 4.69 85.71	14 10.94 87.50	2 1.56 50.00	30 23.44 61.22	31 24.22 40.26	3 2.34 30.00	15 11.72 51.72	10 7.81 71.43	4 3.13 80.00	8 6.25 50.00	5 3.91 83.33	128
Total	7	16	4	49	77	10	29	14	5	16	6	235

Table 14 – Frequency of branch size, branch angle, and crown level used

	Frequency	Percent
<b>Branch Size</b>		
Ground	23	4.57
Clump	94	18.69
Small	220	43.74
Medium	134	28.64
Large	32	6.36
<b>Branch Angle</b>		
Ground	23	4.57
Terminal	85	16.90
Horizontal	247	49.11
Oblique	69	13.72
Vertical	79	15.71
<b>Crown Level</b>		
Ground	23	4.57
L1	90	17.89
L2	144	28.63
L3	91	18.09
M1	38	7.55
M2	31	6.16
M3	53	10.54
U1	7	1.39
U2	9	1.79
U3	17	3.38

Table 15 – Branch size, angle, and crown level during feeding, foraging, and travel

Frequency Column % Row %	Feeding	Foraging	Travel
<b>Branch size</b>			
Ground	6 5.04 26.09	6 4.55 26.09	9 8.11 39.13
Clump	26 21.85 27.66	34 25.76 36.17	30 27.03 31.91
Small	51 42.86 23.18	55 41.87 25.00	33 29.73 15.00
Medium	22 18.49 16.42	32 24.24 23.88	34 30.63 25.37
Large	14 11.76 43.75	5 3.79 15.63	5 4.50 15.63
<b>Branch angle</b>			
Ground	6 5.04 26.09	6 4.55 26.09	9 8.11 39.13
Terminal	24 20.17 28.24	28 21.21 32.94	29 26.13 34.12
Horizontal	49 41.17 19.84	52 39.39 21.05	40 36.04 16.19
Oblique	18 15.13 26.09	20 15.15 28.99	12 10.81 17.39
Vertical	22 18.49 27.85	26 19.70 32.91	21 18.92 26.58
<b>Crown Level</b>			
Ground	6 5.04 26.09	6 4.55 26.09	9 8.11 39.13
L1	30 25.21 33.33	29 21.97 32.22	17 15.32 18.89
L2	20 16.81 13.89	30 22.73 20.83	18 16.22 12.50
L3	23 19.33 25.27	30 22.73 32.97	26 23.42 28.57
M1	12 10.08 31.58	12 9.09 31.58	8 7.21 21.05
M2	6 5.04 19.35	6 4.55 19.35	10 9.01 32.26
M3	8 6.72 15.09	11 8.33 20.75	14 12.61 26.42
U1	4 3.36 57.14	1 0.76 14.29	14 12.61 26.42
U2	4 3.36 44.44	2 1.52 22.22	2 1.80 22.22
U3	6 5.04 35.29	5 3.79 29.41	6 5.41 35.29

Table 16 – Prehensile tail positions on branch size, angle, and crown level

Frequency Column % Row %	Tail wrap	Tail weight- bearing	Tail only
<b>Branch size</b>			
Clump	17	18	3
	27.42	48.65	50.00
	18.09	19.15	3.19
Small	25	15	3
	40.32	40.54	50.00
	11.36	6.82	1.36
Medium	14	4	0
	22.58	10.81	0.00
	10.45	2.99	0.00
Large	6	0	0
	9.68	0.00	0.00
	18.75	0.00	0.00
<b>Branch angle</b>			
Terminal	16	18	3
	25.81	48.65	50.00
	18.82	21.18	3.53
Horizontal	23	8	1
	37.10	21.62	16.67
	9.31	3.24	0.40
Oblique	11	2	1
	17.74	5.41	16.67
	15.94	2.90	1.45
Vertical	12	9	1
	19.35	24.32	16.67
	15.19	11.39	1.27
<b>Crown Level</b>			
L1	14	6	0
	22.58	16.22	0.00
	15.56	6.67	0.00
L2	15	4	1
	24.19	10.81	16.67
	10.42	2.78	0.69
L3	17	15	2
	27.42	40.54	33.33
	18.68	16.48	2.20
M1	5	3	0
	8.06	8.11	0.00
	13.16	7.89	0.00
M2	5	1	0
	8.06	2.70	0.00
	16.13	3.23	0.00
M3	1	2	3
	1.61	5.41	50.00
	1.89	3.77	5.66
U1	0	3	0
	0.00	8.11	0.00
	0.00	42.86	0.00
U2	1	1	0
	1.61	2.70	0.00
	11.11	11.11	0.00
U3	4	2	0
	6.45	5.41	0.00
	23.53	11.76	0.00

Table 17 – Location of food items within tree

Frequency Column % Row %	Fruit	Insects	Leaves
<b>Branch size</b>			
Ground	7	5	0
	6.54	3.91	0.00
	58.33	41.67	0.00
Clump	23	34	1
	21.50	26.56	9.09
	38.33	56.67	1.67
Small	49	53	3
	45.79	41.41	27.27
	46.23	50.00	2.83
Medium	14	33	7
	13.08	25.78	63.64
	25.93	61.11	12.96
Large	14	3	0
	13.08	2.34	0.00
	73.68	15.79	0.00
<b>Branch angle</b>			
Ground	7	5	0
	6.54	3.91	0.00
	58.33	41.67	0.00
Terminal	21	28	1
	19.63	21.88	9.09
	40.38	53.85	1.92
Horizontal	43	49	6
	40.19	38.28	54.55
	42.57	48.51	5.94
Oblique	16	22	0
	14.95	17.19	0.00
	42.11	57.89	0.00
Vertical	20	24	4
	18.69	18.75	38.36
	41.67	50.00	8.33
<b>Crown Level</b>			
Ground	7	5	0
	5.54	3.91	0.00
	58.33	41.67	0.00
L1	22	30	5
	20.56	23.44	45.45
	37.29	50.85	8.47
L2	17	30	2
	15.89	23.44	18.18
	34.00	60.00	4.00
L3	18	33	1
	16.82	25.78	9.09
	33.96	62.26	1.89
M1	13	11	0
	12.15	8.59	0.00
	54.17	45.83	0.00
M2	10	2	0
	9.35	1.56	0.00
	83.33	16.67	0.00
M3	8	10	1
	7.48	7.81	9.09
	42.11	52.63	5.26
U1	0	3	2
	0.00	2.34	18.18
	0.00	60.00	40.00
U2	5	1	0
	4.67	0.78	0.00
	83.33	16.67	0.00
U3	7	3	0
	6.54	2.34	0.00
	63.64	27.27	0.00



Table 18 – Branch size, angle, and location of positional behaviors

Frequency Column % Row %	Cling	Horizontal Tripod	Lie	Quadrupedal Walk	Sit	Squat	Stand	Tail- hindlimb suspend	Tail suspend	Vertical climb
<b>Branch size</b>										
Ground	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	18 15.25 78.26	5 3.16 21.74	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00
Clump	1 8.33 1.06	7 41.18 7.45	0 0.00 0.00	35 29.66 37.23	19 12.03 20.21	1 6.25 1.06	8 16.00 8.51	9 56.25 9.57	2 40.00 2.13	2 6.90 2.13
Small	5 41.67 2.27	8 47.06 3.64	31 58.49 14.09	37 31.36 16.82	73 46.20 33.18	11 68.75 5.00	25 50.00 11.36	5 31.25 2.27	3 60.00 1.36	10 34.48 4.55
Medium	6 50.00 4.48	2 11.76 1.49	17 32.08 12.69	25 21.19 18.66	51 32.28 38.06	2 12.50 1.49	12 24.00 8.96	2 12.50 1.49	0 0.00 0.00	11 37.93 8.21
Large	0 0.00 0.00	0 0.00 0.00	5 9.43 15.63	3 2.54 9.38	10 6.33 31.25	2 12.50 6.25	5 10.00 15.63	0 0.00 0.00	0 0.00 0.00	6 20.69 18.75
<b>Branch angle</b>										
Ground	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	18 15.25 78.26	5 3.16 21.74	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00
Terminal	0 0.00 0.00	7 41.18 8.24	0 0.00 0.00	31 26.27 36.47	17 10.76 20.00	1 6.25 1.18	6 12.00 7.06	9 56.25 10.59	2 40.00 2.35	2 6.90 2.35
Horizontal	0 0.00 0.00	4 23.53 1.62	50 94.34 20.24	48 40.68 19.43	95 60.13 38.46	7 43.75 2.85	27 54.00 10.98	3 18.75 1.22	1 20.00 0.41	1 3.45 0.41
Oblique	0 0.00 0.00	1 5.88 1.45	3 5.66 4.35	16 13.56 23.19	29 18.35 42.03	3 18.75 4.35	11 22.00 15.94	0 0.00 0.00	1 20.00 1.45	2 6.90 2.90
Vertical	12 100.00 15.19	5 29.41 6.33	0 0.00 0.00	5 4.24 6.33	12 7.59 15.19	5 31.25 6.33	6 12.00 7.59	4 25.00 5.06	1 20.00 1.27	24 82.76 30.38
<b>Crown Level</b>										
Ground	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	18 15.25 78.26	5 3.16 21.74	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00
L1	7 58.33 7.78	3 17.65 3.33	4 7.55 4.44	11 9.32 12.22	27 17.09 30.00	4 25.00 4.44	12 24.00 13.33	3 18.75 3.33	0 0.00 0.00	13 44.83 14.44
L2	0 0.00 0.00	2 11.76 1.39	32 60.38 22.22	27 22.88 18.75	55 34.81 38.19	6 37.50 4.17	16 32.00 11.11	2 12.50 1.39	1 20.00 0.69	1 3.45 0.69
L3	1 8.33 1.10	5 29.41 5.49	1 1.89 1.10	29 24.58 31.87	26 16.46 28.57	1 6.25 1.10	7 14.00 7.69	9 56.25 9.89	2 40.00 2.20	1 3.45 1.10
M1	2 16.67 5.26	2 11.76 5.26	0 0.00 0.00	7 5.93 18.42	11 6.96 28.95	2 12.50 5.26	5 10.00 13.16	0 0.00 0.00	0 0.00 0.00	6 20.69 15.79
M2	1 8.33 3.23	0 0.00 0.00	4 7.55 12.90	8 6.78 25.81	11 6.96 35.48	1 6.25 3.23	2 4.00 6.45	1 6.25 3.23	0 0.00 0.00	3 10.34 9.68
M3	0 0.00 0.00	1 5.88 1.89	12 22.64 22.64	18 11.02 24.53	13 8.23 24.53	2 12.50 3.77	3 6.00 5.66	0 0.00 0.00	2 40.00 3.77	2 6.90 3.77
U1	1 8.33 14.29	1 5.88 14.29	0 0.00 0.00	1 0.85 14.29	0 0.00 0.00	0 0.00 0.00	1 2.00 14.29	1 6.25 14.29	0 0.00 0.00	1 3.45 14.29
U2	0 0.00 0.00	1 5.88 11.11	0 0.00 0.00	0 0.00 0.00	4 2.53 44.44	0 0.00 0.00	1 2.00 11.11	0 0.00 0.00	0 0.00 0.00	2 6.90 22.22
U3	0 0.00 0.00	2 11.76 11.76	0 0.00 0.00	4 3.39 23.53	6 3.80 35.29	0 0.00 0.00	3 6.00 17.65	0 0.00 0.00	0 0.00 0.00	0 0.00 0.00